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The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen content of intragravel water and embryo survival

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Abstract:

The accumulation of sediment within salmonid redd gravels can have a detrimental impact on the development of salmonid embryos; therefore, redd sedimentation represents a potential limiting factor for salmonid reproduction. The links between redd sedimentation, the dissolved oxygen content of intragravel water and salmonid embryo survival within the upper and middle parts of the Hampshire Avon catchment in southern England are explored. Measurements of surface and intragravel water quality and redd properties were undertaken for artificial redds constructed at known spawning sites. Salmonid embryos were also planted into artificial redds adjacent to the monitoring equipment. The rate of sedimentation of the newly cleaned redd gravels demonstrated a non-linear decrease over time, which is attributed to a particle-size-selective depositional process. The results of the study confirm that low embryo survival and low dissolved oxygen concentrations in intragravel water can be attributed to the accumulation of sediment within the redd gravels. This was found to produce a reduction in redd permeability, which limited the interchange of surface and intragravel water and, therefore, the supply of dissolved oxygen to the intragravel environment. In view of the diminished status of salmonids within many of the UK's chalk rivers and streams, the results highlight the need for management initiatives aimed at reducing redd sedimentation and thereby optimizing salmonid embryo incubation success. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS salmonid; embryo; redd; dissolved oxygen; permeability; sedimentation; chalk streams

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INTRODUCTION

The input of excessive quantities of sediment into salmonid spawning habitats has been shown to represent a major limiting factor for salmonid fish reproduction (e.g. Cordonne and Kelley, 1961; Chapman, 1988; Bjornn and Reiser, 1991; Waters, 1995). The accumulation of sediment on and within redd gravels can have lethal and sub-lethal affects on the salmonid eggs and sac fry that incubate within the gravel voids. It is widely believed that fine sediment can smother and physically abrade the embryos (McHenry *et al*., 1994; Waters, 1995) and that the accumulation of sediment in the intragravel pores can prevent the emergence of fry from the gravel bed (Hall and Lantz, 1969; Phillips *et al*., 1975; Hausle and Coble, 1976). However, in many situations the principal mechanism whereby redd sedimentation adversely affects embryo survival involves the reduction in the supply of dissolved oxygen (DO) to the egg pocket (e.g. Wicket, 1954, 1958; Coble, 1961; Turnpenny and Williams, 1980; Scrivener and Brownlee, 1989; Rubin and Glimsäter, 1996; Igendahl, 2001). This is because the accumulation of sediment within the voids of the redd gravel reduces redd substrate permeability, thereby reducing intragravel flow rates, the delivery of DO to the incubating embryos and the removal of toxic metabolic waste products from the egg pocket (Rubin and Glimsäter, 1996). As biochemical oxygen demands within the redd consume the available DO, concentrations fall, increasing hypoxial stress and ultimately increasing embryo mortality rates. Low DO concentrations in the intragravel water and entrapment of fry within the redd gravels may not only increase embryo mortality, but also impede embryo development (e.g. Silver *et al*., 1963; Shumway *et al*., 1964; Brannon, 1965; Mason, 1969). Fry that emerge from the gravel bed later and smaller will find it more difficult to compete and are likely to have a lower post-emergence survival than fry that emerge larger or earlier (Silver *et al*., 1963; Mason, 1969; Chapman, 1988).

The negative impact of logging on sediment production and, consequently, salmonid reproduction in North American rivers (e.g. McNeil and Anhell, 1964; Koski, 1966; Hall and Lantz, 1969; Scrivener and Brownlee, 1989) has been a prime motivation for research into the link between sedimentation and salmonid spawning success and has emphasized the links between land use and fish habitat. Sedimentation problems, particularly those resulting from land use change, have also been cited as an influence on salmonid reproduction in the UK

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(e.g. Theurer *et al*., 1998). However, field investigations explicitly aimed at addressing this issue remain limited in number and scale, although related studies of the quality of salmonid spawning habitat have increased (e.g. Carling and McCahon, 1987; Acornley and Sear, 1999; Milan *et al*., 2000; Soulsby *et al*., 2001a,b; Malcolm *et al*., 2003). Further research is required to investigate the causes, nature and scale of sediment-related problems across the range of UK spawning habitats. The groundwater-dominated chalk rivers and streams of southern England are traditional salmonid fisheries. However, increased sediment loadings as a result of changing agricultural activities within these catchments have been cited as a potential cause of diminished salmonid productivity (Theurer *et al*., 1998). To promote greater understanding of these issues, this paper reports an investigation of levels and patterns of sediment accumulation in artificial redds within the upper and middle Hampshire Avon catchment and the links between redd sedimentation, the dissolved oxygen (DO) content of intragravel water and embryo survival.

STUDY AREA

The Hampshire Avon catchment (1701 km^2) extends over parts of the counties of Hampshire, Wiltshire and Dorset in southern England (Figure 1). The main River Avon rises in the Vale of Pewsey and flows south, falling 108 m over 122 km before draining into the English Channel at Christchurch. The study focused on the upper River Avon and its tributaries, the Rivers Wylye, Nadder and Bourne, located in the upper parts of the catchment. This part of the catchment is dominated by the gentle to moderate slopes of the rolling chalk landscape and sheltered valleys of Salisbury Plain and the South Wiltshire Downs.

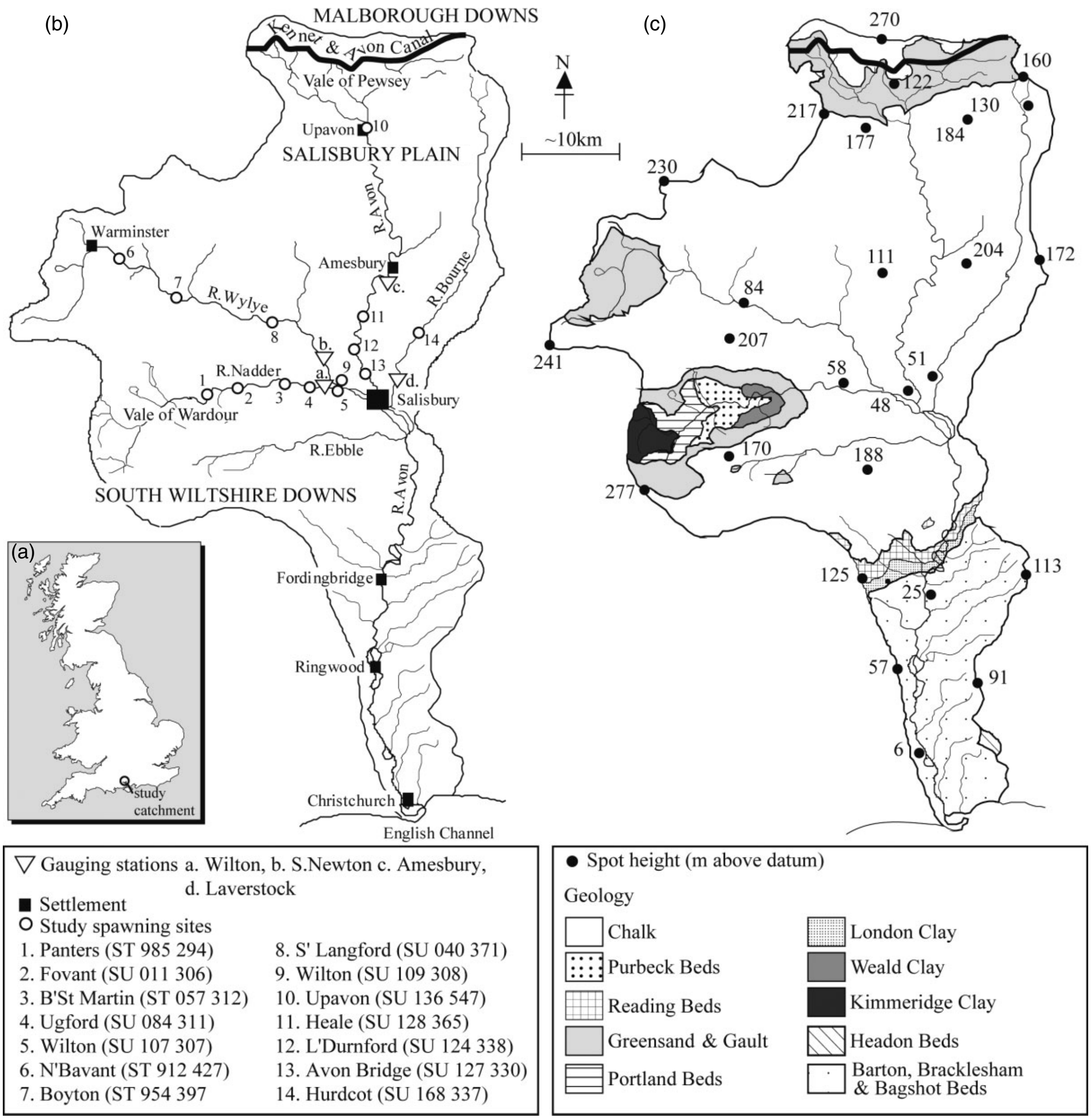

Figure 1. The Hampshire Avon catchment, showing (a) its location within the UK, (b) the location of the study and monitoring sites, and (c) the geology and relief of the catchment

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Above the town of Fordingbridge, Cretaceous chalk is the main rock type (Figure 1), providing an important aquifer that supplies the streams of the upper and middle catchment with a sustained groundwater contribution. Upper Greensand and Gault clay, also of Cretaceous age, underlie the chalk strata and are exposed in the Vale of Pewsey, in the Upper Wylye valley around Warminster and in parts of the Nadder catchment. A more extensive succession of strata beneath the chalk is exposed in the Nadder valley, including Greensand and Weald clay and Jurassic Purbeck and Portland limestones and Kimmeridge clay. Thin, humic, gley and brown rendzina soils and argillic and typical brown earths are the dominant soil types across the study area. The catchments investigated are predominantly rural, with a population of approximately 200 000. Almost 80% of land is in agricultural use, with most of this under arable cultivation (cereals, oil seed rape, short-term grass and set aside). Approximately 30% of the agricultural land is used for grazing, primarily for dairy and beef cattle. Large areas of Salisbury Plain are also used for military training. The rivers represent an important salmonid fishery, although, as with chalk streams in southern England more generally, Atlantic salmon (*Salmo salar*) numbers are perceived to have declined markedly in recent decades (WWF, 2001).

The median (1965–2000) annual discharges at the South Newton, Amesbury, Laverstock and Wilton flow gauging stations (Figure 1) are $4{\cdot}0\ m^3\ s^{-1}$, $3{\cdot}4\ m^3\ s^{-1}$, $0{\cdot}74\ m^3\ s^{-1}$ and $2{\cdot}8\ m^3\ s^{-1}$ respectively. The baseflow index (BFI) values calculated for the South Newton, Amesbury and Laverstock gauging stations on the Rivers Wylye, Avon and Bourne indicate that groundwater contributes ~90% of the total flow, whereas groundwater inputs are estimated to be slightly less important on the River Nadder, contributing ~73% of the flow at Wilton (Environment Agency, personal communication). In accordance with the general perception of chalk stream systems, these rivers are characterized by relatively low suspended sediment concentrations (cf. Heywood and Walling, 2003).

METHODOLOGY

The study involved two field campaigns. The first field campaign (campaign 1) took place between 12 September and 13 December 1999. Although this did not span the natural salmonid spawning and embryo incubation period (ca. October–April), this part of the study was specifically designed to further understanding of the processes associated with spawning gravel sedimentation and the implications of sedimentation for DO concentrations in intragravel water. It provided a study of temporal variations in intragravel water quality and artificial redd sedimentation at two sites, namely Ugford on the River Nadder and Steeple Langford on the River Wylye (Figure 1). The second field campaign (campaign 2) was undertaken between 14 January 2000 and 28 March 2000 and, therefore, covered the natural incubation period. This second campaign aimed to quantify the sedimentation of redd gravels at spawning sites distributed across the Upper River Avon and the Rivers Nadder, Wylye and Bourne (Figure 1) and to investigate the link between salmonid embryo survival and redd sedimentation during this period. This was also accompanied by further measurements of intragravel water quality and assessments of embryo survival at the Ugford and Steeple Langford spawning sites.

Measurement of artificial redd sedimentation

Gravel-filled infiltration baskets (Figure 2), similar to those employed by a number of workers (Carling and McCahon, 1987; Davey *et al.*, 1987; Sear, 1993; Acornley and Sear, 1999), were used to measure sedimentation of artificial redds. The cylindrical infiltration baskets comprised a 23 cm high and 22 cm diameter galvanized steel mesh (2 cm × 2 cm) infiltration cage and a collapsible infiltration bag (23 cm diameter). The infiltration bag

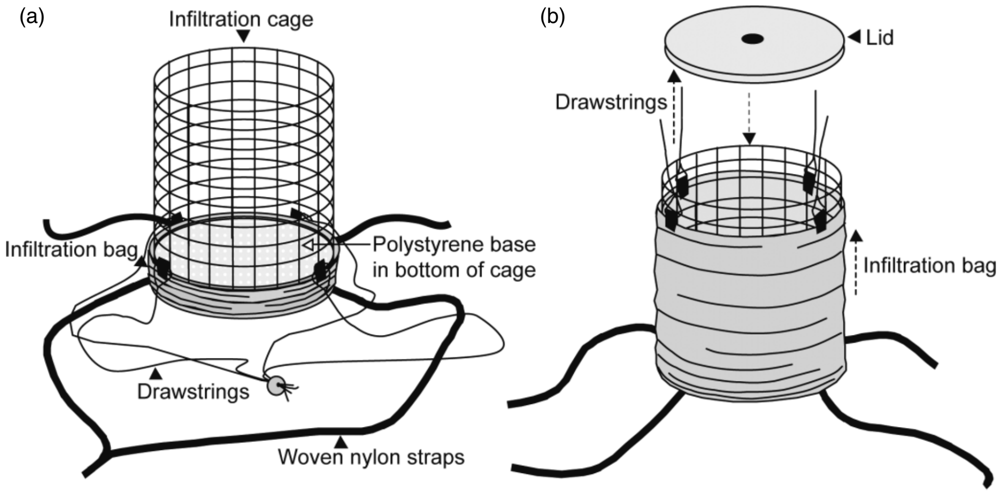

Figure 2. The infiltration basket, showing (a) the infiltration bag folded around the base of the infiltration cage and (b) the infiltration bag partially pulled up around the sides of the infiltration cage and the Perspex lid

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was constructed from flexible polyvinyl chloride (PVC) ducting fixed to a plywood disc base (1 cm thick). The ducting contained an integral stainless steel coil that enabled the bag to be neatly folded in a concertina fashion around the base of the infiltration basket, prior to installation into an artificial redd (Figure 2). Immediately prior to removing the basket and contents from the artificial redd, drawstrings attached to top of the bag provided a means of pulling it up around the infiltration cage and a Perspex lid was also placed on top of the basket (Figure 2). This prevented the loss of fine sediment from the basket upon removal. Four woven nylon straps were attached to the base of the infiltration bag to provide additional lift for extracting the entire infiltration basket and contents from the redd. Upon removal from a redd, the contents of the infiltration basket were retained in sealed plastic containers for subsequent wet sieving, drying and weighing.

Suitable spawning sites in which to carry out measurements were identified with the help of Environment Agency fisheries personnel and redd maps for previous years. Artificial redds were constructed at each of the sites selected (Figure 3). This involved cleaning the gravels by winnowing the fine sediment and moulding the gravels into a form imitating that of a natural redd. The artificial redd dimensions (Figure 3) were based on observations of natural redds and conform to general accepted dimensions for Atlantic salmon redds (e.g. Crisp and Carling, 1989). Following redd construction, an infiltration basket was filled with a representative sample of the redd substrate that had been wet sieved to remove material less than 2 mm in size. This included two or three larger gravel- or cobble-sized particles placed at the base of each infiltration basket in an attempt to represent the coarser lag of the egg pocket (cf. Chapman, 1988). Depending on the field campaign, either one or two gravel-filled infiltration baskets were then installed in the centre of the redd (Figure 3) in a position representing the likely location of the natural egg pocket, with the top of the basket flush with the redd surface. The infiltration baskets remained in the artificial redds for predetermined lengths of time, according to the aims of the investigation. During field campaign 1, removal of the baskets from the redds at both the Ugford and Steeple Langford sites was staggered so that the two baskets in a particular redd were both removed after 10, 22, 46, 68 and 92 days. This afforded a means of comparing the accumulation of fine sediment within progressively older redds, thereby establishing temporal patterns of sediment accumulation. However, it is acknowledged that variation in the characteristics of the artificial redds within each site may compromise the results obtained. During field campaign 2, 45 artificial redds, each containing a single infiltration basket, were created at the sites indicated on Figure 1. These infiltration baskets were retrieved after a 74-day period.

The contents of the infiltration baskets removed from artificial redds were wet sieved through 64, 32, 16, 8, 4, 2, 1, 0·5, 0·25 and 0·125 mm mesh sieves. The resulting size fractions were air dried and then weighed. The remaining water–sediment mixture, containing all material $<0{\cdot}125$ mm, was left to settle for a period of 7 days in a cool dark environment before two-thirds of the supernatant was decanted. The remaining sample was transferred to a centrifuge bottle and centrifuged at 2500 rpm for 1 h in the laboratory. The resulting 'sludge' was then freeze-dried and subsequently weighed. To determine the silt and clay ($<0{\cdot}063$ mm) content of the $<0{\cdot}125$ mm sediment, a portion of the dried sediment was rewetted and disaggregated by adding a dispersing agent (sodium hetametaphosphate) and placing the sample in an ultrasonic bath for 10 min prior to analysis using a Coulter LS130 laser diffraction particle size analyser. This process was repeated three times and the average proportion of sediment $<0{\cdot}063$ mm by volume was calculated. Disaggregation was necessary because a large proportion of the silt and clay particles removed from the redd were present as composite particles $>0{\cdot}063$ mm in size. The weights of each size fraction were used to establish how much fine sediment had accumulated within the redd gravel and to determine the overall redd substrate quality. The organic matter content of sediment samples retrieved from the infiltration baskets was also determined using a standard loss-on-ignition procedure. Samples of a known weight of sediment <2 mm were placed in a furnace for 4 h at 550 °C, before being reweighed to determine the loss of organic matter.

Measurement of intragravel and stream water quality

Samples of intragravel water were extracted from the artificial redds, using a modified version of the intragravel water sampling technique described by Hoffman (1986). The technique involved installing a horizontal sampling pipe (Figure 3) at a depth of approximately 25 cm in the centre of an artificial redd tailspill and perpendicular to the direction of flow, so that only the top of the vertical access tube remained above the redd surface. The pipe comprised a rigid outer PVC pipe (700 mm long, 35 mm internal diameter), which had 372 slots (37 mm long and 0·3 mm wide) cut perpendicular to its long axis. This essentially served as an outer casing that prevented fine sediment from entering the sampling system. One end of the outer casing was sealed using a U-PVC cap, and the other end was threaded to accept a circular removable U-PVC union. A rigid plastic internal pipe (710 mm long, 13 mm internal diameter) was centred axially within the outer casing and secured by the union nut. This inner plastic pipe was perforated with three 0·5 cm diameter holes equally spaced along its length and one end was capped. Hoffman (1986) found that this design allowed equal volumes of water to enter each of the internal tube holes simultaneously during sampling. A 10 mm portion of the non-capped end of the internal pipe protruded from the union and this was connected to a 30 cm length of the same piping by a 90° elbow joint. This provides the vertical access tube, linking the sampling pipe to the riverbed

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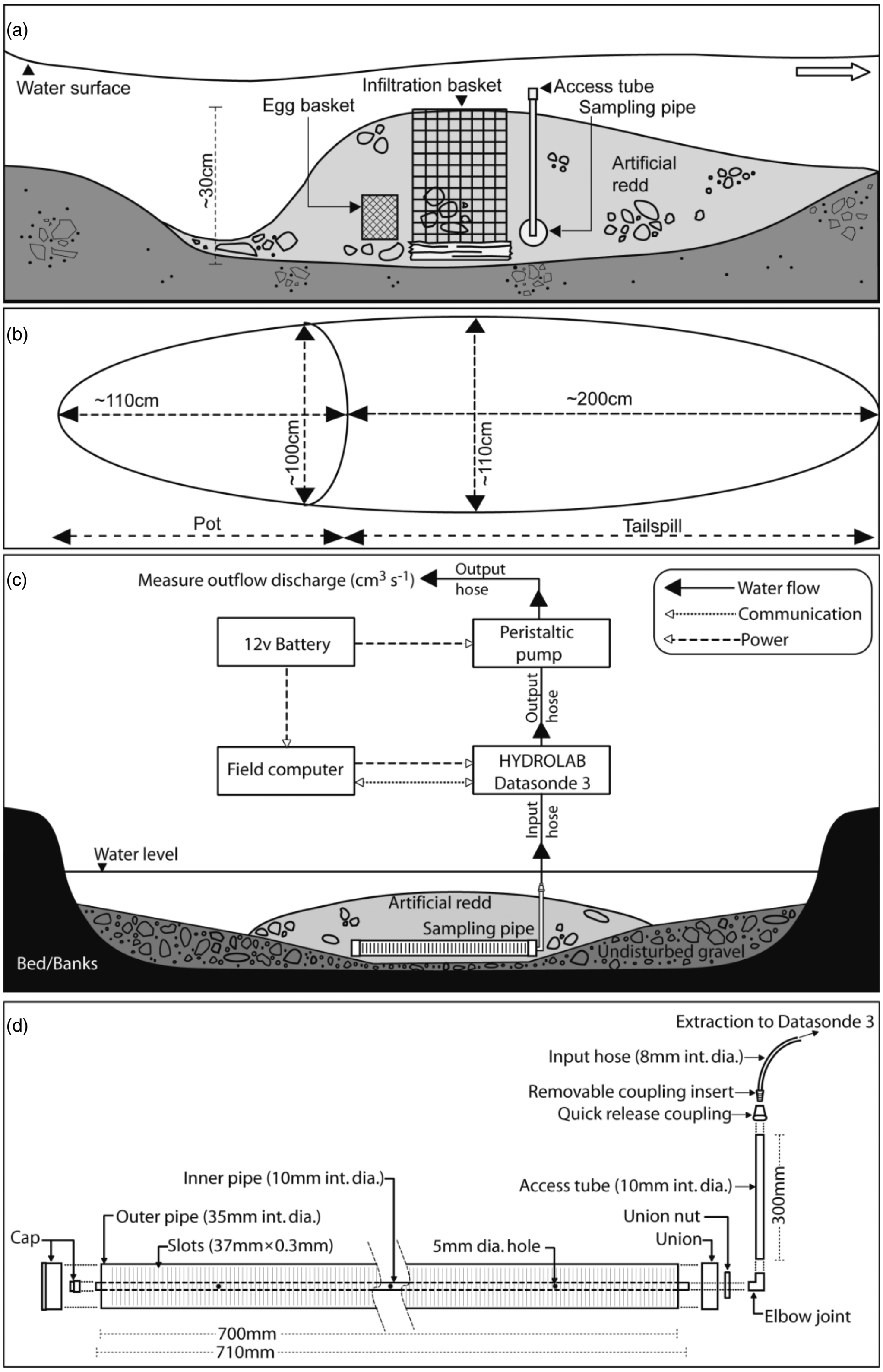

Figure 3. Details of the redd sampling strategy showing (a) a schematic representation of a longitudinal section of an artificial redd depicting the installation of an egg basket, an infiltration basket and an intragravel water sampling pipe, (b) a plan view of an artificial redd showing its approximate dimensions, (c) the approach used for intragravel water sampling and (d) the intragravel water sampling pipe and its components

surface. A quick-release coupling (RS-Components Ltd) was attached to the access tube. The coupling acted as a one-way valve to prevent inflow of surface water into the access pipe, while permitting samples of intragravel water to be extracted during sampling. Therefore, one end of the extraction hose (Figure 3) was fitted with a removable coupling insert (RS-Components Ltd) for easy attachment to and detachment from the access pipe. Unless threaded, all fittings were glued and sealed using Tangit U-PVC adhesive.

The remainder of the water quality sampling apparatus (Figure 3) consisted of a multiprobe water quality monitor (HYDROLAB Datasonde3), a peristaltic pump (Watson Marlow Ltd, 5045, IP55), a 2 m long input hose (non-reinforced PVC tubing, ARCO, 0·8 mm internal diameter), a 1 m long output hose (Marprene, 0·5 mm internal diameter) and a portable field computer (HUSKY, FC486, Husky Computers Ltd). The pump, computer and water quality monitor were powered by a (12 V) battery. The input hose was used to connect the intragravel sampling pipe to the water quality monitor via the quick release coupling, whilst the output hose connected the water quality monitor to the peristaltic pump. The monitoring equipment was deployed in the river on a portable table, which was weighted for stability. However, it was also possible to sample the redds from a bankside location by extending the length of the input hose.

The water quality monitor was programmed to measure and record DO concentration (percentage saturation and mg l^{-1}), temperature (°C) and specific electrical conductance (SEC; μS cm^{-1}) every 5 s. The DO probe was recalibrated to a constant temperature before each sampling exercise, to take account of the influence of changing water temperatures on absolute DO measurements. DO concentrations have been presented as mg l^{-1} values in this study, on the basis that these provided the strongest relationships between DO and the other variables reported. Although limited in scope, the measurement of temperature, DO and SEC may provide a tentative indication of whether upwelling groundwater represented a significant source of hyporheic water in the redd under investigation, based upon the premise that large temperature gradients or water quality differences reflect greater separation of water sources (Hoffman and Scopettone, 1988; Peterson and Quinn, 1996, Acornley, 1999; Geist *et al.*, 2001). In addition, a significant disparity between surface and subsurface values could provide a further indication of limited interaction between streamflow and intragravel flow, due to a reduction in redd permeability, to supplement observed DO patterns.

Before collecting a sample of intragravel water, the water quality monitor and hoses were first purged of air by pumping stream water from a well-mixed part of the flow, through the system for approximately 5 min. This provided data on stream water quality, and, therefore, background data with which the intragravel water quality data could be compared. The input hose was then attached to the intragravel sampling pipe and water was withdrawn using a constant pump setting. A low pumping rate was used to minimize drawdown of stream water into the gravels. This corresponded to an average extraction rate of 2·5 cm^3 s^{-1}, but the rate was found to vary according to the permeability of the redd substrate. For this reason, extraction rates were considered to provide a useful surrogate measure of relative redd gravel permeability and were quantified by recording the time taken to extract 1 l of water from the redd. During extraction, real-time records of DO concentration were logged by the portable field computer and examples of these are shown in Figure 4. These were consistently characterized by a DO sampling curve, where the minimum DO concentration recorded represents the DO concentration of intragravel water in the redd. Minimum DO concentrations were always registered after 1·05 l of water had been discharged from the output hose. This corresponds to the amount of water required to displace the water contained within the Datasonde reservoir, the intragravel sampling pipe and the sampling hoses by water sampled from the intragravel pores surrounding the intragravel sampling pipe. After continued pumping, DO concentrations commonly began to rise and eventually reached background stream water concentrations, as the extracted intragravel water was replaced by stream water being

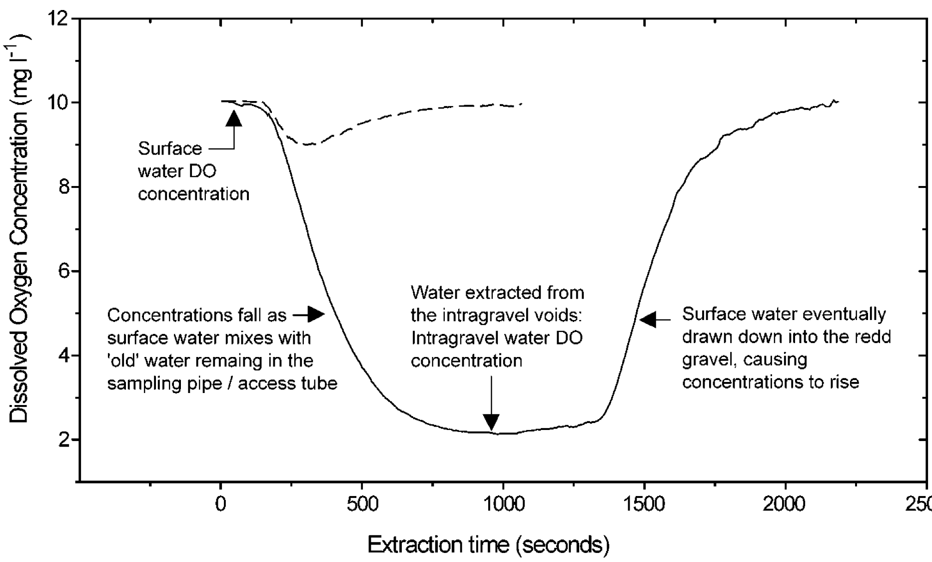

Figure 4. Examples of DO records. The dashed line represents a typical DO record for a highly permeable redd, characterized by a short extraction time and intragravel water with a high DO concentration. The solid line represents a relatively low permeability redd, characterized by a longer extraction time and intragravel water with a lower DO concentration

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drawn down into the gravels. The two curves shown in Figure 4 emphasize that extraction rates could be highly variable. The upper (dashed) curve represents more permeable gravel characterized by a high extraction rate and high DO concentrations in the intragravel water, whereas the second, longer, curve reflects a less permeable redd characterized by a lower extraction rate and lower DO concentrations.

During field campaign 1, three artificial redds each containing an intragravel water-sampling pipe were constructed alongside the five artificial redds containing infiltration baskets at the Ugford and Steeple Langford sites. Seven sets of water quality measurements were taken from each site over the duration of field campaign 1, where each set of measurements involved measuring background surface water quality and the quality of intragravel water in the three artificial redds. During field campaign 2, three intragravel water-sampling pipes were each installed into an artificial redd at the Ugford and Steeple Langford sites. However, unlike field campaign 1, each of these three redds also contained an infiltration basket and an egg basket containing Atlantic salmon embryos. Three sets of water quality measurements were made over the duration of field campaign 2.

Embryo survival survey

An embryo survival investigation was carried out alongside measurements of redd sedimentation and the DO content of intragravel water during field campaign 2, in order to investigate the potential for redd sedimentation to affect embryo survival adversely during this period. This involved planting eyed salmon eggs contained in gravel-filled egg boxes (cf. Harris, 1973) into artificial redds alongside infiltration baskets and DO monitoring equipment. Eggs were sourced from the UK Environment Agency Kielder hatchery in Northumbria, due to the critically low levels of local salmonid stocks. Egg boxes (10 cm high, 6 cm diameter) were constructed from a supple plastic mesh (2 mm × 2 mm) (Netlon Ltd), heat welded together to form a cylindrical basket. Egg box lids were also constructed in a similar fashion. Each egg box was filled with a sample of the artificial redd gravel on the riverbank. At the same time, 50-eyed eggs were carefully transferred from an ice-filled egg carrier into the egg box gravels. Care was taken to distribute the eggs evenly throughout the gravel layers. Once filled with gravel and eggs, the egg box was placed into a hole in the artificial redd, immediately upstream of the infiltration basket, and subsequently carefully covered with gravel. Egg baskets were placed into 35 of the 45 artificial redds created in field campaign 2. At the Ugford and Steeple Langford sites, egg boxes were also installed alongside intragravel water sampling equipment, in addition to the infiltration baskets. Egg boxes were retrieved after a 74-day incubation period, along with the infiltration baskets. The numbers of live and dead eggs and alevins were then determined.

To establish whether embryo survival rates in artificial redds were less than survival rates under favourable conditions, and to provide an indication of whether the handling of eggs in the field was a cause of increased mortality, Atlantic salmon embryos were also incubated under controlled conditions in a trout-rearing facility near Fordingbridge on the River Avon. Two rearing tanks containing slowly flowing water pumped from the River Avon were established to contain embryos. One tank contained three batches of 100 eggs kept loosely within nylon mesh egg trays. The egg trays were enclosed to prevent alevin escaping. A second rearing tank held three batches of 50 eggs housed in gravel-filled egg boxes. Embryo survival rates were established upon completion of the field experiment (28 March 2000).

RESULTS

Background hydraulic conditions and sediment transport during the study

Discharge and suspended sediment concentration data from nearby gauging stations (Figure 1) have been used to characterize flow conditions and suspended sediment transport at the Ugford and Steeple Langford sites during the two field campaigns (Figure 5). During field campaign 1 there were nine principal storm events over the 92-day period, with a particularly wet period between 18 September and 4 October. Discharges of $2{\cdot}4\ m^3\ s^{-1}$ and $2{\cdot}2\ m^3\ s^{-1}$ were equalled or exceeded for 50% of the campaign period at the Ugford and Steeple Langford respectively. At both sites, storm event flows were superimposed on a gradual increase in baseflow discharge in response to groundwater recharge, particularly on the River Wylye. Suspended sediment concentrations equalled or exceeded $48\ mg\ l^{-1}$ and $7\ mg\ l^{-1}$ for 5% of the campaign period for the Rivers Nadder and Wylye respectively, and maximum concentrations reached $256\ mg\ l^{-1}$ and $22\ mg\ l^{-1}$ respectively. Mean daily suspended sediment loads for the River Nadder and River Wylye sites over field campaign 1 were $4{\cdot}9\ t\ day^{-1}$ and $0{\cdot}68\ t\ day^{-1}$ respectively.

Field campaign 2 began with high water levels, although nevertheless declining, following a large annual maximum storm, which led to substantial recharge of the groundwater stores and, together with a number of other significant wet periods, contributed to high baseflow conditions that persisted over the remainder of the field campaign (Figure 5). Over the 74-day period there were seven main storm events and flows were greater than in field campaign 1. Discharges equalled or exceeded for 50% of the period at the Ugford and Steeple Langford sites were $4{\cdot}5\ m^3\ s^{-1}$ and $7\ m^3\ s^{-1}$ respectively. Suspended sediment concentrations in the River Nadder and River Wylye equalled or exceeded $70\ mg\ l^{-1}$ and $9\ mg\ l^{-1}$ for 5% of the campaign period respectively, and maximum concentrations were $251\ mg\ l^{-1}$ and $25\ mg\ l^{-1}$ respectively. Suspended sediment transport was greater in field campaign 2, with mean daily loads of $10{\cdot}5\ t\ day^{-1}$ for the River Nadder and $2{\cdot}5\ t\ day^{-1}$ for the River Wylye.

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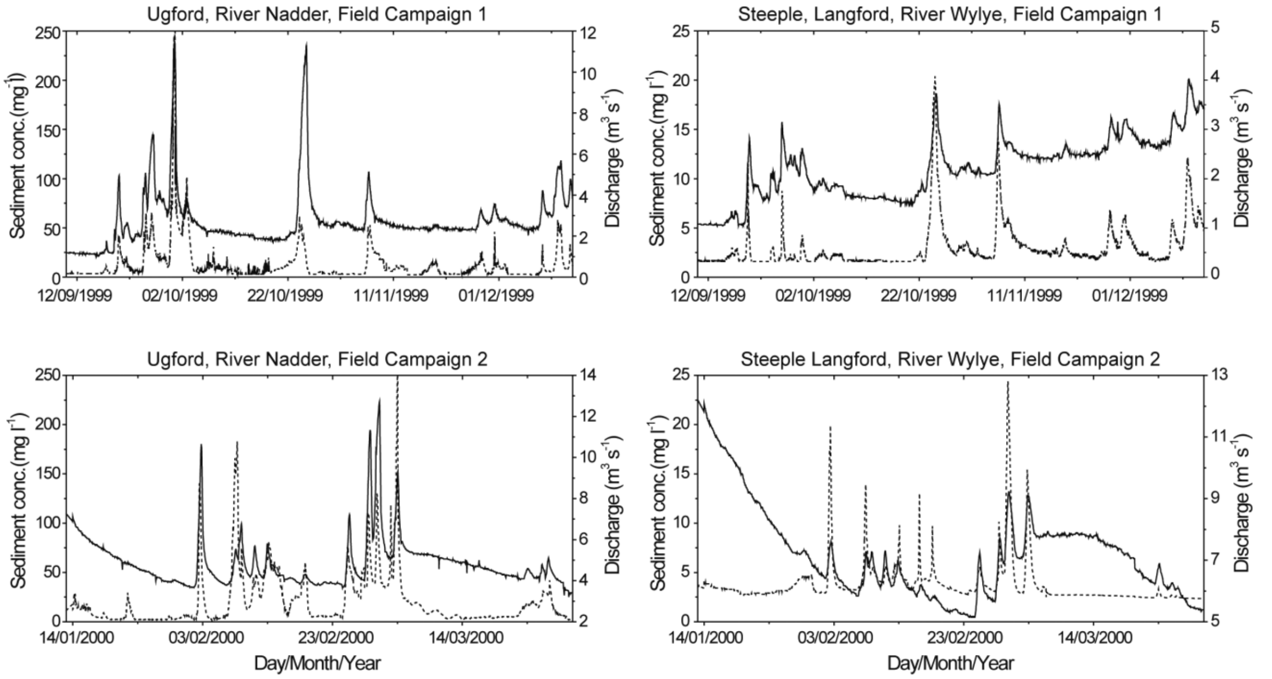

Figure 5. Discharge (solid line) and suspended sediment concentration (dashed line) records for the Ugford and Steeple Langford monitoring sites during the periods covered by field campaigns 1 and 2

The accumulation of sediment in redd gravels

Figure 6 shows the percentage of the infiltration basket content comprising sediment <2 mm and <1 mm upon removal from the artificial redds at Ugford and Steeple Langford during field campaign 1. This shows that redd sedimentation was greater at Ugford than at Steeple Langford. At both spawning sites, sedimentation of the artificial redds was especially rapid for the first 22 days, after which rates of sediment accumulation declined, particularly at Ugford. The percentage of sediment <2 mm in the infiltration baskets removed from artificial redds after 22 days was ~9% at Ugford and ~1·7% at Steeple Langford. The equivalent values for infiltration baskets removed after 92 days were ~8% and ~5% respectively. In some instances, the amounts of fine sediment in the infiltration baskets were smaller in older redds. However, it is possible that this reflects spatial variation in sedimentation between the different redds within each site, as opposed to remobilization of deposited sediment from the redd gravels by hydraulic flushing.

The mean particle size distribution of the sediment <2 mm accumulating within the artificial redds during field campaign 1 was similar for both sites. Coarse sand-sized particles (0·5–2 mm) comprised 55% (standard deviation SD = 17%) of the sediment, fine sand-sized particles (0·5–0·063 mm) made up 30% (SD = 10%), and silt- and clay-sized particles (<0·063 mm) made up 15% (SD = 8%). The results from the loss on ignition indicated that ~16% (SD = 2·0%) of sediment <2 mm comprised organic matter.

Figure 7 shows the percentage levels of sediment <2 mm and <1 mm contained in the infiltration baskets

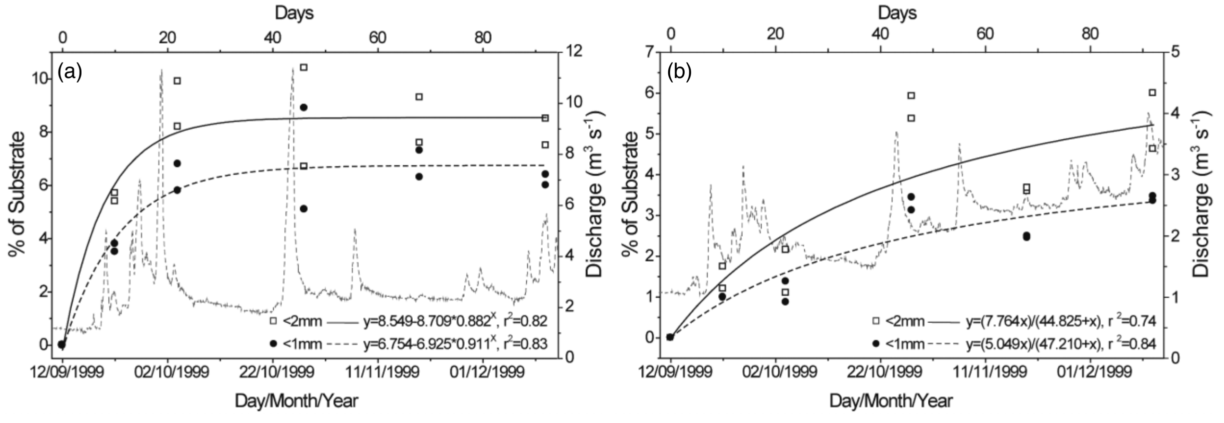

Figure 6. The proportions of sediment <1 mm and <2 mm in the infiltration baskets recovered from artificial redds of different age at (a) Ugford and (b) Steeple Langford, during field campaign 1. The dashed lines represent the discharge records for the monitoring sites during the period covered by field campaign 1

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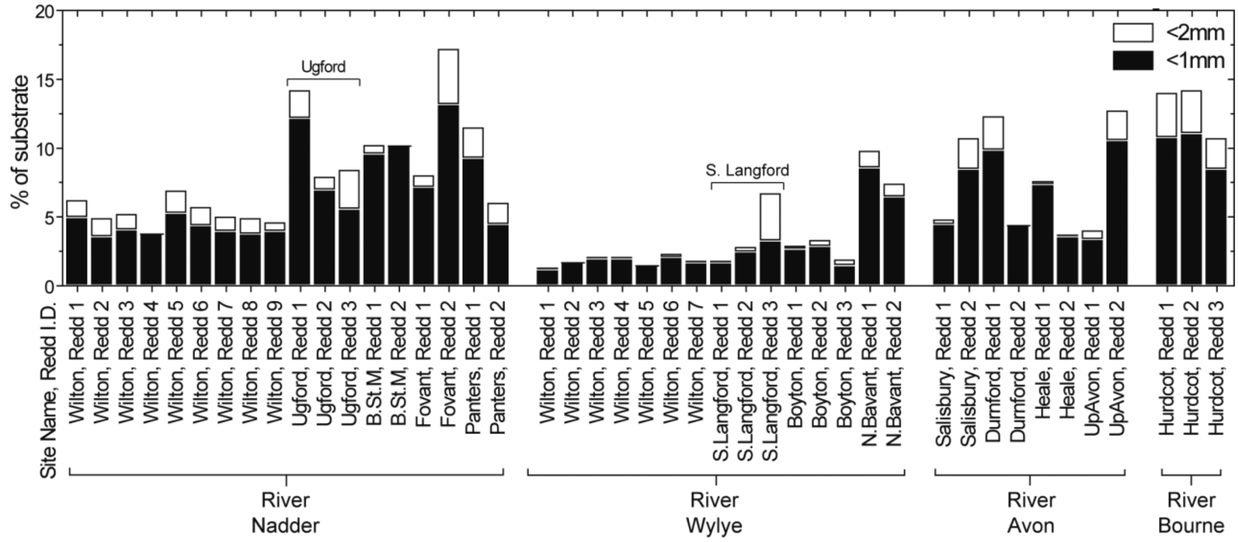

Figure 7. The proportion of sediment <1 mm and <2 mm in the infiltration baskets removed from the redds after 74 days in field campaign 2

removed from artificial redds in the Rivers Wylye, Nadder, Avon and Bourne during field campaign 2, including those at Ugford and Steeple Langford. The mean amounts of sediment <2 mm in the infiltration baskets after the 74-day period were 7·8%, 3·3% and 7·5% for the Rivers Nadder, Wylye and Avon respectively, with values for individual baskets ranging from 1·3 to 17·2%. Only one site was successfully sampled on the River Bourne, and this was characterized by a mean level of sediment <2 mm of 13%. The mean particle size distribution of sediment <2 mm accumulating within infiltration baskets during field campaign 1 was 28% (SD = 15%) coarse sand-sized particles, 41% (SD = 14%) fine sand-sized particles and 31% (SD = 14%) silt- and clay-sized particles. Particulate organic matter comprised 14% (SD = 4·9%) of the <2 mm sediment fraction.

The levels of sedimentation at both the Ugford and Steeple Langford sites during field campaign 2 (Figure 7) were generally similar to those observed during field campaign 1 (Figure 6), with the exception of one redd at each site where relatively high levels of sedimentation were observed. However, for each of these redds there were no distinguishing features that could help to explain these elevated levels of sedimentation. The particle size distribution of sediment <2 mm at both sites was finer than in field campaign 1, with coarse sand-sized particles comprising 34% (SD = 19%) of the sediment, fine sand-sized particles 36% (SD = 13%), and silt- and clay-sized particles 30% (SD = 16%). Organic matter comprised 13% (SD = 2·4%) of the <2 mm sediment.

Extraction rates and surface and intragravel water quality during field campaign 1: 12 September–10 December 1999

Extraction rates for each intragravel water sample collected during field campaign 1 are presented in Figure 8 and these demonstrate that substrate permeability was consistently lower at Ugford than at Steeple Langford. The mean extraction rates at Ugford and Steeple Langford during field campaign 1 were 1·68 cm^3 s^{-1} and 4·53 cm^3 s^{-1} respectively. Extraction rates at Ugford did not show a statistically significant trend (linear regression, $P = 0{\cdot}12$) over the duration of field campaign 1, tending to decline steadily until 28 October 1999 and then to recover slightly. Conversely, extraction rates for the redds at Steeple Langford showed a significant decline (linear reression, $P < 0{\cdot}01$) over the duration of field campaign 1.

Figure 8 presents information on DO, temperature and SEC for surface water and intragravel water collected from Ugford and Steeple Langford during field campaign 1. The mean difference between the surface water and intragravel water quality measurements is also presented for each set of measurments. The DO concentrations of stream water samples were not significantly different between the Ugford and Steeple Langford sites ($P = 0{\cdot}19$, *t*-test), with mean concentrations of 10·9 mg l^{-1} and 11·3 mg l^{-1} respectively. The mean DO content of intragravel water at Ugford was 5·0 mg l^{-1} over the 92 days and ranged from 2·5 to 9·1 mg l^{-1}. At Steeple Langford, DO concentrations in intragravel water were significantly higher ($P < 0{\cdot}001$, *t*-test), with a mean value of 10·2 mg l^{-1} and values ranging from 7·4 to 11·9 mg l^{-1}. Although the DO concentrations in intragravel water did not provide evidence of a significant decline (linear regression, $P > 0{\cdot}05$) over the 92-day period at either site, Figure 8 demonstrates that, at both Ugford and Steeple Langford sites, the mean difference between the DO concentrations in surface and intragravel water for each set of measurements did show a general increase over time.

Temporal variations in surface water and intragravel water temperatures were almost identical (Figure 8). At Ugford, the mean difference between surface water and intragravel water temperature for each set of measurements ranged from −1 to +0·28 °C; the equivalent mean

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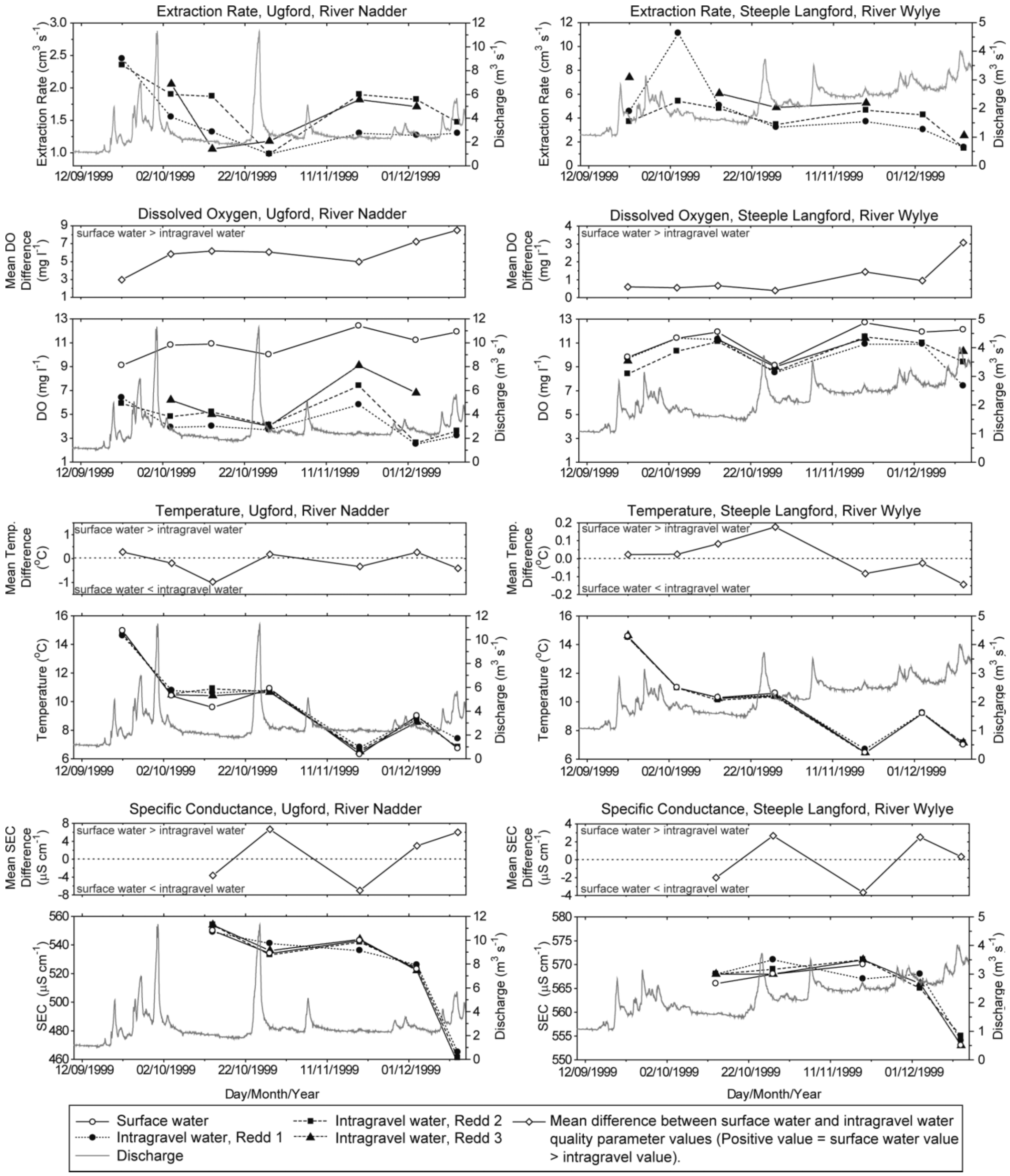

Figure 8. Extraction rates and the DO concentration, temperature and specific conductance of surface water and intragravel water samples collected during field campaign 1. For each water quality parameter, the mean difference between the surface water and intragravel water quality measurements is also presented for each set of measurements

differences at Steeple Langford were smaller, ranging between $-0{\cdot}14$ and $0{\cdot}18\,^{\circ}C$. SEC measurements were not available for the two first sampling occasions. However, temporal changes in the SEC of surface water and intragravel water were generally similar. As with DO and temperature, the mean difference between the SEC of surface water and intragravel water for each set of measurements was greatest at Ugford, where the mean differences ranged from around -7 to 7 $\mu S\ cm^{-1}$, as opposed to only $-3{\cdot}7$ to $2{\cdot}7$ $\mu S\ cm^{-1}$ for redds at Steeple Langford.

Extraction rates and water quality during field campaign 2: 14 January–28 March 2000

Extraction rates in field campaign 2 were comparable to those in field campaign 1 (Figure 9). As in the case of field campaign 1, redd permeability was consistently greater for redds at the Steeple Langford site, where the average extraction rate was $5{\cdot}83\ cm^3\ s^{-1}$ compared with only $2{\cdot}48\ cm^3\ s^{-1}$ at Ugford. With the exception of one redd at Steeple Langford, extraction rates declined

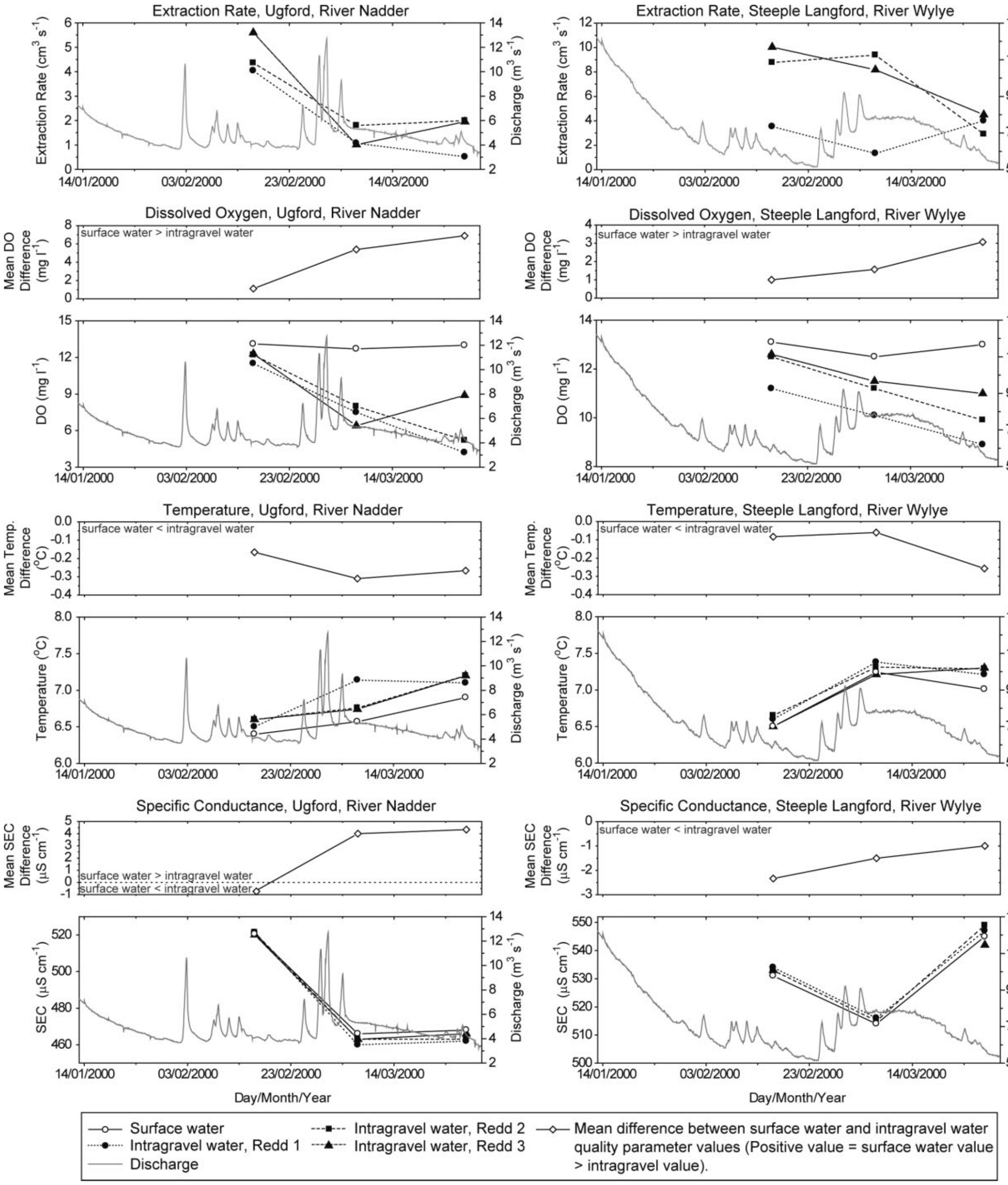

Figure 9. Extraction rates and the DO concentration, temperature and specific conductance of surface water and intragravel water samples collected during field campaign 2. For each water quality parameter, the mean difference between the surface water and intragravel water quality measurements is also presented for each set of measurements

between successive measurements in field campaign 2, indicating a progressive reduction in redd permeability.

Surface water DO concentrations were characterized by limited spatial and temporal variability during field campaign 2, averaging around 12·9 mg l^{-1} at both sites (Figure 9). At both Ugford and Steeple Langford, the DO concentrations in intragravel water decreased (linear regression, $P < 0{\cdot}02$) between the three successive sets of measurements and, as in the case of field campaign 1, DO concentrations in intragravel water remained significantly (t-test, $P < 0{\cdot}02$) higher for the Steeple Langford redds than for the Ugford redds. DO concentrations in intragravel water within artificial redds at Ugford approximated surface water concentrations (11·5–12·3 mg l^{-1}) in newly constructed artificial redds on 14 January 2000, and concentrations were 4·2, 5·2 and 8·9 mg l^{-1} on the 28 March 2000. At Steeple Langford, DO concentrations in intragravel water were generally equal to surface water DO concentrations (11·2–12·6 mgl^{-1}) in newly constructed redds and were 8·8, 9·9 and 11 mg l^{-1} 74 days later on 28 March 2000.

Surface water and intragravel water temperature and SEC measurements tended to demonstrate similar temporal trends (Figure 9). As in the case of field campaign

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1, the difference between SEC measurements for surface water and intragravel water were small, but greater at Ugford than at Steeple Langford. At Ugford, the temperature difference ranged from $-0{\cdot}16$ to $-0{\cdot}31\,^{\circ}$C and the SEC differences from -7 to 4 μS cm^{-1}. The respective values at Steeple Langford were $-0{\cdot}06$ to $-0{\cdot}26\,^{\circ}$C and -1 to $-2{\cdot}3$ μS cm^{-1}.

Embryo survival

The median rate of survival of the eyed embryos planted into 35 artificial redds in January 2000 was 66% (Figure 10). Survival ranged from 0 to 86% and half of the survival values fell between 26 and 74%. Survival was <10% in 20% of cases and was zero in three cases. All embryos that had survived were present as fry, with the yolk sacs absorbed, and in many cases fry had migrated to near the top of the egg basket, most probably indicating a readiness for emergence. Dead embryos were almost always found in the egg stages. There were no significant differences in survival between the Rivers Wylye, Nadder and Avon (Kruskal–Wallis, $P = 0{\cdot}56$). Survival of embryos incubated under hatchery conditions was high (>99%), indicating that survival in the artificial redds was lower than the viable levels under favourable conditions.

The influence of redd sedimentation on the quality of intragravel water and embryo survival

The relationships between DO concentrations in intragravel water, redd permeability and sediment accumulation are presented in Figure 11. The percentage content of fine sediment <1 mm has been used to represent sediment accumulation on the basis that this provided the optimum coefficient of determination values. Owing to the destructive nature of the infiltration basket sampling method and the investigation of temporal patterns of sediment accumulation in field campaign 1, it was necessary to compare the measurements of permeability and the DO content of intragravel water obtained for the three redds within each site with the corresponding values of percentage sediment <1 mm obtained for an adjacent redd. Comparing data between adjacent redds was considered acceptable on the basis that two-way analysis of variance (unbalanced design, Minitab, V13·31) confirmed ($P < 0{\cdot}05$) that the variation in the DO concentrations in intragravel water, extraction rates and redd sedimentation was greatest between the two sampling sites and greater between the successive sets of measurements than between the individual redds within each site. The data on redd sedimentation, permeability and the DO concentrations of intragravel water for field campaign 2, presented in Figure 11, were all collected from the same redd, because the amount of fine sediment in the redd gravels was only determined once, namely at the end of the field campaign immediately following the final measurements of extraction rates and water quality. For the purpose of regression analysis in this study, the data were first tested for normality using the Kolmogorov–Smirnov test. In cases where a normal distribution cannot be assumed ($P \geq 0{\cdot}15$), the data have either been normalized using logarithmic transformations or a non-linear regression has been used.

Figure 11 confirms that both substrate permeability and the DO concentrations in intragravel water were negatively related to the accumulation of fine sediment within the redd gravels. Examination of the different data series shows that differences in the amount of sediment accumulated within the redds were an important factor in accounting for the contrasts in the DO concentrations in intragravel water and in the permeability measurements between the Ugford and Steeple Langford spawning sites. However, sediment accumulation did not explain much of the variability between redds observed within each of the spawning sites for the field campaign 1 data series. It seems likely that at least some of this unexplained residual variability can be attributed to the use of sediment accumulation data from adjacent redds for field campaign 1 data. Importantly, therefore, examination of the data series from field campaign 2 helps to validate the observed relationships.

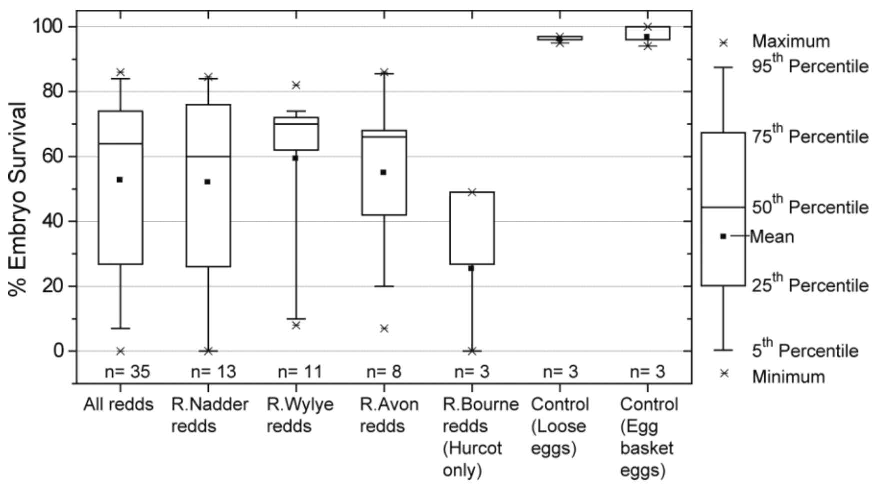

Figure 10. The survival of Atlantic salmon embryos planted into artificial redds in field campaign 2. The survival of embryos kept under hatchery conditions (control) is also shown

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DO concentrations in intragravel water increased with increasing extraction rate in a non-linear fashion (Figure 11). The relationships between the DO concentration in intragravel water and substrate permeability and sediment accumulation are slightly improved by using the difference between the DO concentration of surface water and intragravel water as the dependent variable. This suggests that the DO concentrations in surface water represented an additional influence on DO concentrations in the redd. There is also some indication that the difference between the temperature and SEC of surface water and intragravel water were also weakly related to the permeability of the redd, with absolute differences being greater for less permeable redds (Figure 11). As in the case of DO concentrations, much of the variation occurs between the high-permeability redds at Steeple Langford and the less-permeable redds at the Ugford site.

It is generally recognized that embryo survival is more likely to be related to the overall textural composition of the redd, as opposed to the relative amounts of fine sediment of a defined particle size found within the redd (e.g. Platts *et al.*, 1979; Shirazi and Seim, 1979; Young *et al.*,

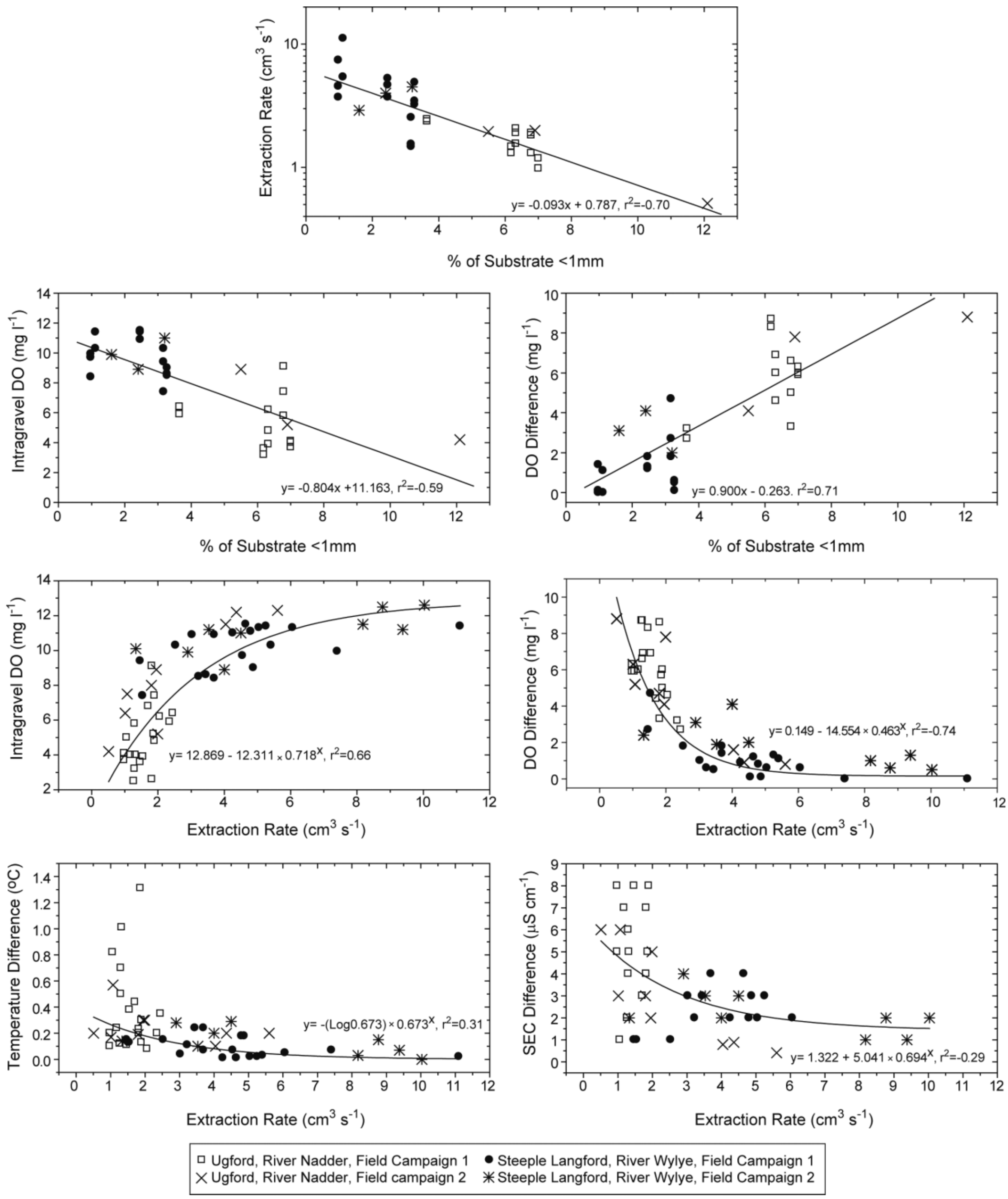

Figure 11. The relationships between intragravel water quality and redd substrate characteristics. The DO, temperature and specific conductance differences refer to the absolute difference between the corresponding values for surface water and intragravel water provided by each set of measurements

1991; Kondolf *et al*., 1993). For this reason, embryo survival has been related to two descriptors of redd textural composition commonly used by fisheries researchers to characterize spawning gravel quality (namely the geometric mean diameter and the Fredle index), in addition to the proportions of fine sediment <1 mm and <2 mm within the redd (Figure 12). The geometric mean particle diameter d_g and the Fredle index FI both provide a more meaningful surrogate measure of substrate porosity and permeability than percentage fines and have been calculated using the method of Lotspeich and Everest (1981):

$$d_g = d_1^{W_1} \times d_2^{W_2} \times \ldots \times d_n^{W_n}$$

$$\mathrm{FI} = d_g/\mathrm{SO}$$

$$\mathrm{SO} = (D_{75}/D_{25})^{0{\cdot}5}$$

where d is the midpoint diameter of particles retained by a given sieve and W is the decimal fraction by weight of particles retained by a given sieve. The percentiles D_{75} and D_{25} refer to the particle diameters below which 75% and 25% of the sample lies. The sorting coefficient SO represents the variance in the grain size distribution, whereby values greater than unity indicate that the voids between grains are filled with smaller grains, which reduces the gravel permeability.

Although embryo survival was significantly ($P < 0{\cdot}001$) related to the percentage fines, d_g and FI, Figure 12 shows that percentage fines <1 mm and <2 mm proved to be a slightly more successful predictor of embryo survival. This is contrary to the findings and perceptions of other investigators (e.g. Lotspeich and Everest, 1981; Young *et al*., 1991). Embryo survival fell below 50% when sediment <2 mm and <1 mm composed more than about 9% and 8% of the redd respectively and reached zero at around 14% sediment <2 mm and 12% sediment <1 mm. Although limited by a lack of data, Figure 12 conforms to expectations, in that embryo survival is positively related to both the DO concentrations in intragravel water and extraction rates. During field campaign 2, those redds at Ugford that were characterized by lower DO concentration of 4·2 mg l^{-1} and 5·2 mg l^{-1}, were also characterized by low embryo survival rates of 0% and 24% respectively. At Steeple Langford, measured DO concentrations remained above 8·9 mg l^{-1} for all three redds, for which survival rates ranged from 10 to 72%.

DISCUSSION

The study reported here aimed to investigate the patterns of redd sedimentation and its role as a control on the supply of DO to incubating salmonid embryos. The results confirm that the survival of salmon embryos in the study rivers can be adversely affected by the excessive accumulation of sediment with the redd gravels and,

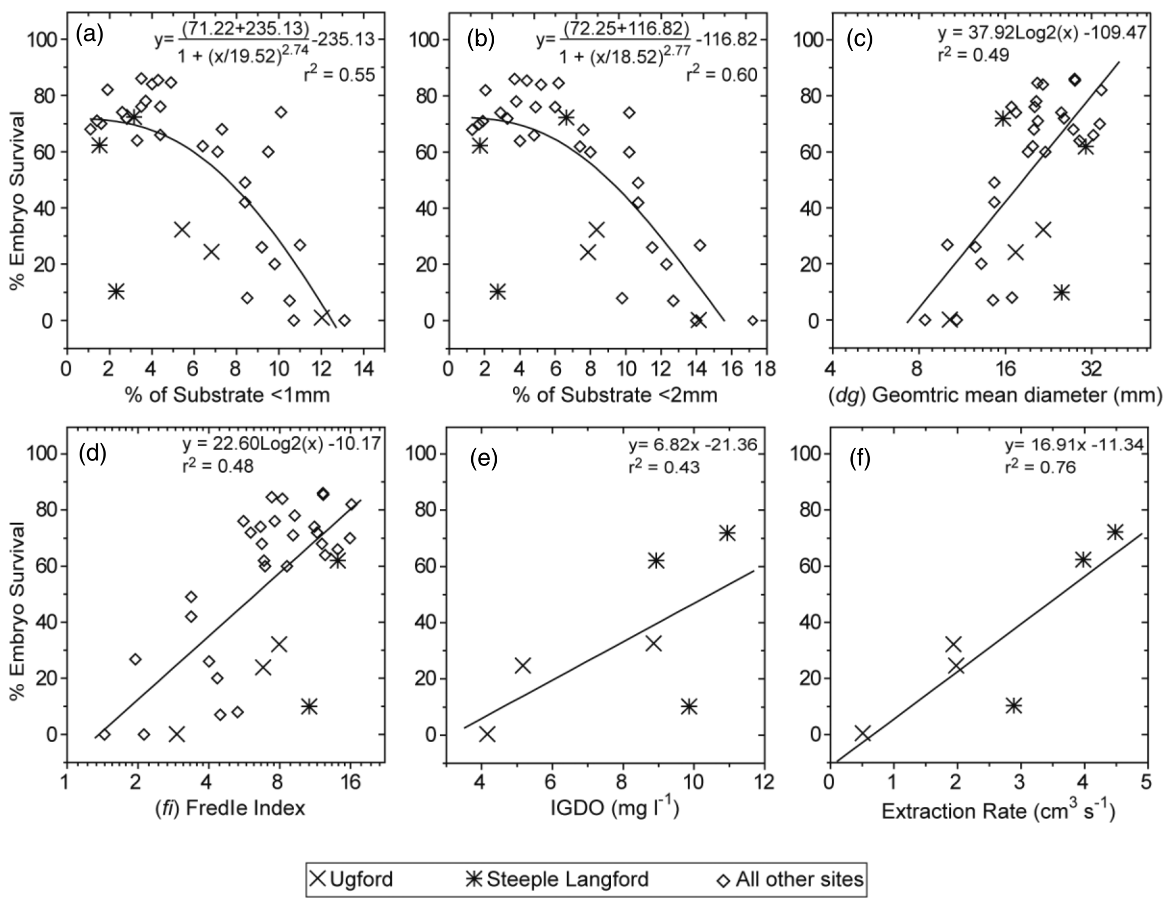

Figure 12. The relationships between embryo survival and redd substrate characteristics and the intragravel DO (IGDO) concentration

therefore, conform to the findings of other investigations (e.g. Turnpenny and Williams, 1980; Scrivener and Brownlee, 1989; Rubin and Glimsäter, 1996), in that the most likely cause of reduced embryo survival was low DO concentrations in intragravel water. Furthermore, as in other investigations (e.g. Tagart, 1984; Chapman, 1988), the relationship between survival and sediment accumulation was highly sensitive, indicating that a small increase in the fine sediment content of the redd could produce a large decrease in embryo survival.

Reduced DO concentrations in intragravel water were seen to reflect the reduction in redd permeability due to the accumulation of sediment within the redd gravel voids. This limited the interchange of surface water and intragravel water through the redd surface, thereby reducing the DO supply to the intragravel environment. The non-linear relationship between the difference between the DO concentration of intragravel water and of surface water and redd permeability indicates that DO concentrations in intragravel water increased with an increase in redd permeability until a threshold is reached, whereby redd permeability no longer limits the exchange of surface and intragravel water. Further evidence of a reduction in the interchange of water through the redd surface is provided by the increasing difference between the temperature and SEC of surface water and intragravel water as redd permeability is reduced. However, the relationships involved were weak, reflecting the importance of other controls on these water quality variables. Water temperatures within the streambed partly depend on heat exchange by conductance and advection via intragravel flow, both of which will be influenced by the streambed textural composition and porosity (Acornley, 1999). Because of this, Acornley (1999) highlights a number of studies which suggest that temperature gradients and lag times between surface and intragravel water can increase due to sedimentation of the streambed.

For the DO concentration of intragravel water to fall, the biochemical oxygen demand within the redd needs to exceed the DO supply rate. Hoffman and Scoppettone (1988) point out that these oxygen demands include the oxidation of dissolved and particulate carbonaceous organic matter by heterotrophic bacteria, in addition to the incubating embryos themselves. In this study, organic material comprised around 15% of sediment infilling the gravels. The precise significance of the sediment oxygen demand associated with this, as well as the oxygen demands exerted by the incubating embryos in field campaign 2, remains uncertain, and further research is required to investigate the influence of organic material quantity and quality on incubation conditions within the redd.

The DO concentrations in redds were greater at Steeple Langford than at Ugford. This can be attributed to the greater amount of fine sediment accumulating in the redds at the Ugford site, which resulted in lower permeability redd gravels. However, the greater permeability of the redds at Steeple Langford may also reflect the coarser particle size composition of the gravel framework (e.g. Cooper, 1965), which implies that the size of intragravel pores within the redd would also be greater. The geometric mean diameter of particles (>2 mm) used initially to fill the infiltration baskets at Steeple Langford was 33 mm (SD = 2·2 mm), as opposed to 27 mm (SD = 1·4 mm) at Ugford. Furthermore, observation of the infiltration baskets upon removal confirmed the tendency for coarser sand-sized particles to accumulate near the surface rather than at depth in some cases. This was more obvious for infiltration baskets removed from redds at Ugford than at Steeple Langford. The formation of a sediment seal within the surface horizon of the channel bed has been previously reported as causing a reduction in the exchange of surface and intragravel water (e.g. Alonso *et al.*, 1996; Packman and MacKay, 2003).

The DO concentration of the surface water supplying the redd gravels also exerted a control on the DO concentration of intragravel water. This influence is most pronounced for more permeable redds, where there is a greater exchange of flow between the water column and the intragravel environment. Furthermore, it seems that increasing surface water DO concentrations over the duration of field campaign 1, partly counteracted the influence of redd sedimentation by preventing an overall reduction in the DO supply rate, despite a reduction in the rate of exchange between the surface and intragravel water. Independent of redd sedimentation, changes in the DO content of intragravel water may occur over the incubation period, as well as between different spawning years, in response to different hydrological conditions. Although the variation in the measured surface water DO concentrations was generally small ($N = 20$; maximum difference: 4 mg l^{-1}; interquartile range: 1·8 mg l^{-1}), the influence of such differences on the DO content of intragravel water may have large implications for embryo development, particularly in those redds where levels of fine sediment already pose a threat. Both Wicket (1958) and McNeil (1962) reported that lower DO concentrations in intragravel water were generally associated with low flow periods, and McNeil (1962) demonstrated that this could produce differences in intragravel water DO concentrations between different years.

Recent research has highlighted that, at some spawning sites, the relative importance of upwelling groundwater and downwelling surface water sources within the hyporheic zone can exert a control on intragravel water quality and, therefore, also on embryo development (cf. Soulsby *et al.*, 2001a). For instance, Soulsby *et al.* (2001a) and Malcolm *et al.* (2003) showed that the upwelling of chemically reduced groundwater into the hyporheic zone of some spawning sites in tributaries of the Rivers Dee and Don in Aberdeenshire, Scotland, represented a cause of low DO concentrations in intragravel water and, as a result, reduced embryo survival (Malcolm *et al.*, 2003). In this study, the magnitude or patterns of differences in temperature and SEC measurements between surface and intragravel water did not provide any obvious indication that groundwater upwelling exerted a

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significant control on the quality of intragravel water at the two sites investigated. However, it must be acknowledged that this is difficult to confirm, given the limited nature of the data and that recent research (e.g. Soulsby *et al.*, 2001a; Malcolm *et al.*, 2003) has demonstrated that water quality differences between stream water and intragravel water in groundwater-affected areas can be subtle, although nevertheless significant. Furthermore, the effects of upwelling groundwater can be localized (Sear *et al.*, 1999; Malcolm *et al.*, 2003), and so the relative importance of groundwater and surface water sources in controlling intragravel water quality within the study rivers remains a key uncertainty.

The pattern of redd sedimentation observed in this study showed that the sedimentation of the newly constructed redds was particularly rapid, and that sedimentation rates gradually decreased over the investigation period. It seems likely that the initially high sedimentation rates observed here principally reflect the efficiency of the newly cleaned redd gravels in trapping fine sediment (e.g. Cooper 1965; Beschta and Jackson, 1979; Carling, 1984) and the high sediment transport rates associated with a number of large storm events within the first 46 days of field campaign 1, since sedimentation rates have also been shown to be supply controlled (e.g. Carling, 1984; Sear, 1993; Larkin and Slaney, 1996; Acornley and Sear, 1999). It is believed that the gradual reduction in sediment accumulation rates observed during field campaign 1 reflects the gradual reduction in the size of the gravel framework pores and pore openings, as sediment progressively accumulated within the redd. For a sediment particle to infiltrate stable openwork gravels, via either the gravel surface pores or interstitial flow (Carling, 1984; Sear, 1993; Alonso *et al.*, 1996), the particle must encounter a sufficiently large pore opening. Therefore, both the amount and the pattern of sediment infiltration will depend, in part, on the particle size composition of the transported sediment and the pore size distribution of the surface and subsurface redd gravels (cf. Frostick *et al.*, 1984; Diplas and Parker, 1985; Lisle, 1989). Jobson and Carey (1989) refer to this filtering effect as 'particle straining'. For instance, some studies have highlighted the formation of an impenetrable sediment seal near the surface of the framework gravels, due to larger particles lodging near the gravel surface and filtering out progressively finer particles, commonly with unfilled pore space below and clogged gravel above (cf. Frostick *et al.*, 1984; Diplas and Parker, 1985; Lisle, 1989; Alonso *et al.*, 1996). In this study, the temporal pattern of sediment accumulation and the tendency for coarse sands to accumulate nearer the top of the infiltration basket, together, suggest the formation of a sediment seal. This evidence is further supported by the more rapid reduction in sedimentation rates at Ugford, where the smaller size of the gravels (and associated pores) and greater amounts of fine sediment in the redd will mean that particle straining is likely to represent a more significant influence than at Steeple Langford.

The amounts of fine sediment recovered from infiltration baskets removed from progressively older redds during field campaign 1, suggest that in some instances there was a slight reduction in the amounts of fine sediment stored in the redd gravels through time, although it is not possible to confirm whether this reflects spatial variation between redds within each site rather than a real temporal trend. Diplas and Parker (1985), indicate that without mobilization of the surface pavement, hydraulic removal of fine sediment will be limited to the surface layer of the bed, whilst mobilization of the pavement may enable flushing of fine sediment from the subsurface gravels. In this study, disturbance of the redd gravels was evident from the gradual degradation of the redd morphology over the 92-day period. It seems possible that, during this process, the loss of the surface gravels will have been associated with some loss of finer sediment from the subsurface gravel framework. Furthermore, disturbance of the redd gravels and flushing of matrix sediment from the gravel framework would be required to generate the increases in redd permeability for those occasions where extraction rate measurements were found to increase between subsequent sampling events.

The sediment infilling the redd gravels was found to comprise primarily fine to coarse sand (0·063–2 mm) rather than silt- and clay-sized particles (<0·063 mm). This conforms to the findings of other studies of UK spawning gravel, which have also found sand to be the dominant size fraction of matrix sediment contained within the gravel framework (e.g. Milan *et al.*, 2000; Soulsby *et al.*, 2001b). Also in common with other UK rivers (e.g. Wass and Leeks, 1999; Walling *et al.*, 2000), the *absolute* particle size distribution of storm-period suspended sediment samples collected for the study rivers was comprised almost entirely (>98%) of silt and clay particles <0·063 mm (unpublished data). This suggests that the majority of sediment accumulating within the redd was derived from the fine-grained bedload, rather than from suspended sediment. The presence of fine bedload particles within redd gravels can be attributed to their greater degree of contact with the channel bed and, therefore, with the better access to the surface pores, relative to suspended sediment (Diplas and Parker; 1985; Lisle, 1989; Alonso *et al.*, 1996). In this study, the particle size composition of sediment accumulating within the artificial redds in field campaign 2 was finer than in field campaign 1, due to a greater abundance of clay- and silt-sized particles, presumably as a result of the increased suspended sediment loads during this period. Despite the dominance of sand-sized material in the matrix sediment, it is pertinent to note that the significance of the cohesive nature and the biological and chemical properties of silt- and clay-sized sediment (cf. Droppo, 2001), in terms of the gravel sedimentation process (cf. Phillips and Walling, 1999), incubation conditions and embryo survival, remains largely unexplored for natural spawning habitats.

There is a general paucity of published information on the grain size composition of natural redds and the

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relationships between embryo survival and redd textural composition for UK salmonid spawning habitats that could be used as a basis for comparisons with this study. Benchmark data regarding acceptable levels of fine sediment in UK spawning habitats tend to refer to undisturbed spawning gravels (e.g. Milan *et al*., 2000), whereas it is generally accepted that redd gravels will contain lower levels of fine sediment than undisturbed gravels, due to the winnowing of fines during redd construction (Grost *et al*., 1991; Barnard, 1992; Kondolf *et al*., 1993). Further difficulties in comparing studies arise because of differences in the methods used for substrate sampling (e.g. freeze coring, bulk coring, infiltration baskets) and sample processing (gravimetric or volumetric processing methods) and differences in the variables reported for defining spawning gravel quality. However, the percentage levels of fine sediment <1 mm in the artificial redds observed in this study are closely comparable to those found by Crisp and Carling (1989) for natural redds in a range of UK rivers. In particular, Crisp and Carling (1989) reported that sediment <1 mm comprised between 2·3 and 12·4% of the surface redd gravels in the River Piddle, a chalk stream akin to those investigated in this study. The proportions of fine sediment <1 mm reported in this study are also similar to those reported for natural redds in many other studies, primarily relating to North American salmonid rivers (e.g. McNeil and Anhell, 1964; Grost *et al*., 1991; Kondolf *et al*., 1993; McHenry *et al*., 1994; Thurow and King, 1994; Kondolf, 2000).

There is a lack of consistency among reported relationships between embryo survival and redd substrate composition from different studies. The reasons for this variability include the inherent differences between field- and laboratory-based studies (Cederholm *et al*., 1981), as well as variations in spawning habitat, water quality, salmonid species, egg burial depth and egg physiology and viability across different river systems and stocks in different years (Tappel and Bjornn, 1983; Irving and Bjornn, 1984; Chapman, 1988; Young *et al*., 1990; Rubin and Glimsäter, 1996). These differences mean that it is inappropriate to seek a universally applicable threshold level of fine sediment in redd gravel (Kondolf, 2000). This uncertainty is also compounded by research showing that the various measures of overall redd textural composition (e.g. d_g, FI, SO) are commonly more suitable for assessing incubation conditions than the relative proportion of fine sediment within the redd (e.g. Platts *et al*., 1979; Shirazi and Seim, 1979; Lotspeich and Everest, 1981; Chapman, 1988; Young *et al*., 1991; Waters, 1995). As a result, some studies recommend that a range of substrate descriptors should be presented (e.g Chapman, 1988; Crisp and Carling, 1989; Kondolf, 2000). The regression model shown in Figure 12 suggests that embryo survival fell below 50% when sediment <1 mm composed around 8% of the redd substrate. Although lower than the 'critical' levels of around 12–14% reported by Kondolf (2000), McHenry *et al*. (1994) and McNeil and Anhell (1964), this value is not alarming given the above discussion and considering the large residual variance in the relationship (Figure 12). Although this unexplained variance could be attributed, at least partly, to the influence of other controls on embryo survival, it is also possible that the scatter may reflect the fact that the amount of sediment recovered from the infiltration baskets may not be fully representative of that immediately around the planted egg baskets. This is emphasized by research reported by Meyer (2003), which demonstrated that embryo survival tends to be more strongly related to the level of sediment within the egg pocket itself, as opposed to the redd in general.

The disturbance of natural redds in UK spawning habitats for research purposes is contentious, due to the commonly low numbers of spawning salmonids in many rivers. As a result, artificial redds are useful for investigating the process of redd sedimentation and the controls on embryo survival and indicating likely survival rates. This is particularly so given the ability to install and manipulate eggs and equipment in the artificial redd. However, the degree to which artificial redds are able to simulate natural conditions is uncertain. Meyer (2003) compared artificial redds with natural redds in a stream in north-western California and concluded that it was not possible to confirm or refute the representativeness of the former. In addition, although the research presented here clearly demonstrates the significance of redd sedimentation in influencing the DO content of intragravel water supply and embryo survival in the redd, this investigation did not address the potential problems of sediment entrapping fry within the redd gravels. The dominance of sand-sized matrix particles within the artificial redds highlights the need for research specifically addressing this issue (Hall and Lantz, 1969; Philips *et al*., 1975; Hausle and Coble, 1976).

PERSPECTIVE

This study sheds further light on the process of redd sedimentation and, importantly, confirms the supposition that the sedimentation of redd gravels can represent a critical factor influencing the survival of incubating embryos in UK spawning habitat. Overall, the findings support the need for sustained development of initiatives aimed at optimizing salmonid reproduction, including the identification of sediment sources and reduction of sediment mobilization and delivery from these sources, and the restoration of impacted spawning habitats. However, the effective design and implementation of such sediment control and management strategies requires continued research to provide an improved understanding of incubation and emergence conditions for salmonid embryos in these rivers. Further research needs specifically to address intragravel DO demands within the redd, the emergence success of fry potentially entrapped within redd gravels as a result of the accumulation of sands, and the influence of groundwater upwelling on water quality within redd gravels in these groundwater-dominated chalk stream systems.

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