Reduced flow impacts salmonid smolt emigration in a river with low-head weirs

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Abstract

The impacts of large dams on the hydrology and ecology of river systems are well understood, yet the impacts of low-head structures are poorly known. While impacts of small weirs on upstream-migrating fish have long been mitigated by fish ladders, it is assumed that downstream migration of surface-oriented fishes is unaffected under natural flow regimes. To test this, the effects of low-head weirs and the influence of river flow on the migration of brown trout (*Salmo trutta*) smolts in the River Tweed, UK, was examined. Movements of acoustic tagged smolts were quantified in 2010 and 2011 using automatic listening stations and manual tracking throughout the migration route. In both years smolts exhibited major losses, most likely due to predators, with escapement rates of 19% in 2010 and 45% in 2011. Loss rates were greater in 2010 when flows were frequently below Q95 (20% of study period), compared to 2011 when more typical flows predominated (0% of study period below Q95). Smolts experienced significantly longer delay at weirs during 2010 than 2011, associated with the different hydrographs during emigration as well as weir design. Flow comparisons within the study periods and historical records shows that low flows experienced in 2010 were not unusual. The swimming behaviour of smolts in relation to flow conditions differed between years, with smolts in 2010 increasing their rate of movement in relation to increasing flow at a faster rate than smolts in 2011. This is the first study to demonstrate river flow impacts on the migration success of wild salmonid smolts at small weirs. Because small weirs are common in rivers and because spring-summer low flow periods may become more frequent with climate change (based on UKCIP09 models) and altered river hydrology, further research and improved management is needed to reduce the impacts of low river flows in combination with low-head weirs on salmonid smolt migration.

Keywords: *Salmo trutta*, smolt migration, habitat fragmentation, river obstructions, low flow

1. Introduction

In many developed countries there is a long history of river modification and, as a result, in-river structures such as dams and weirs are present in half of the world’s rivers (Dynesius and Nilsson, 1994; Nilsson et al., 2005). Such modification has been integral to human population growth through processes such as flood defence; power generation and farming in floodplains (Nilsson et al., 2005; Poff and Hart, 2002). However, in-river barriers such as dams and weirs have a major role in the fragmentation of fluvial ecosystems (Dynesius and Nilsson, 1994; Fullerton et al., 2010; Jungwirth, 1998; Kemp and O'Hanley, 2010). In-river barriers can have major impacts on fish populations by preventing or restricting movement to habitats required for essential stages of fish life history (Branco et al., 2012; Lucas and Baras, 2001; Lucas and Batley, 1996; Lucas et al., 2009; Wollebaek et al., 2011). In-river barriers not only impact fish populations by restricting essential movement, there is also major impacts on fish habitat due to alteration of the downstream flux of water and sediment, nutrient movement, and water temperatures within rivers (Poff and Hart, 2002). The effects of migration obstacles depend on factors such as fish species; river hydrology and barrier type, with effects varying from short delays to complete blockage (Kemp and O'Hanley, 2010; Northcote, 1998). In Europe, legislation such as the Water Framework Directive (WFD; 2000/60/EC) requires free passage for migratory fish travelling between areas of river essential for their life history, such as juvenile emigration from natal areas and adult spawning migrations. Failure to comply can result in the river being assigned less than “Good ecological status” and may result in sanctions.

The seaward migration of juvenile anadromous salmonids (smolts) is a crucial event in their life history. Smoltification is a period of great morphological, behavioural and physiological change when juvenile salmonids develop various adaptations that enable them to survive at sea (Debowski et al., 1999a; Debowski et al., 1999b; Denton and Saunders, 1972; Lysfjord and Staurnes, 1998; McCormick et al., 1998). The smolt migratory period is precisely timed with photoperiod, river discharge and temperature playing determinate roles in its commencement (Björnsson et al., 1995;

Björnsson et al., 2010; McCormick, 1994; McCormick et al., 2000; McCormick et al., 2007; McCormick et al., 2002). Throughout migration smolts are subject to elevated predation risk from mammalian; avian and fish predators (Aarestrup et al., 1999; Aarestrup and Koed, 2003; Carss et al., 1990; Dieperink et al., 2002; Dieperink et al., 2001; Harris et al., 2008; Heggenes and Borgstrom, 1988; Koed et al., 2002; Steinmetz et al., 2003; Svenning et al., 2005a; Svenning et al., 2005b; Wiese et al., 2008). Delays at river obstructions during such a timing-specific and vulnerable life history stage can potentially have large impacts on the survival of smolts and the health of salmonid stocks as a whole.

The impacts of large dams on the hydrology and ecology of temperate river systems, including downstream fish passage, especially of economically important salmonids, are relatively well known. In general downstream salmonid passage efficiency over dams is high (74.6%) based on recent quantitative assessment (Noonan et al., 2012). However, high smolt mortalities due to both physical damage and predation have been observed at major impoundments and hydro-power facilities (Aarestrup et al., 1999; Hockersmith et al., 2003; Keefer et al., 2012; Muir et al., 2001a; Muir et al., 2001b; Raymond, 1979; Raymond, 1988; Smith et al., 2006; Smith et al., 2002; Williams et al., 2001). Low flows due to regulation in river reaches also cause delays in smolt emigration and result in increased duration of exposure to mortality risks (Aarestrup and Koed, 2003; Keefer et al., 2012). However, the impacts of low-head structures, such as simple overflow weirs are poorly known for downstream migrants (Lucas and Baras, 2001) with the exception of bottom-orientated freshwater eels (Acou et al., 2008). While impacts of small weirs on upstream-migrating fish (Lucas and Frear, 1997; Ovidio and Philippart, 2002) have been partially mitigated by fish ladders designed specifically to assist upstream passage (Clay, 1995), average passage efficiencies are relatively low (41.7%) (Noonan et al., 2012) and presence of passage fascilities is not always guaranteed to mitigate passage concerns (Roscoe and Hitch, 2010). However, it is generally assumed that downstream migration of wild surface-oriented fishes such as salmonid smolts is relatively unaffected and that they will pass simple overflowing weirs unhindered under reasonably natural flow regimes (Lucas and Baras, 2001). Some studies on passage of hatchery-reared smolts past small weirs, in particular that of Aarestrup and Koed (2003), strongly contradict this. To test this assumption for wild fish, the effects of low-head weirs and the influence of natural variations in river flow on the migration behaviour and survival of anadromous brown trout (*Salmo trutta*) smolts were examined in the River Tweed, UK, a catchment with very strong wild migratory salmonid stocks.

2. Study areas

The study was carried out on the River Tweed in southern Scotland, which drains west to east and empties to the North Sea. The Tweed is the sixth largest river in mainland Britain and the second largest in Scotland and has some of the largest Atlantic salmon (*Salmo salar*) and anadromous brown trout populations in the UK (Gardiner, 1989; Sheail, 1998). The Tweed catchment covers 5000 km^2 with an estimated 2160 kilometres of the main channel and tributaries accessible to fish (Gardiner, 1989). The water quality of the river is very high, with there being very little pollution present (Currie, 1997). The River Tweed is a designated Site of Special Scientific Interest (SSSI) within the UK and is an EU Special Area of Conservation (SAC) for Atlantic salmon and lampreys. Compared to many rivers, there are relatively few anthropogenic impacts and the hydrology, although modified, retains high natural variability in discharge. Several low-head engineered structures occur within the River Tweed's main channel, downstream of one of the key spawning tributaries, the Ettrick Water, as well as in the Ettrick itself (Figure 1). The Ettrick is a regulated river and its main tributary the Yarrow Water is also regulated at its outflow from St Marys Loch, 23 km upstream of its confluence with the Ettrick. The average annual flow on the Yarrow is 5.58 m^3 s^{-1}, while on the Ettrick it is 15.1 m^3 s^{-1} and their combined catchment areas come to 501 km^2. The course of the river under investigation is characterised by multiple low-head structures which are remnants of light industry, most of which are now redundant (Figure 1, Table 1)

-Figure 1 here-

-Table * here-

3. Methods

3.1. Smolt capture and tagging

Trout smolts were captured in a trap on the Yarrow between the 1st of April and the 1st of June in 2010 and 2011. The smolt trap consisted of a meshed box trap placed in the outwash of the smolt and debris screen of a fish farm.

The smolts were removed from the trap and immediately placed in a holding tub filled with highly aerated river water. The fish were placed in an induction tank and anaesthetised using Phenoxyethanol (0.3 ml l^{-1}), their fork length (mm) and weight (g) were recorded before those sufficiently large for tagging (over 145 mm in fork length) were placed on a V-shaped surgical table. An incision (12-14 mm) was made on the ventral side of the fish anterior to the pelvic girdle. A miniature coded acoustic transmitter (either Model V7-2x, 7 mm diameter, 18 mm length, 1.4 g weight in air, Vemco Ltd, Nova Scotia, Canada or Model LP-7.3, 7.3 mm diameter, 18 mm length, 1.9 g weight in air, Thelma Biotel AS, Trondheim, Norway) was then implanted in to the peritoneal cavity through the incision. Tags were chosen to have code repeat periods of 20-60 seconds and estimated lives of 100 days. The incision was closed with three independent sutures (4-0 Vicryl Rapide, Ethicon Ltd, Livingston, UK). The gills were aspirated with a mixture of dilute Phenoxyethanol and river water during the early stages of the procedure before switching to 100% river water during the later stages of the procedure. All tagging was carried out under UK Home Office License and complied with the UK Animals (Scientific Procedures) Act 1986.

Once the procedure was complete the fish were returned to a recovery tub filled with highly aerated water. When recovered the fish were placed in a keep box in the intake channel overnight before release into the river; no mortalities occurred during these procedures. Details of the fish released in the two seasons are given in Table 2. There was no significant difference between the lengths of smolts tagged in 2010 and 2011 (Mann-Whitney U; n=103, Z=-0.445,p>0.05). Release was always in groups that included untagged fish (since smolts migrate in aggregations), within 24 hours of tagging, in to a section of the river 100 m below the point of capture. Due to high losses of tagged smolts within the upper study section in 2010, tagged smolts were released at two additional release sites, one 2 km below the point of capture and another 200 m downstream of the the Murray Cauld as a way to test the impact of the weir on migration in 2011 (Table 2, Figure 1). The Murray Cauld is the only intact in-river structure on the migration route and so has only a fish pass as an alternative to passage over its crest. The lengths of smolts in the three release groups in 2011 were not significantly different (Kruskall-Wallis; n=60, χ^2= 1.0892, df = 2, p>0.05).

-Table 2 here-

3.2. Acoustic tracking

Acoustic tracking was carried out via a combination of fixed automatic listening stations (ALS) and manual tracking at 69 KHz. Fixed ALS positions (Models VR2 & VR2W, Vemco Ltd, Nova Scotia, Canada) were set approximately 11 km apart along the migration route. Sites were chosen to detect fish as they approached cross-river weirs or other features of interest, with acoustic loggers located in calm water to give reliable recording of tags, based upon field tests. Positioning of loggers at some sites was limited by the availability of calm, deep water as well as site access. Logging stations at weirs were located 50-100 m upstream of obstructions. In the estuary multiple stations were placed in both the inner and outer estuary to give effective coverage. ALS stations were downloaded on a weekly basis during the study period, these data allowed for the locations of each fish to be estimated and help determine areas to target for manual tracking.

Manual tracking was carried out on foot using a Vemco VR100 (Vemco Ltd, Nova Scotia, Canada) with a VH110 Directional Hydrophone attached (Vemco Ltd, Nova Scotia, Canada). Range testing was conducted by placing a test tag in a known position and then measuring the distance at which the test tag became undetectable on manual tracking equipment, this was repeated in several different river sections with varying hydromorphological conditions. In field tracking conditions, with the hydrophone kept fully submerged, the range varied between 100 m in deep pools to less than 10 m in fast flowing riffles. Fish locations were recorded by the VR100 inbuilt GPS unit and later stored in a GIS database.

In 2010, 10 tags were deployed in mesh bags in the river to estimate tag failure rate. As a further control, 10 tags were deployed loose on the river bed to determine whether, and under what circumstances, tags lost by fish, or following predation and subsequent tag egestion, were moved passively by flows and what their detectability was.

3.3. Environmental data

River flow is recorded along the smolt migration route at the Philiphaugh gauging station of the Scottish Environment Protection Agency (SEPA) on the lower Yarrow and also at their Lindean (Ettrick), Boleside and Sprouston (Both Tweed) and at the Norham gauging station of the Environment Agency of England and Wales (EA)(Figure 1). Historic flow records for these stations were obtained from the Centre for Ecology and Hydrology (CEH) National River Flow Archive (NRFA).

4. Results

4.1. Inter-annual variations in survival out to sea and passage efficiencies at weirs

Through the combined use of stationary ALS receivers and manual tracking, survival estimates were calculated for the 43 tagged smolts released in 2010 and the 60 released in 2011. The approximate distance travelled by each smolt was measured from its last known location. Tags that were either missing after repeated manual tracking trips or repeatedly found at the same site, without any movement on successive manual tracking trips were assumed to be smolt mortalities. In total, seven tags in 2010 and three tags in 2011 were assumed to be dead after repeatedly being found in the same location in the river. Conversely, 28 tags in 2010 and 30 tags in 2011 were assumed to have been removed from the system by terrestrial predators after a cessation in logged movements and not being detected after several manual tracking trips. All of the tags deployed in the river as controls in retrievable mesh bags operated for their expected durations and 90% of the tags deployed loose on the river bed could be detected over their study period, none moving more than 1 m.

In 2010 only 19% of the 43 released smolts were detected leaving the river on the outer estuary logger whereas 45% of the 60 released smolts reached there in 2011. One notable difference between years was the variation in mortality around the Murray Cauld; in 2010 a 44% decline in survival was observed there compared to a 9% decline in 2011 (Figure 2). There was a slight variation in survival out to sea for release sites A and B (above the Murray Cauld) and C (below it) in 2011, which had relatively normal flow, with 40%; 55% and 40% survival being observed respectively (Figure 2). In 2010 there was a significant difference in smolt length between successful migrants and unsuccessful migrants, with successful smolts being larger (Mann-Whitney U; n=43, Z=-2.07, p=0.044). This trend may be a result of the low number of successful smolts compared to the much larger number of unsuccessful smolts. However, In 2011 there was no difference in length between successful and unsuccessful migrants (Mann-Whitney U; n=60, Z =-0.647, p>0.05).

For both years a significant negative relationship between distance travelled from release site and cohort survival was recorded (2010: linear regression; n=43, R^2= 0.495, F= 12.064, p= 0.005; Figure 2, 2011: linear regression; n=60, R^2=0.84, F=84.731, p<0.001; Figure 2). For all three release sites in 2011 there were significant negative relationships between the distance travelled from release sites and cohort survival (release site A: linear regression; n=20, R^2=0.52, F=15.263, p=0.002; Figure 2, release site B: linear regression; n=20, R^2=0.72, F=37.305, p<0.001; Figure 2, release site C: linear regression; n=20, R^2=0.73, F=25.536, p=0.001; Figure 2). Subsequently, two of the smolts tagged in 2011 were detected 20 km up the estuary of the River Tees on an acoustic array associated with a separate study. The Tees estuary is approximately 144 km south of the Tweed estuary, along the North Sea coast, and the tags were detected for periods of 4.3 and 60.4 hours, after respective periods of 20 and 10 days following escapement from the Tweed estuary. These detections fit in with prior Carlin tag data from the Tweed that shows smolts moving down the UK coastline close to shore and in neighbouring estuaries (Campbell, *unpublished data*).

The passage efficiencies at three different weirs differed between years, at Murray Cauld passage efficiency differed markedly between years with 46% and 100% passage efficiency being observed in 2010 and 2011 respectively. Differences in passage efficiency between 2010 and 2011 were also observed on the other two weirs studied but were not as pronounced (Table 3). What is important to note is that weir design differs between all three weirs and Murray Cauld is the only fully intact weir.

-Figure 2 here-

4.2. The delay of smolts during seaward migration in 2010 and 2011 and its impact on smolt movement rate

When comparing the mean ground speeds of migrating smolts in 2010 and 2011, using the first detection of each smolt on each ALS position along the migration route and factoring in each river section in to the analysis, a significant difference was observed (ANOVA; n=205, F=5.673, p<0.001; Figure 3) with smolts in 2011 moving significantly faster along the migration route. Ground speed data for 2011 in the river sections between release site B and logging station 1 as well as release site C and logging station 2 were not included in the analysis due to the stated release sites not being used in 2010.

Records of the migration delays experienced by smolts at localities in both 2010 and 2011 were retrieved from stationary ALS receivers. Delay was quantified by the duration of time between the first recording and the last recording on an ALS for each tagged smolt. Data from station 5 were not included, since this logger was inefficient due to noise resulting from its suboptimal location. In general, smolts experienced more delay in 2010 than 2011. Smolts were more significantly delayed in 2010 compared to 2011 on all freshwater ALS stations; station 1 (Mann-Whitney U; n=54, Z=-5.0, p<0.001; Table 3), station 2 (Mann-Whitney U; n=47, Z=-2.33, p=0.02; Table 3), station 3 (Mann-Whitney U *;* n=32, Z=-2.712, p=0.011; Table 3), station 4 (Mann-Whitney U; n=19, Z=-2.966, p=0.002; Table 3), station 6 (Mann-Whitney U; n=23, Z=-3.244, p=0.001; Table 3) and station 7 (Mann-Whitney U; n=34, Z=-2.315, p=0.02; Table 3). However, there was no significant difference in delay in the Tweed estuary between 2010 and 2011 (Mann-Whitney U; n=33, Z=-0.336, p>0.05; Table 3), suggesting that either the factors influencing delay within the river were not present or were of less importance within the estuary or that a different set of factors govern estuarine movements.

-Table 3 here-

-Figure 3 here-

4.3. Variation in flow conditions between 2010 and 2011 and its influence on smolt ground speed

Using mean daily flow data retrieved from SEPA and the EA and flow duration curves from the CEH NRFA, the flow conditions along the migration route during the typical smolt migration period (1 April to 30 June) in 2010 and 2011 were analysed. The Lindean SEPA gauging station was used as a proxy for the flow at the Murray Cauld as it is approximately 6 km downstream from the weir and there are no large tributaries joining the Ettrick in this section of river. The two years' flows at Lindean, during the key migration period, differed markedly, with mean daily flows declining below the Q95 flow for 18 days in 2010 and not at all in 2011. There were several high flow events in 2011 whereas the only flow increases in 2010 were the results of artificial weekly freshets from St Mary's Loch on the Yarrow system (Figure 4).

-Figure 4 here-

Using historical flow records from the CEH NRFA for Lindean extending back to 1962 the prevalence of daily flows under Q95 was calculated for each year in the 49 year period. Days where flow was low there during the migration period were not uncommon (Figure 5). Short periods of flow restriction occurred frequently and periods where at least 15 days out of the 90 day period were below Q95 daily flows occurred at least once a decade (Figure 5). There have therefore been periods of flow restriction similar to that experienced in 2010 previously and they are likely to reoccur.

-Figure 5 here-

The influence of flow conditions on smolt migration speed was calculated from the net ground speed of individual smolts between two successive ALS positions using the first record of each smolt at each ALS as it moved downstream and then matching the speed to the mean flow conditions during the period of transit using 15-minute gauged flows from the nearest SEPA flow gauging stations to the fixed ALS positions. This was carried out for all sequential pairs of ALSs. For both years a positive relationship between elevated flow (m^3s^{-1}) and increased net ground speed (km h^{-1}) was observed; 2010 (Regression; n=88, R=0.719, p<0.001; Figure 6), 2011 (Regression; n=218, R=0.579, p<0.001; Figure 6). However, when the relationships between net groundspeed and mean flow were compared between years using an ANCOVA there was a highly significant difference in slope (n=306, F=147.73, p<0.001). These results suggest that smolts released in 2010 undertook increasingly more active swimming within the flows in which they exhibited downstream migration than the smolts released in 2011.

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5. Discussion

This study shows, for the first time, that surface-orientated wild fishes, migrating downstream, can be markedly impeded by small overflowing weirs, and that the effects of this are dramatically increased during low-flow conditions. These delays are associated with losses of migrating fishes, again substantially elevated during low-flow conditions. While these effects are known for salmonids at large impoundments, especially hydroelectric dams, with or without surface bypasses (Hockersmith et al., 2003; Muir et al., 2001a; Muir et al., 2001b; Raymond, 1979; Raymond, 1988; Smith et al., 2006; Williams et al., 2001), and also for benthically orientated eels (Acou et al., 2008; Boubée and Williams, 2006; Gosset et al., 2005), they have not been recorded for wild juvenile salmonids in relatively natural river systems. However, manipulative studies with smolts have shown that modified surface bypasses reduce the delay in passing weirs compared to conventional bypasses (Haro et al., 1998). These results strongly suggest that small obstructions can have much larger than expected impacts on seaward escapement of anadromous brown trout smolts and given the observation that low flows dramatically exacerbate these problems, any climate scenario (such as UKCIP02 and UKCP09) that results in increased frequency of low river flows during spring and early summer is a very real concern (Arnell, 2004; Christierson et al., 2012; Marsh, 2004; Wilby and Harris, 2006). However, it is possible that climate change may bring an increase in water availability for the UK in some scenarios (IPCC SRES A2 and B2) (Xenopoulos et al., 2005).

The results from the automated acoustic tracking of the smolts migrating to the sea in 2010 and 2011 clearly showed a disparity in the degree to which they were delayed in different river sections between the two seasons. These also showed that obstructions in river sections, such as weirs, also exacerbate delays during periods of reduced river flow. In general very little work has been conducted to link overflowing barriers to the passage and behaviour of freshwater fish during downstream movement. In Australian studies Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*) displaced above weirs displayed a reluctance to move past low-head weirs when attempting to home downstream (O'Connor et al., 2006). Negative impacts of weirs were also observed in hatchery reared Atlantic salmon and anadromous brown trout smolts released in small Danish rivers where they suffered from increased delay and mortality in proximity to small fish farm weirs (Aarestrup and Koed, 2003). Low flows spread across the breadth of obstructions such as overflowing weirs spanning whole channels, give depths over their crests that are very shallow, which may reduce the behavioural stimuli (one or more combinations of velocity, depth, velocity gradient, turbulence) needed to get fish to continue past the barrier. Haro et al., (1998) found American shad (*Alosa sapidissima*) to be unwilling to approach the small surface water bypasses that would allow them to move downstream at large barriers, while Enders et al. (2009) demonstrated a similar unwillingness for salmonid smolts under experimental conditions, showing that hydraulic changes at surface bypasses do not necessarily promote effective downstream passage of surface-orientated fishes.

In the current study it was inferred that acoustic tag loss was very likely due to removal of tagged fish from the river by terrestrial predators because; 1) transmitters were lost well within the quoted lifetime of the tags; 2) control transmitters deployed in the river showed zero failure rate within the quoted life; 3) loose control tags on the river bed could be reliably detected by tracking gear and moved little and, 4) predation by aquatic predators (in this study area, large brown trout), would have resulted in acoustic tags being retained in the aquatic environment and detectable. The most common avian predators on the Tweed are goosander (*Mergus merganser*) and grey heron (*Ardea cinerea*), the former occurs in large numbers during the smolt migration season when they can form large feeding aggregations. Their diet on the Tweed has been investigated by Marquiss, et al (1998), who estimated their consumption of smolt-sized salmonids could be up to 4.79 per goosander per day in March and April and up to 1.8 per day in May. The survival of smolts during migration was radically different between the two seasons studied, that of 2010 (19%) being below half that of 2011 (45%). These levels can be compared with those of conventionally tagged anadromous brown trout smolts in Norway which were estimated to have a survival rate of 24% for their first seaward migration (Berg and Berg, 1987) and with the survival of chinook salmon

(*Oncorhynchus tshawytscha*) smolts migrating down the Snake and Columbia rivers where survival to the sea was estimated to be around 27.5% (Welch et al., 2008). However, the Columbia River system is of much greater size and has much larger impoundments than the Tweed catchment.

The mortality of Atlantic salmon smolts during in-river migration has been estimated for several different rivers in previous studies. Overall mortality, calculated on a kilometre by kilometre basis ranged from 0.3 to 5% per kilometre (Davidsen et al., 2009; Dieperink et al., 2002; Koed et al., 2002; Martin et al., 2009; Moore et al., 1998; Thorstad et al., 2012a; Thorstad et al., 2012b). In comparison anadromous brown trout smolts tracked in the Tweed in 2010 and 2011 suffered 0.88% and 0.55% mortality per km respectively, well within the range of mortality observed for salmon. It is important to note that these studies only included the lower reaches and estuary of their rivers where predation is expected to be more intense while the present study examined migration over 100.29 km of river and estuary.

Mortality at individual weirs during migration varied within and between years, with mortality ranging between 2-44% per cohort of fish arriving at each weir with an ALS near it (the Murray Cauld, Melrose Cauld and Mertoun Cauld) in 2010 and 5-9% in 2011. In comparison, stocked brown trout smolt mortality at various fish farm weirs in Denmark varied between 15-64%, although it is important to note that piscivorous predators such pike (*Esox lucius*) and zander (*Sander lucioperca*) are present in Danish rivers (Aarestrup and Koed, 2003) but are absent in the studied section of the River Tweed. Passage efficiencies at these weirs also varied between 46-90% in 2010 and 92-100% in 2011. Murrays Cauld was particularly inefficient in 2010 with downstream passage efficiency being only 46%, well below the average downstream passage efficiency of 68.5% seen in Noonan et al., (2012). This low efficiency during low flow periods is most probably the consequence of Murray Cauld being the only fully intact weir along the migration route, with other weirs either being in a ruinous state or cut.

The flow conditions in the period of study were markedly different between years. The April to June water levels of 2010 were characterised by low flows that dipped below Q95 for a total of 18 days whilst the 2011 flows for the same period exceeded Q10 flows for two consecutive days during the largest spate and had other elevated periods. From a historical perspective, low flows similar to those that were prevalent in 2010 for the study period have been recorded regularly on the Ettrick between 1962 and 2011. The use of Q95 flows as an estimation of low flows is now widely practised in Europe (Gustard et al., 1992; Laaha and Blöschl, 2007; Smakhtin, 2001). Studies into the migration of chinook salmon on rivers with large barriers have shown a positive relationship between increased river flow and increased smolt survival during migration (Connor et al., 2003; Smith et al., 2003).While the Tweed is a much smaller river, with small barriers, the same pattern is apparent – higher smolt mortality in seasons with low flows and *vice-versa*.

Smolt swimming speed increased in relation to flow in both years of the study. However, smolts in 2010 showed a steeper relationship of ground speed to river discharge than smolts in 2011. This may be a consequence of the overall lower flow conditions in the river in 2010 compared to 2011 possibly meaning that smolts moving downstream in 2010 did so more actively than smolts released in 2011. Conversely, smolts in 2011 displayed more active swimming behaviour at lower flow levels than smolts in 2010, this is possibly due to smolts in 2011 not suffering the same flow restriction as smolts in 2010 and therefore movement may not be as impeded by in river structures. Similarly, previous research into anadromous brown trout and Atlantic salmon smolt migration has also found a correlation between river discharge and smolt net ground speeds (Aarestrup et al., 2002; Martin et al., 2009). Smolt ground speeds were low in sections from release to detections upstream of Philiphaugh weir in both 2010 and 2011, but these low speeds include periods during which smolts may have been preparing to emigrate and exhibited holding behaviour.

The conclusion of this study is that passage of downstream-migrating salmonid smolts is not only impacted by the large dams with which river managers are familiar, but probably also by much smaller low head weirs that Lucas et al. (2009) report as being much more abundant and which impound water and create zones of reduced flow rate. Current passage provision for downstream-migrating salmonid smolts is probably inadequate at many weirs and periodic low flows during the smolt migratory period should be a management concern, especially for areas where salmonid stocks are a highly prized economic asset. Most fish passage facilities, such as technical fish ladders, are designed for upstream migrants, and while downstream fish bypasses exist, they have been little used on low-head overflowing weirs and have rarely been evaluated for their efficiency (Haro et al., 1998; Scruton et al., 2002, 2007). In the face of climate change and un- certain variability in river flows,where low-head structures are no lon- ger needed, removal should be strongly considered along with the construction of bypasses for reducing emigration delays and mortality in salmonid smolts (Arnell, 2004; Christierson et al., 2012; Garcia de Leaniz, 2008; Kemp and O'Hanley, 2010; Marsh, 2004; Wilby and Harris, 2006; Xenopoulos et al., 2005). To ultimately test the impact of weirs, future studies should consider a tenable before–after control impact (BACI) design, using multiple years worth of smolt migration data for each treatment. Further to this, more detailed information on smolts lost while migrating downstream would also be very useful for management purposes, unless definite causes can be assigned for losses it is difficult to take measures against them.

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Tables

Table 1: Descriptions of in river structures along the studied smolt migratory route. * Structure crosses river at an angle to the flow.

Name of structure	Structure status	Year structure built	Structure width (m)	Structure head-loss (m)	Fish pass present	Location (latitude, longitude ,°)
Murray Cauld	Intact	1847	65	3	Pool and spill	55.537667, -2.874796
Melrose Cauld	Ruinous	Not known	102	1	None	55.602007, -2.726349
Mertoun Cauld	Cut	Rebuilt in 1990s	98	3	Pool and spill	55.582512,-2.623382
Rutherford Cauld	Ruinous	Not known	153	1	None	55.57769, -2.550825
Kelso Cauld	Cut	Middle ages	300*	2	Multiple pool and spill	55.599875,-2.439349
Hendersyde Cauld	Cut	Not known	230	2	Pool and spill	55.624852, -2.382158
The Lees Cauld	Cut	Not known	100	ca. 1	None	55.642852, -2.250394
Coldstream bridge apron	Cut	1784	96	ca. 1	None	55.654607, -2.241373
Milne Graden Cauld	Ruined	Not known	98	ca. 1	None	55.691506, -2.195022

Table 2: Summary data for smolts tagged in 2010 and 2011. The release sites are shown on Figure 1. * Tag to body weight ratio is calculated from masses in air.

Release site	Tagging date	Number tagged	Fork length [mean ± SD (range), mm]	Weight [mean ± SD (range), g]	Tag/body weight ratio [mean (range), %]*
Release site A	29/04/2010	14	163.2 ± 16.5 (145-190)	45.6 ± 15.2 (30-77)	4.5 (2.5 – 6.3)
Release site A	07/05/2010	20	161.5 ± 15.5 (140-202)	41.4 ± 13.4 (23-82)	5.0 (2.3 -8.3)
Release site A	13/05/2010	9	175.8 ± 18.3 (156-200)	54.6 ± 18.6 (29-81)	3.9 (2.3 – 6.6)
2010	Total	43	165 ± 17 (140-202)	45.5 ± 15.7 (23-82)	4.6 (2.3 – 8.3)
Release site A	21/04/2011	3	155 ± 8.7 (150-165)	38 ± 9.5 (32-49)	5.2 (3.9 – 5.9)
Release site A	22/04/2011	6	164.3 ± 19.5 (142-199)	45.7 ± 16.7 (31-77)	4.5 (2.5 – 6.1)
Release site A	26/04/2011	4	182.2 ± 17 (159-198)	59.3 ± 17.5 (35-76)	3.5 (2.5 – 5.4)
Release site A	04/05/2011	7	165 ± 33.9 (140-220)	50.4 ± 32.6 (23-97)	5.1 (2.0 – 8.3)
Release site A	Total	20	166.7 ± 24.3 (140-220)	48.9 ± 22.6 (23-97)	4.6 (2.0 – 8.3)
Release site B	21/04/2011	3	160 ± 15 (145-175)	44 ± 11.5 (31-53)	4.6 (3.6 – 6.1)
Release site B	22/04/2011	6	161.5 ± 20.3 (147-197)	41.8 ± 12.5 (32-62)	4.8 (3.1 – 5.9)
Release site B	26/04/2011	4	161.5 ± 7.3 (154-171)	42 ± 7 (33-49)	4.6 (3.9 – 5.8)
Release site B	04/05/2011	7	170.3 ± 16.9 (154-202)	50.3 ± 17.7 (34-86)	4.1 (2.2 – 5.6)
Release site B	Total	20	164.4 ± 15.9 (145-202)	45.2 ± 13.3 (31-86)	4.5 (2.2 -6.1)
Release site C	21/04/2011	3	163.3 ± 20.2 (140-175)	43.3 ± 13.9 (28-55)	4.8 (3.5 -6.8)
Release site C	22/04/2011	6	171.7 ± 8.1 (160-182)	50.5 ± 8.3 (40-62)	3.8 (3.1 – 4.8)
Release site C	26/04/2011	4	173.8 ± 21.6 (142-190)	58.5 ± 19.7 (31-78)	3.7 (2.4 – 6.1)
Release site C	04/05/2011	7	167.4 ± 20.7 (145-205)	46.9 ± 20.5 (20-85)	4.8 (2.2 – 9.5)
Release site C	Total	20	169.4 ± 16.8 (142-205)	49.8 ± 16.1 (28-85)	4.3 (2.2 – 9.5)
2011	Total	60	166.8 ± 19.2 (140-220)	47.9 ± 17.6 (23-97)	4.5 (2.0 – 9.5)

Table 3. Delay and barrier passage efficiencies at ALS positions along the smolt migration route through the river and estuary. Station 5 not listed due to insufficient sample size recorded there.

ALS Station	Immediately Upstream of in-river structure	In-river structure characteristics	2010 Delay (median(Q_1- Q_3), minutes)	2011 Delay (median(Q_1- Q_3), minutes)	2010 Passage efficiency (%)	2011 Passage efficiency (%)
1	Yes	Intact	4497.3 (109.9-25029.4)	5.8 (2.7-26.4)	46	100
2	Yes	Ruinous	7.1 (1.8-18.8)	2.1 (0.9-4.6)	76	92
3	Yes	Cut	1.11 (0.2- 2.7)	0.1 (0.1-0.5)	90	94
4	No	-	2.5 (1.3-81.6)	0.6 (0.1-0.8)	-	-
6	No	-	5 (3.1-18.9)	0.9 (0.1-1.1)	-	-
7	No	-	4.7 (2.7-11.7)	1.7 (0.9-2.7)	-	-
8	No	-	460 (61.8-1244.8)	314.3 (4.6-1719.9)	-	-

Figures

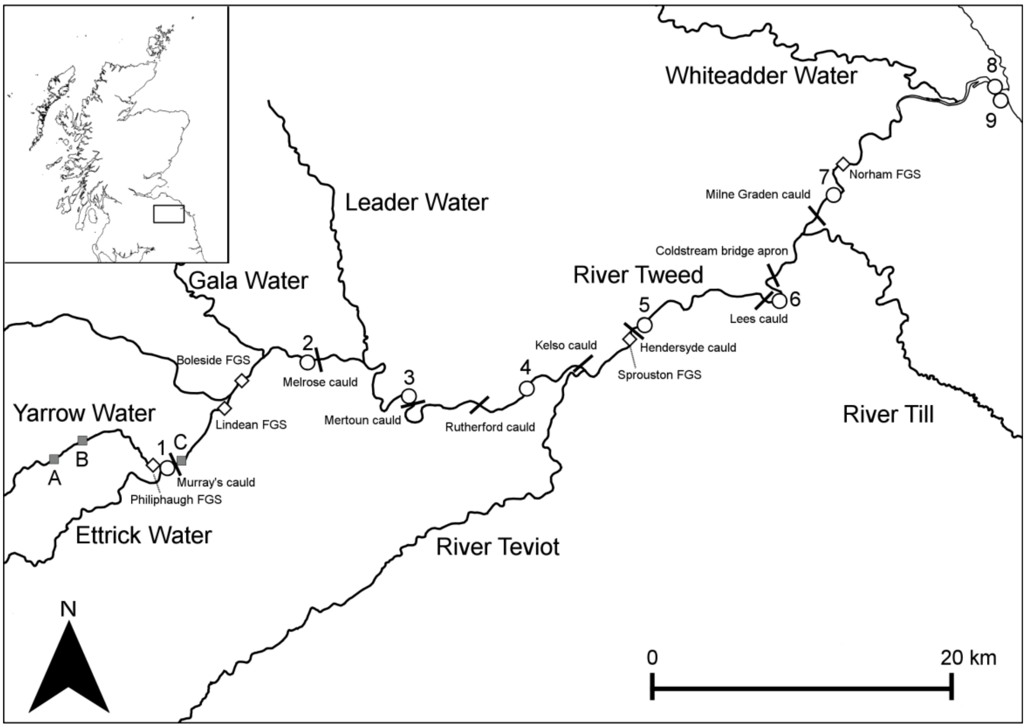

Figure 1: Map of the River Tweed showing all the major tributaries as well as the migration route downstream from the Yarrow Water. Grey boxes denote the release sites along with white circles denoting the ALS positions and white diamonds for SEPA flow gauging stations (FGS). Black bars indicate the sites of in-river structures.

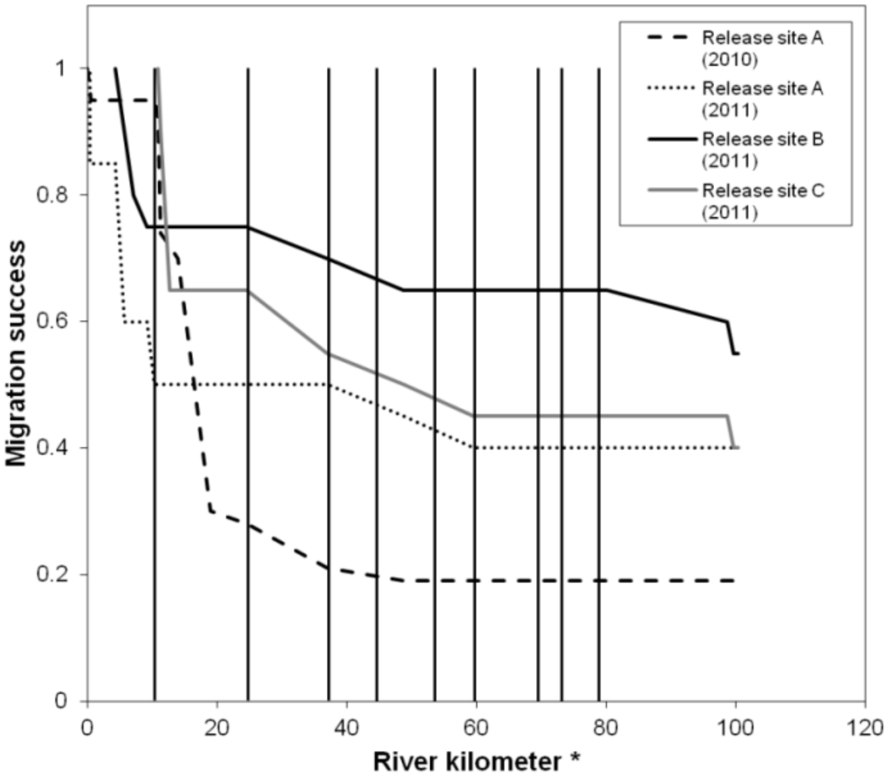

Figure 2. Cumulative survival of acoustically tagged brown trout smolts migrating out to sea in 2010 and for three separate release groups in 2011. Black vertical bar represent weirs along the migration route. * Measured from the furthest upstream release point down to the estuary.

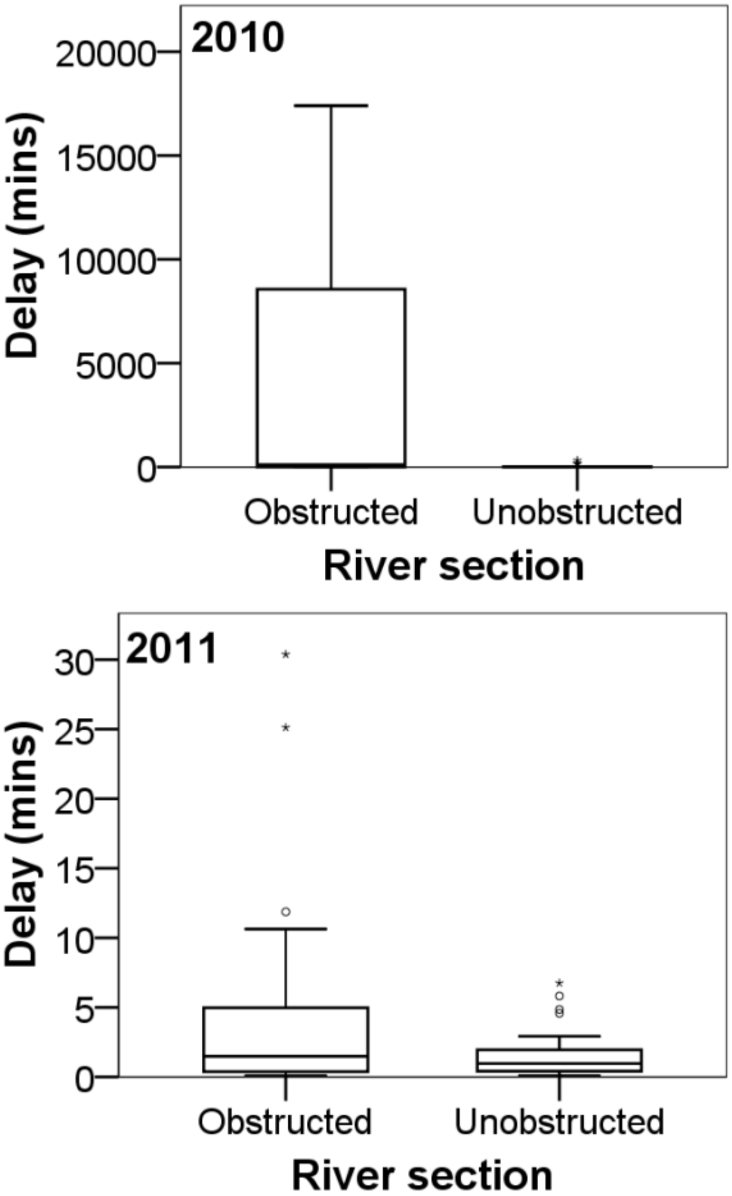

Figure 3. Time spent by individual smolts at ALS positions (delay) that were within the impoundment zones of in river structures (obstructed) compared with those that were not (unobstructed). Data are presented as box plots, showing median, upper and lower quartiles, upper and lower 5 percentiles, mild outliers (circles; Q3 + 1.5 × IQR) and extreme outliers (asterisks; Q3 + 3 × IQR). In the 2010, panel medians are obscured by other lines. Data do not include records from station 5 due to insufficient sample size.

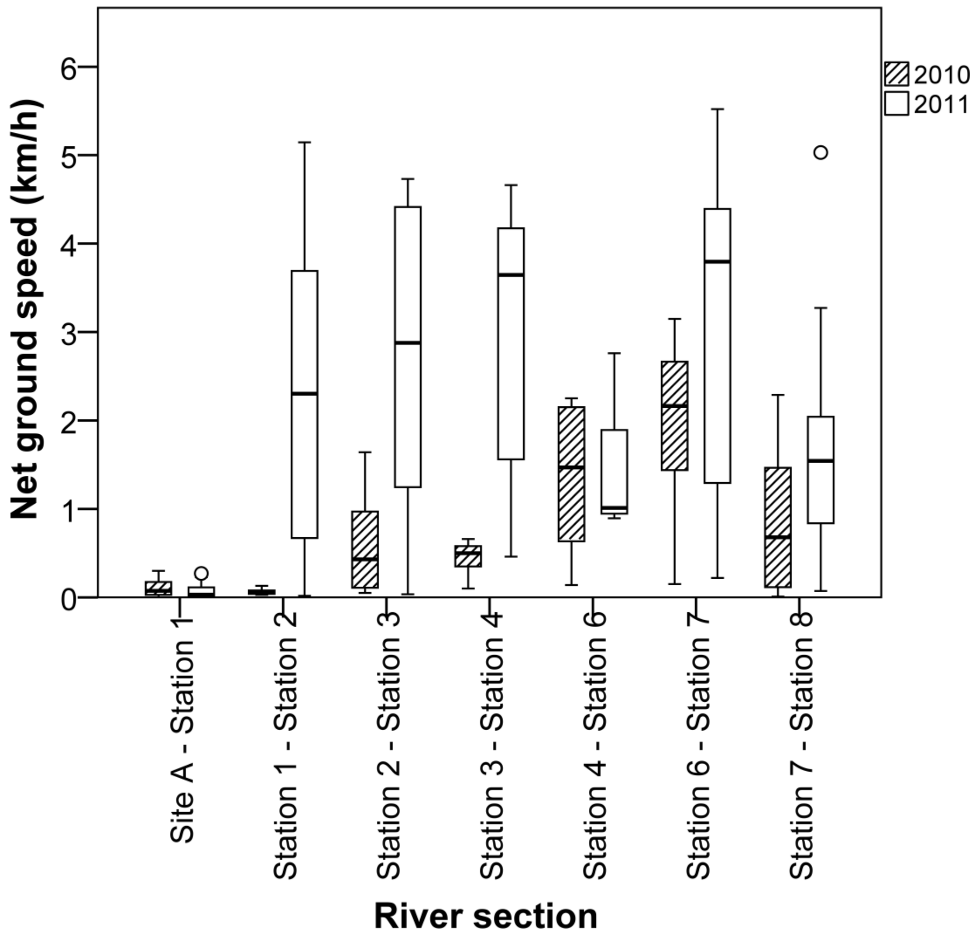

Figure 4. Box plot displaying the median net ground speeds of tagged trout smolts moving through each river section in both 2010 and 2011. Boxes represent upper and lower quartiles and T-bars represent the upper and lower 5 percentiles and round dots signify outliers. *Section of river between ALS stations, station 5 removed from analysis due to insufficient sample size.

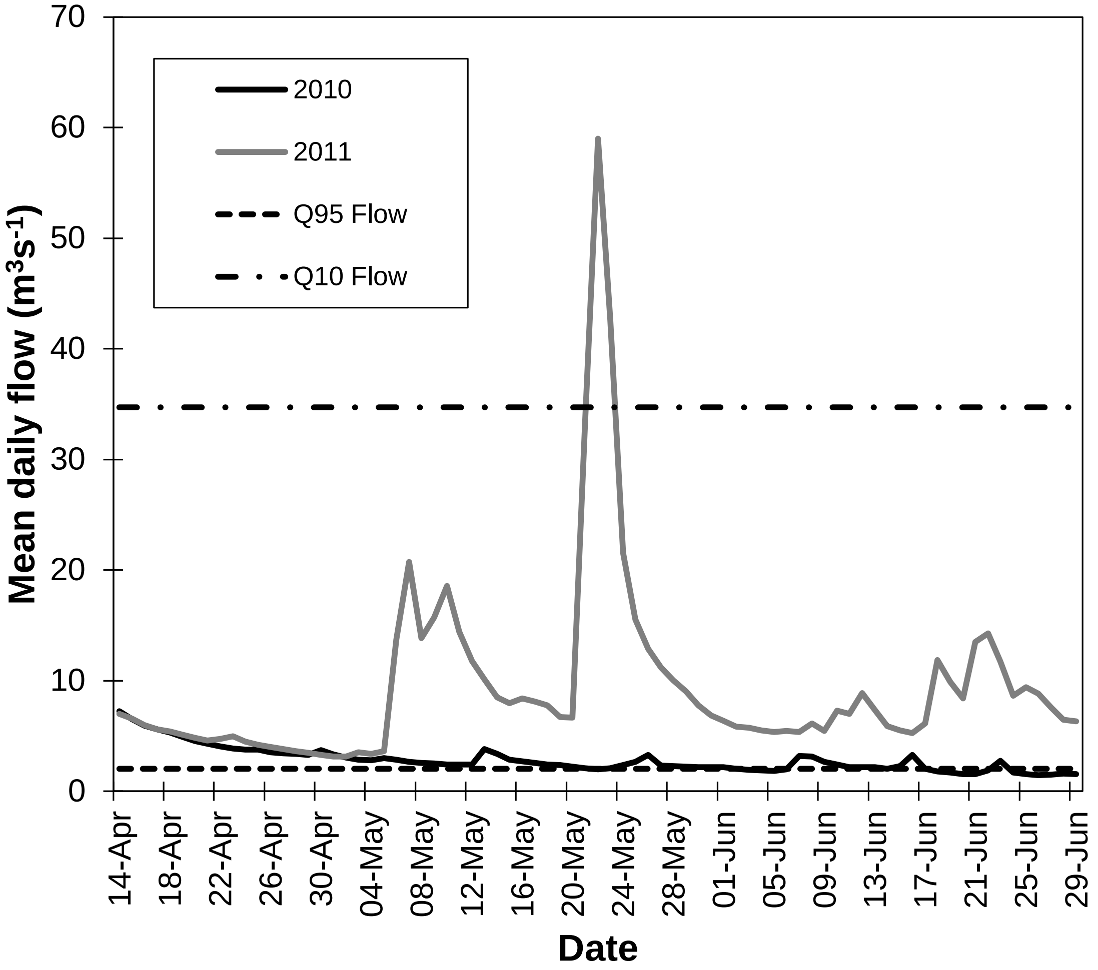

Figure 5. Mean daily flows at the flow gauging station at Lindean on the Ettrick Water, reflecting water flow at Murray's Cauld, during the period of study in both 2010 and 2011 as well as the Q95 and Q10 flows for the Lindean station.

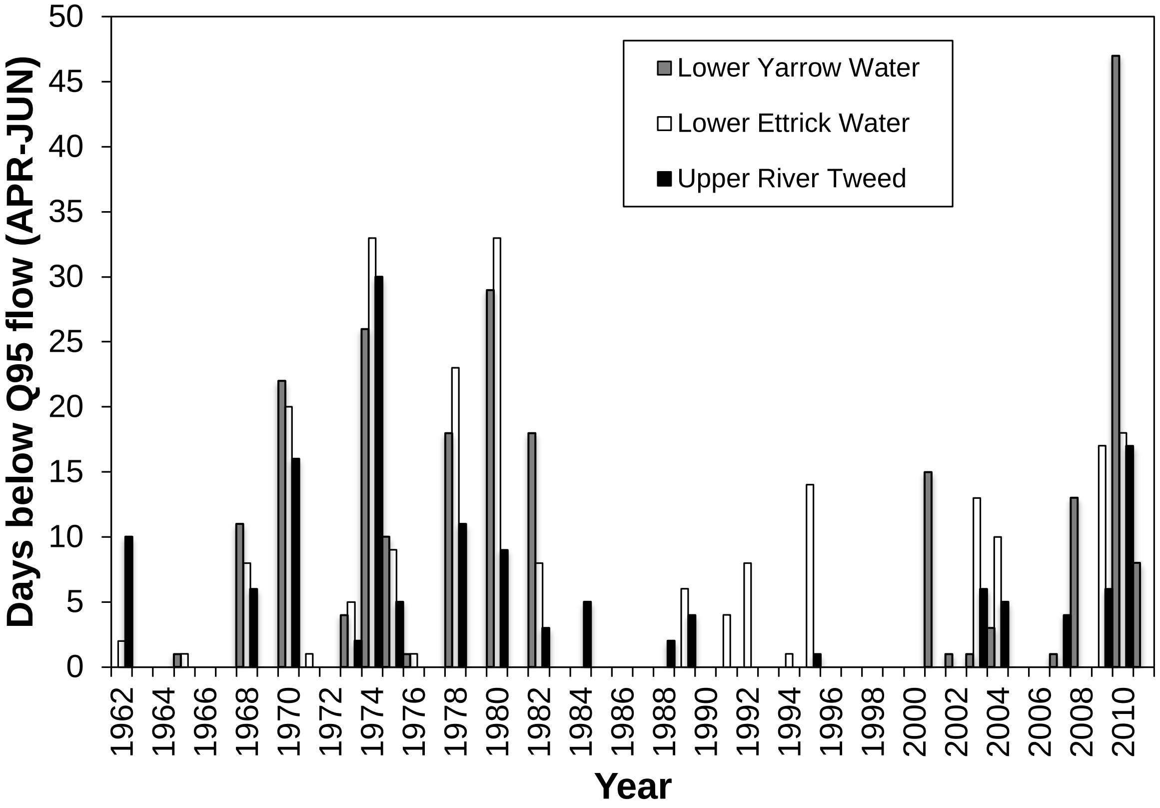

Figure 6. Total number of days below Q95 flows for the smolt migration period 1 April to 30 May between 1962 and 2011 on the lower Yarrow Water at the Philiphaugh flow gauging station, lower Ettrick Water at the Lindean flow gauging station and the upper Tweed at the Boleside flow gauging station.

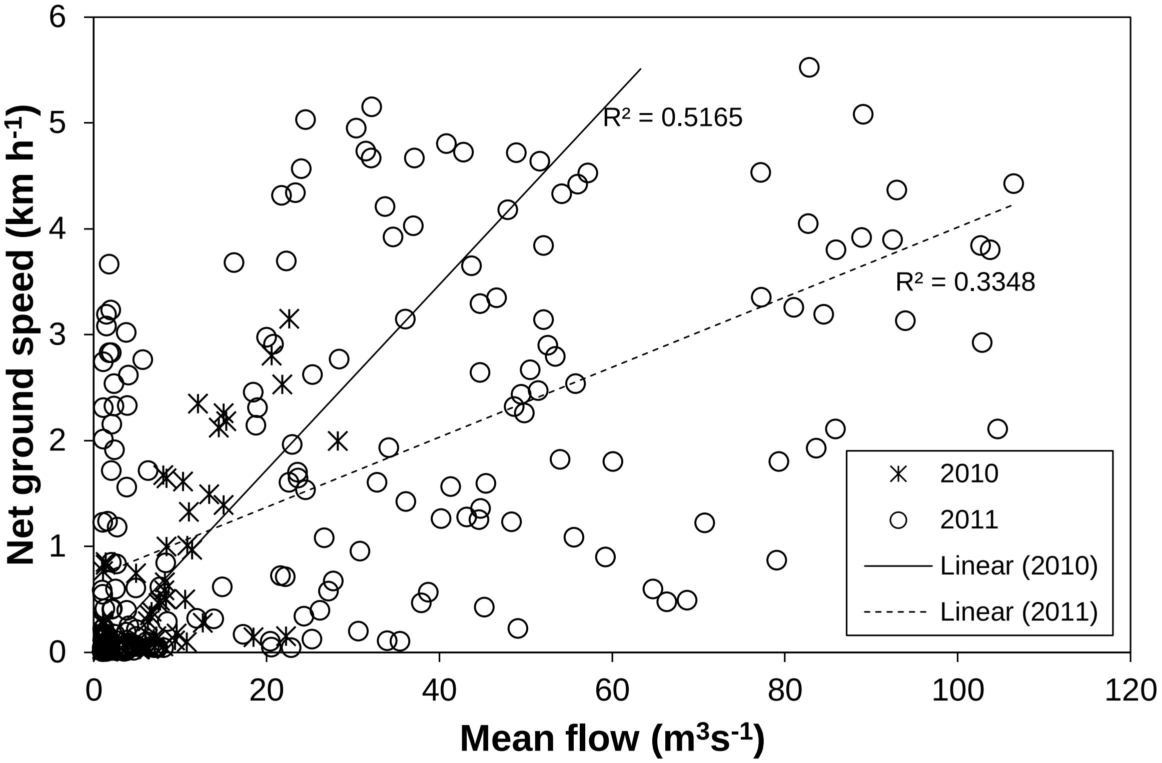

Figure 7. The net ground speed (km h^{-1}) of migrating smolts in relation to the estimated mean flow conditions (m^3s^{-1}) during the period of transit throughout the migratory route. Flows are based upon the nearest 15-minute gauged flow, at the closest gauging station.