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

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HIGHLIGHTS

- First evidence of impacts of small weirs on wild salmonid smolt emigration.
- Weirs delayed trout smolt migration, especially at low river flows.
- Emigration success was reduced in a low-flow season compared to a normal flow season.
- Weir passage efficiencies differed with weir design.
- Smolt migration response to daily flow differed between high and low-flow years.

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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, were 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 delays 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 show 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.

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;

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Northcote, 1998). In Europe, legislations such as the Water Framework Directive (WFD; 2000/60/EC) require 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, 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, 2007, 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, 2001; Harris et al., 2008; Heggenes and Borgstrom, 1988; Koed et al., 2002; Steinmetz et al., 2003; Svenning et al., 2005a, 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 past dams through bypass facilities 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, 2001b; Raymond, 1979, 1988; Smith et al., 2006, 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 long been 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 the presence of passage facilities is not always guaranteed to mitigate passage concerns (Roscoe and Hinch, 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 (Fig. 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 (Fig. 1, Table 1).

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. Individual fish likely to be large enough for tagging were placed in an induction tank and anaesthetised using Phenoxyethanol (0.3 ml l^{-1}), and 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 s 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 h 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: 2 km below the point of capture and 200 m downstream of the Murray Cauld as a way to test the impact of the weir on migration in 2011 (Table 2, Fig. 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

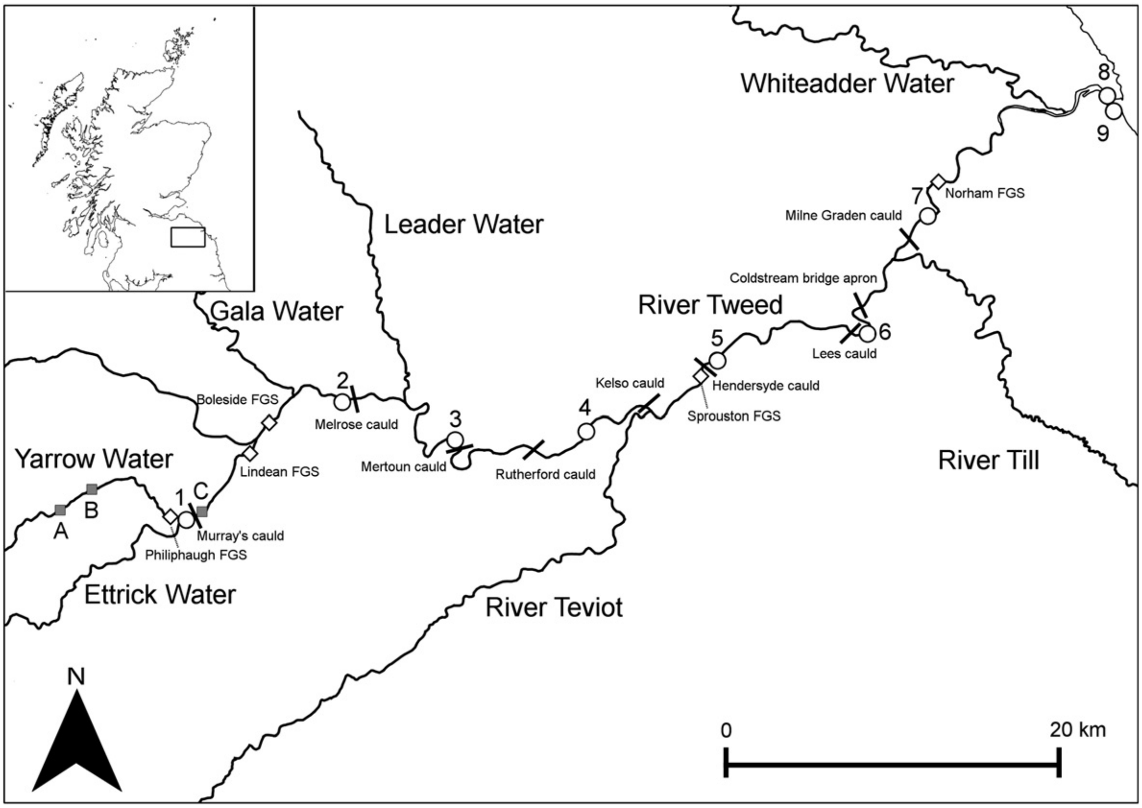

Fig. 1. Map of the River Tweed showing all the major tributaries as well as the migration route downstream from the Yarrow Water. Grey boxes denote the release sites along with white circles denoting the ALS positions and white diamonds for SEPA flow gauging stations (FGS). Black bars indicate the sites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

significantly different (Kruskal–Wallis; $n = 60$, $\chi^2 = 1.0892$, $df = 2$, $p > 0.05$).

3.2. Acoustic tracking

Acoustic tracking was carried out via a combination of fixed automatic listening stations (ALS) and manual tracking at 69 KHz to track fish survival to sea. 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. Average detection efficiencies for the ALSs were 89% in 2010 (100% excluding station 5) and 91% in 2011.

Manual tracking was carried out on foot by wading in shallow stretches and by boat in the deeper sections using a Vemco VR100 (Vemco Ltd, Nova Scotia, Canada) with a VH110 Directional Hydrophone attached (Vemco Ltd, Nova Scotia, Canada). The hydrophone was placed in the calmest water locally available and slowly rotated. 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; thus repeated scans were made at distances of equating to the effective range. Fish locations were recorded

Table 1
Descriptions of in river structures along the studied smolt migratory route.

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

* Structure crosses river at an angle to the flow.

Table 2
Summary data for smolts tagged in 2010 and 2011. The release sites are shown on Fig. 1.

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)

* Tag to body weight ratio is calculated from masses in air.

by the VR100 inbuilt GPS unit and later stored in a GIS database. Blind operator training was also used to ensure manual trackers could detect tags in various river sections, enabling maximum confidence that tags were not missed during manual tracking.

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)(Fig. 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 fish (16%) in 2010 and three fish in 2011 (5%) were assumed to be dead in the river after repeatedly being found in the same location in the river. Conversely, 28 tagged fish (65%) in 2010 and 30 tagged fish (50%) 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 (Fig. 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 (Fig. 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

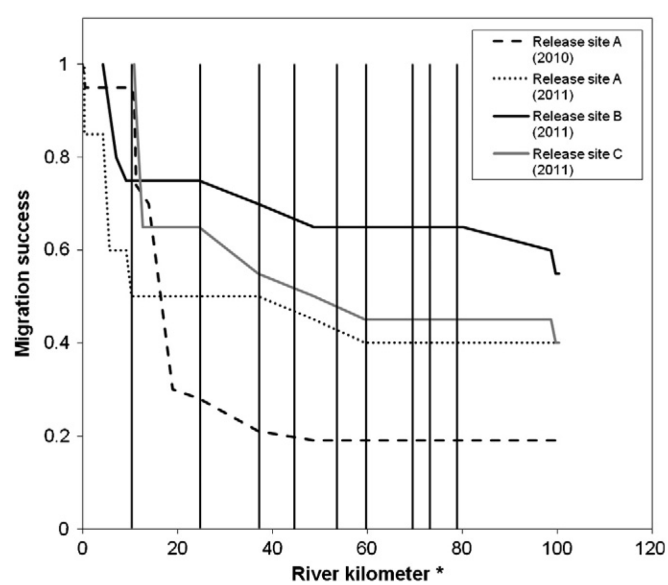

Fig. 2. Cumulative survival of acoustically tagged brown trout smolts migrating out to sea in 2010 and for three separate release groups in 2011. Black vertical bar represent weirs along the migration route. *Measured from the furthest upstream release point down to the estuary.

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: $n = 43$, $R^2 = 0.495$, $F = 12.064$, $p = 0.005$, Fig. 2; 2011: linear regression: $n = 60$, $R^2 = 0.84$, $F = 84.731$, $p < 0.001$, Fig. 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; $n = 20$, $R^2 = 0.52$, $F = 15.263$, $p = 0.002$; Fig. 2, release site B: linear regression; $n = 20$, $R^2 = 0.72$, $F = 37.305$, $p < 0.001$; Fig. 2, release site C: linear regression; $n = 20$, $R^2 = 0.73$, $F = 25.536$, $p = 0.001$; Fig. 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 h, 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 the weirs with ALS positions immediately above them 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 both Melrose Cauld and Mertoun Cauld 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.

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; $n = 205$, $F = 5.673$, $p < 0.001$; Fig. 4) 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, reflected through residence times experienced by smolts at logger 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. Regrouping the ALS delay data into two groups, "obstructed" where the ALS stations are within 100 m of an in river structure (stations 1, 2 and 3) and "unobstructed" where the ALS stations are in a free flowing section of river (stations 4, 6 and 7), it is observed that delay was significantly higher at obstructed sections compared to unobstructed sections in 2010 (Mann–Whitney U; median obstructed = 108.9, median unobstructed = 4.7, $n = 80$, $Z = -2.865$, $p = 0.004$; Fig. 3). Conversely, there was a lack of significant difference in delay duration between obstructed and unobstructed river sections in 2011 (Mann–Whitney U; median obstructed = 1.49,

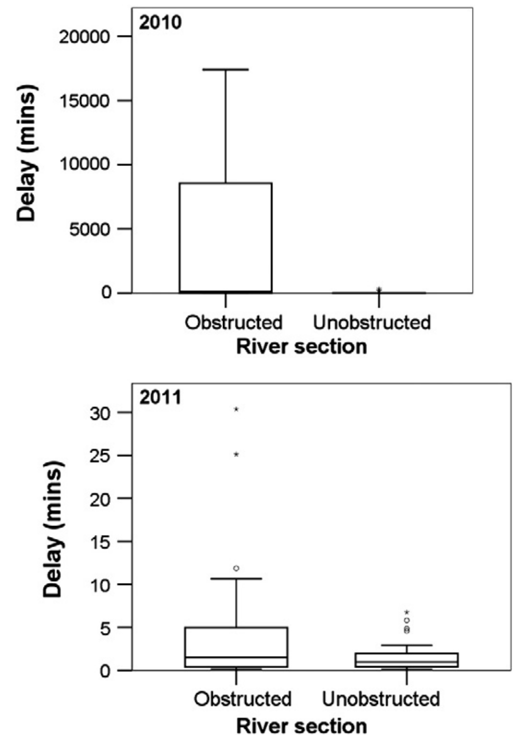

Fig. 3. Time spent by individual smolts at ALS positions (delay) that were within the impoundment zones of in river structures (obstructed) compared with those that were not (unobstructed). Data are presented as box plots, showing median, upper and lower quartiles, upper and lower 5 percentiles, mild outliers (circles; $Q_3 + 1.5 \times IQR$) and extreme outliers (asterisks; $Q_3 + 3 \times IQR$). In the 2010, panel medians are obscured by other lines. Data do not include records from station 5 due to insufficient sample size.

Table 3
Delay and barrier passage efficiencies at ALS positions along the smolt migration route through the river and estuary (station 5 was 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) (min)	2011 Delay, median (Q_1–Q_3) (min)	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)	–	–

median unobstructed = 0.97, $n = 129$, $Z = -1.767$, $p = 0.077$; Figs. 3 and 4).

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 (Fig. 5).

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 (Fig. 6). 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 (Fig. 6). There have therefore been periods of flow restriction similar to that experienced in 2010 previously and they are likely to reoccur.

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-min 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; $n = 88$, $R = 0.719$, $p < 0.001$; Fig. 7), 2011 (Regression; $n = 218$, $R = 0.579$, $p < 0.001$; Fig. 7). 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.

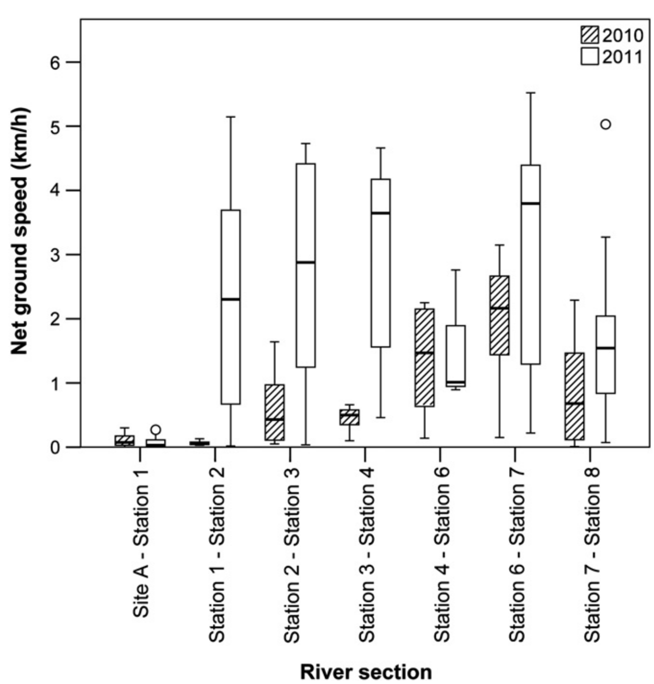

Fig. 4. Box plot displaying the median net ground speeds of tagged trout smolts moving through each river section in both 2010 and 2011. Boxes represent upper and lower quartiles and T-bars represent the upper and lower 5 percentiles and round dots signify outliers. *Section of river between ALS stations,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

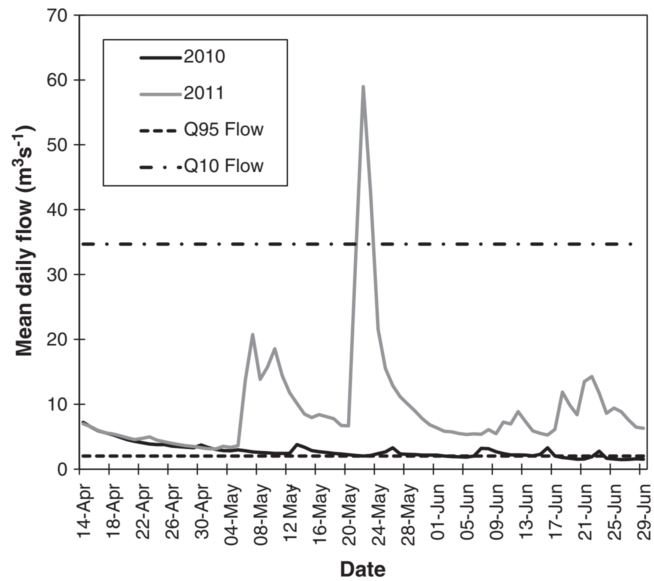

Fig. 5. Mean daily flows at the flow gauging station at Lindean on the Ettrick Water, reflecting water flow at Murray's Cauld, during the period of study in both 2010 and 2011 as well as the Q95 and Q10 flows for the Lindean station.

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, 2001b; Raymond, 1979, 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 Atlantic salmon 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 A1B) 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

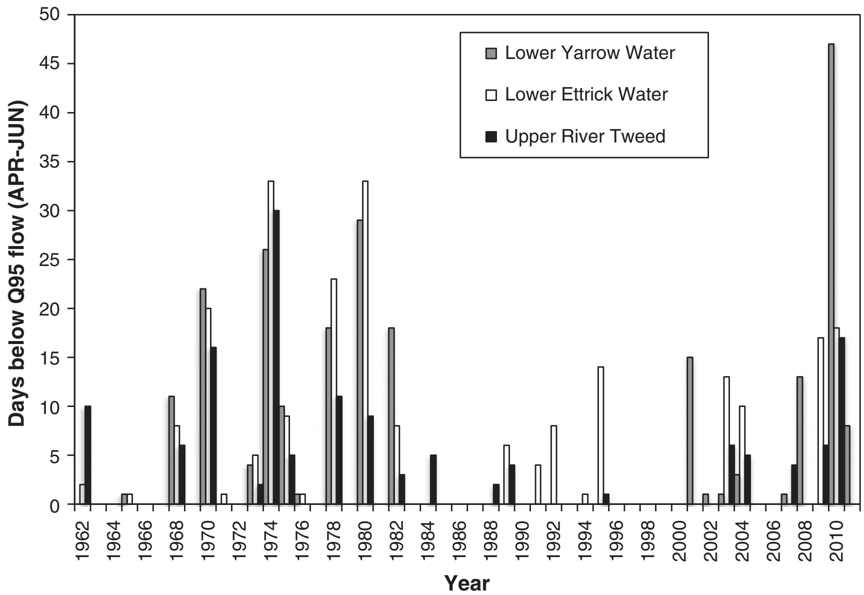

Fig. 6. Total number of days below Q95 flows for the smolt migration period 1 April to 30 May between 1962 and 2011 on the lower Yarrow Water at the Philiphaugh flow gauging station, lower Ettrick Water at the Lindean flow gauging station and the upper Tweed at the Boleside flow gauging station.

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 and 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.

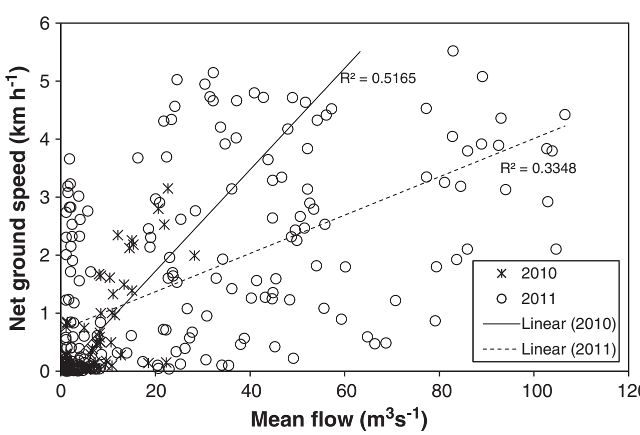

Fig. 7. The net ground speed (km h^{-1}) of migrating smolts in relation to the estimated mean flow conditions (m^3s^{-1}) during the period of transit throughout the migratory route. Flows are based upon the nearest 15-min gauged flow, at the closest gauging station.

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. In 2010, seven fish (16%) were repeatedly confirmed as stationary within the river, and 28 (65%) were assumed as removed from the system due to repeated null detections. Likewise in 2011, three fish (5%) were repeatedly confirmed as stationary whilst 30 tags (50%) were apparently removed from the river system after repeated null detections. 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, 2006; Martin et al., 2009; Moore et al., 1998; Thorstad et al., 2012a, 2012b). In comparison, anadromous brown trout smolts tracked in the Tweed in 2010 and 2011 suffered 0.88% and 0.55% mortality per kilometre, 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% and 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% and 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% and 90% in 2010 and between 92% and 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 the 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) reported 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 uncertain variability in river flows, where low-head structures are no longer 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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References

Aarestrup K, Koed A. Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. Ecol Freshw Fish 2003;12:169–76.

Aarestrup K, Jepsen N, Rasmussen G. Movements of two strains of radio tagged Altlantic salmon, *Salmo salar* L., smolts through a reservoir. Fish Manag Ecol 1999;6:97-107.

Aarestrup K, Nielsen C, Koed A. Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. Hydrobiologia 2002;483:95-102.

Acou A, Laffaille P, Legault A, Feunteun E. Migration pattern of silver eel (*Anguilla anguilla*, L.) in an obstructed river system. Ecol Freshw Fish 2008;17:432–42.

Arnell NW. Climate-change impacts on river flows in Britain: the UKCIPO2 scenarios. Water Environ J 2004;18:112–7.

Berg OK, Berg M. Migrations of sea trout, *Salmo trutta* L., from the Vardnes river in northern Norway. J Fish Biol 1987;31:113–21.

Björnsson B, Stefansson S, Hansen T. Photoperiod regulation of plasma growth hormone levels during parr-smolt transformation of Atlantic salmon: implications for hypoosmoregulatory ability and growth. Gen Comp Endocrinol 1995;100: 73–82.

Björnsson BT, Stefansson SO, McCormick SD. Environmental endocrinology of salmon smoltification. Gen Comp Endocrinol 2010;170:290–8.

Boubée JAT, Williams EK. Downstream passage of silver eels at a small hydroelectric facility. Fish Manag Ecol 2006;13:165–76.

Branco P, Segurado P, Santos JM, Pinheiro P, Ferreira MT. Does longitudinal connectivity loss affect the distribution of freshwater fish? Ecol Eng 2012;48:70–8.

Carss DN, Kruuk H, Conroy JWH. Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland. J Fish Biol 1990;37:935–44.

Christierson BV, Vidal J-P, Wade SD. Using UKCP09 probabilistic climate information for UK water resource planning. J Hydrol 2012;424–425:48–67.

Clay CH. Design of fishways and other fish facilities. Boca Raton: Lewis Publishers; 1995.

Connor WP, Burge HL, Yearsley JR, Bjornn TC. Influence of Flow and Temperature on Survival of Wild Subyearling Fall Chinook Salmon in the Snake River. N Am J Fish Manag 2003;23:362–75.

Currie J. Pollution prevention on the River Tweed: past, present and future. Sci Total Environ 1997;194–195:147–54.

Davidsen JG, Rikardsen AH, Halttunen E, Thorstad EB, Ã˜Kland F, Letcher BH, et al. Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. J Fish Biol 2009;75:1700–18.

Debowski P, Dobosz S, Robak S. Estimation of smoltification of hatchery-reared sea trout (*Salmo trutta morpha trutta* L.) based on body morphology. Arch Pol Fish 1999a;7:257–66.

Debowski P, Glogowski J, Robak S, Dobosz S. Smoltification of hatchery-reared Atlantic salmon (*Salmo salar* L.)-indices and methods of estimation. Arch. Pol. Fish. 1999b;7:267–79.
Denton EJ, Saunders RL. On the organization of silvery layers in the skin of the Atlantic salmon (*Salmo salar*) during smoltification and on the regeneration of these layers under abnormal lighting conditions. J Mar Biol Assoc UK 1972;52:889–98.
Dieperink C, Pedersen S, Pedersen MI. Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. Ecol Freshw Fish 2001;10:177–83.
Dieperink C, Bak BD, Pedersen LF, Pedersen MI, Pedersen S. Predation on Atlantic salmon and sea trout during their first days as postsmolts. J Fish Biol 2002;61:848–52.
Dynesius M, Nilsson C. Fragmentation and flow regulation of river systems in the northern third of the world. Science 1994;266:753–62.
Enders EC, Gessel MH, Williams JG. Development of successful fish passage structures for downstream migrants requires knowledge of their behavioural response to accelerating flow. Can J Fish Aquat Sci 2009;66:2109–17.
Fullerton AH, Burnett KM, Steel EA, Flitcroft RL, Pess GR, Feist BE, et al. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshw Biol 2010;55:2215–37.
Garcia de Leaniz C. Weir removal in salmonid streams: implications, challenges and practicalities. Hydrobiologia 2008;609:83–96.
Gardiner R. Tweed juvenile salmon and trout stocks. In: Mills D, editor. Tweed towards 2000. Melrose: The Tweed Foundation; 1989. p. 105–14.
Gosset C, Travade F, Durif C, Rives J, Elie P. Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. River Res Appl 2005;21: 1095–105.
Gustard A, Bullock A, Dixon JM. Low flow estimation in the United Kingdom. Report No. 108. Wallingford: Institute of Hydrology; 1992.
Haro A, Odeh M, Noreika J, Castro-Santos T. Effect of water acceleration on downstream migratory behavior and passage of Atlantic salmon smolts and juvenile American shad at surface bypasses. Trans Am Fish Soc 1998;127:118–27.
Harris CM, Calladine JR, Wernham CV, Park KJ. Impacts of piscivorous birds on salmonid populations and game fisheries in Scotland: a review. Wildl Biol 2008;14:395–411.
Heggenes J, Borgstrom R. Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic salmon, *Salmo safar* L., and brown trout, *S. trutta* L., in three small streams. J Fish Biol 1988:885–94.
Hockersmith EE, Muir WD, Smith SG, Sandford BP, Perry RW, Adams NS, et al. Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling chinook salmon in the snake and Columbia rivers. N Am J Fish Manag 2003;23:404–13.
Jungwirth M. River continuum and fish migration- going beyond the longitudinal river corridor in understanding ecological integrity. In: Jungwirth M, Schmutz S, Weiss S, editors. Fish Migration and Fish Bypasses. Oxford: Fishing News Books; 1998. p. 19–32.
Keefer ML, Taylor GA, Garletts DF, Helms CK, Gauthier GA, Pierce TM, et al. Reservoir entrapment and dam passage mortality of juvenile Chinook salmon in the Middle Fork Willamette River. Ecol Freshw Fish 2012;21:222–34.
Kemp PS, O'Hanley JR. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fish Manag Ecol 2010:297–322.
Koed A, Jepsen N, Aarestrup K, Nielsen C. Initial mortality of radio-tagged Atlantic salmon (Salmo salar L.) smolts following release downstream of a hydropower station. Hydrobiologia 2002;483:31–7.
Koed A, Baktoft H, Bak BD. Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. River Res Appl 2006;22:69–78.
Laaha G, Blöschl G. A national low flow estimation procedure for Austria. Hydrol Sci J 2007:37–41.
Lucas MC, Baras E. Migration of Freshwater Fishes. Blackwell Science Oxford: Oxford; Malden, MA; 2001.
Lucas MC, Batley E. Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: implications for river management. J Appl Ecol 1996: 1345–58.
Lucas MC, Frear PA. Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. J Fish Biol 1997;50:382–96.
Lucas MC, Bubb DH, Jang M-H, Ha K, Masters JEG. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. Freshw Biol 2009;54:621–34.
Lysfjord G, Staurnes M. Gill Na + –K + -ATPase activity and hypoosmoregulatory ability of seaward migrating smolts of anadromous Atlantic salmon (Salmo salar), sea trout (*Salmo trutta*) and Arctic char (Salvelinus alpinus) in the Hals river, northern Norway. Aquaculture 1998;168:279–88.
Marquiss M, Carss DN, Armstrong JD, Gardiner R. Fish-eating birds and salmonids in Scotland. Edinburgh: The Scottish Office Agriculture and Fisheries Department; 1998.
Marsh TJ. The UK, drought of 2003: a hydrological review. Weather 2004;59:224–30.
Martin F, Hedger RD, Dodson JJ, Fernandes L, Hatin D, Caron F, et al. Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. Ecol Freshw Fish 2009;18:406–17.
McCormick SD. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. Estuaries 1994;17:26–33.
McCormick SD, Hansen LP, Quinn TP, Saunders RL. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 1998;55:77–92.
McCormick SD, Moriyama S, Björnsson BT. Low temperature limits photoperiod control of smolting in atlantic salmon through endocrine mechanisms. Am J Physiol Regul Integr Comp Physiol 2000;278:R1352–61.
McCormick SD, Shrimpton JM, Moriyama S, Björnsson BT. Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. J Exp Biol 2002;205:3553–60.
McCormick SD, Shrimpton JM, Moriyama S, Bjornsson BT. Differential hormonal responses of Atlantic salmon parr and smolt to increased daylength: a possible developmental basis for smolting. Aquaculture 2007;273:337–44.
Moore A, Ives S, Mead TA, Talks L. The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton Water, southern England. Hydrobiologia 1998;371/372:295–304.
Muir WD, Smith SG, Williams JG, Hockersmith EE, Skalski JR. Survival estimates for migrant yearling chinook salmon and steelhead tagged with passive integrated transponders in the lower snake and lower Columbia Rivers, 1993–1998. N Am J Fish Manag 2001a;21:269–82.
Muir WD, Smith SG, Williams JG, Sandford BP. Survival of juvenile salmonids passing through bypass systems, turbines, and spillways with and without flow deflectors at Snake River dams. N Am J Fish Manag 2001b;21:135–46.
Nilsson C, Ca Reidy, Dynesius M, Revenga C. Fragmentation and flow regulation of the world's large river systems. Science 2005;308:405–8.
Noonan MJ, Grant JWA, Jackson CD. A quantitative assessment of fish passage efficiency. Fish Fish 2012;13:450–64.
Northcote TG. Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. In: Jungwirth M, Schmutz S, Weiss S, editors. Fish Migration and Fish Bypasses. Oxford: John Wiley & Sons; 1998. p. 3-18.
O'Connor JP, O'Mahony DJ, O'Mahony JM, Glenane TJ. Some impacts of low and medium head weirs on downstream fish movement in the Murray–Darling Basin in southeastern Australia. Ecol Freshw Fish 2006;15:419–27.
Ovidio M, Philippart J-C. The impact of small physical obstacles on upstream movements of six species of fish. Hydrobiologia 2002;483:55–69.
Poff NL, Hart DD. How dams vary and why it matters for the emerging science of dam removal. Bioscience 2002;52:659–68.
Raymond HL. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans Am Fish Soc 1979;108:505–29.
Raymond HL. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. N Am J Fish Manag 1988;8:1-24.
Roscoe DW, Hinch SG. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. Fish Fish 2010;11:12–33.
Scruton DA, McKinley RS, Kouwen N, Eddy W, Booth RK. Use of telemetry and hydraulic modeling to evaluate and improve fish guidance efficiency at a louver and bypass system for downstream-migrating Atlantic salmon (*Salmo salar*) smolts and kelts. Hydrobiologia 2002;483:83–94.
Scruton DA, Pennell CJ, Bourgeois CE, Goosney RF, Porter TR, Clarke KD. Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at a hydroelectric facility on the Exploits River, Newfoundland, Canada. Hydrobiologia 2007;582:155–69.
Sheail J. The Tweed fisheries: an historical perspective. Sci Total Environ 1998;210:469–82.
Smakhtin VU. Low flow hydrology: a review. J Hydrol 2001;240:147–86.
Smith SG, Muir WD, Williams JG, Skalski JR. Factors associated with travel time and survival of migrant yearling chinook salmon and steelhead in the lower Snake River. N Am J Fish Manag 2002;22:385–405.
Smith SG, Muir WD, Hockersmith EE, Zabel RW, Graves RJ, Ross CV, et al. Influence of river conditions on survival and travel time of Snake River subyearling fall Chinook salmon. N Am J Fish Manag 2003;23:939–61.
Smith SG, Muir WD, Marsh DM, Williams JG, Skalski JR. Survival estimates for the passage of spring-migrating juvenile salmonids through Snake and Columbia River dams and reservoirs, 2005. Report of the National Marine Fisheries Service to the Bonneville Power Administration, Portland, Oregon; 2006.
Steinmetz J, Kohler SL, Soluk DA. Birds are overlooked top predators in aquatic food webs. Ecology 2003;84:1324–8.
Svenning M, Borgstrom R, Dehli T, Moen G, Barrett R, Pedersen T, et al. The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, lesser sandeel (*Ammodytes marinus*). Fish Res 2005a;76:466–74.
Svenning M, Fagermo S, Barrett R, Borgstrom R, Vader W, Pedersen T, et al. Goosander predation and its potential impact on Atlantic salmon smolts in the River Tana estuary, northern Norway. J Fish Biol 2005b;66:924–37.
Thorstad EB, Uglem I, Finstad B, Chittenden CM, Nilsen R, Okland F, et al. Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. Fish Manag Ecol 2012a;19:400–9.
Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. J Fish Biol 2012b;81:500–42.
Welch DW, Rechisky EL, Melnychuk MC, Porter AD, Walters CJ, Clements S, et al. Survival of migrating salmon smolts in large rivers with and without dams. PLoS Biol 2008;6:e265.
Wiese FK, Parrish JK, Thompson CW, Maranto C. Ecosystem-based management of predator-prey relationships: piscivorous birds and salmonids. Ecol Appl 2008;18: 681–700.
Wilby RL, Harris I. A framework for assessing uncertainties in climate change impacts: low-flow scenarios for the River Thames, UK. Water Resour. Res. 2006;42. [W02419].
Williams JG, Smith SG, Muir WD. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966–1980 and 1993–1999. N Am J Fish Manag 2001;21:310–7.
Wollebaek J, Heggenes J, Roed KH. Population connectivity: dam migration mitigations and contemporary site fidelity in arctic char. BMC Evol Biol 2011;11.
Xenopoulos MA, Lodge DM, Alcamo J, Märker M, Schulze K, Van Vuuren DP. Scenarios of freshwater fish extinctions from climate change and water withdrawal. Glob Chang Biol 2005;11:1557–64.