Available online at www.sciencedirect.com
SCIENCE @ DIRECT®
Science of the Total Environment 344 (2005) 241–258
Science of the Total Environment
An International Journal for Scientific Research into the Environment and its Relationship with Humankind
www.elsevier.com/locate/scitotenv

The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management

S.M. Greig[a], D.A. Sear[b,*], P.A. Carling[b]

[a]Scottish Environment Protection Agency, Edinburgh, Scotland, UK
[b]School of Geography, University of Southampton, Highfield, Southampton, SO17 1BJ, UK

Abstract

This paper draws on results from a recent research programme on the impact of fine sediment transport through catchments to present a case for the development of new approaches to improving the quality of salmonid spawning and incubation habitats. To aid the development of these programmes, this paper summarises the mechanisms by which fine sediment accumulation influences the availability of oxygen (O_2) to incubating salmon embryos. The results of the investigation indicate that incubation success is inhibited by: (i) the impact of fine sediment accumulation on gravel permeability and, subsequently, the rate of passage of oxygenated water through the incubation environment; (ii) reduced intragravel O_2 concentrations that occur when O_2 consuming material infiltrates spawning and incubation gravels; and (iii) the impact of fine particles (clay) on the exchange of O_2 across the egg membrane. It is concluded that current granular measures of spawning and incubation habitat quality do not satisfactorily describe the complexity of factors influencing incubation success. Furthermore, an assessment of the trends in fine sediment infiltration indicates that only a small proportion of the total suspended sediment load infiltrates spawning and incubation gravels. This casts doubt over the ability of current catchment-based land use management strategies to adequately reduce fine sediment inputs.

Keywords: Fine sediment spawning gravels; Oxygen supply; Land use management

1. Introduction

Population estimates indicate that wild salmon stocks are in decline (Huntington et al., 1996; Shea and Mangel, 2001; WWF, 2001). Within the UK, 7 of the 76 rivers in England and Wales believed to have supported Atlantic salmon (*Salmo salar*) no longer have populations, 10 are classified as critical and 19 as endangered (WWF, 2001). In Scotland and Ireland, a number of salmon runs are also in recession (WWF, 2001; Youngson et al., 2002). Poor marine recruitment is frequently cited as the dominant factor limiting survival; however, low productivity during freshwater life stages has also been linked to declining populations. In the freshwater environment, a number of factors have been linked to poor productivity, includ-

---

* Corresponding author. Tel.: +44 23 80592215.
E-mail address: d.sear@soton.ac.uk (D.A. Sear).

0048-9697/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.scitotenv.2005.02.010

ing barriers to migration, loss of habitat and degradation of the incubation environment (Bjorn and Reiser, 1991).

Under natural processes, small quantities of silt and clay are delivered to the river system. Aquatic communities are typically adapted to these conditions and are able to cope. Anthropogenic activities and in particular land management actions have been shown to increase the supply and delivery of fine sediment (sand, silt and clay) from the catchment surface to the river network (Theurer et al., 1998; Walling and Amos, 1999), though the influence of bank erosion sources may be locally as well as regionally significant (Walling et al., 2001; Walling, this volume). Causes of fine sediment runoff from catchment surfaces are associated with changes in agricultural practice towards larger areas of arable cultivation. Also critical for salmonid survival have been changes in the timing of arable cultivation, which in Europe has moved from spring to autumn sown cereals, a time that coincides with the incubation of salmon eggs within the river gravel. In addition to the growth in arable cultivation, there has been an increase in stock density and mechanised farm practices that compact the soil under pasture, resulting in increased runoff and soil erosion (McMellin et al., 2002). Similarly, runoff from land under livestock farming can be associated with delivery of organic waste to the river network (Theurer et al., 1998). The delivery of fine sediment from agricultural sources is also associated with enhanced levels of sediment-bound nutrients (including phosphorus, Haygarth et al., this volume), pesticides and herbicides whose impact on salmon incubation remains largely unknown. The increasing recognition of catchment and in particular agricultural land use as a primary source of fine sediment delivery to the river network has initiated a move towards managing land use practice to reduce delivery of fines (Heaney et al., 2001; McMellin et al., 2002).

Salmon and other fish species lay their eggs in gravel nests called redds. The process of redd-cutting creates pockets of eggs overlain by loose gravels from which the fine sediments have either been removed by entrainment during the cutting process, or redeposited at the base of the redd by a process of kinematic sieving. Successful incubation requires that the ambient oxygen (O_2) concentration within the redd is sufficient to support the O_2 gradient required to drive diffuse O_2 exchange across the egg membrane at different water temperatures and stages of embryonic development (Silver et al., 1963; Daykin, 1965; Wickett, 1975; Turnpenny and Williams, 1980; Chevalier and Carson, 1984). The concentration gradient required to support diffuse O_2 exchange is maintained by the bulk movement of O_2 through the riverbed. Fine sediment intrusion into the incubation zone will the passage of oxygenated water by blocking interstitial pore spaces and reducing interstitial flow velocities within the incubation zone (Chapman, 1988; Alonso et al., 1996; Bjorn and Resier, 1991; Acornley and Sear, 1999; Theurer et al., 1998) and, if O_2 consuming materials are introduced into the riverbed, by lowering O_2 concentrations (Whitman and Clark, 1982; Chevalier and Carson, 1984; Štěrba et al., 1992). These two processes are not discrete, and lowered interstitial flow velocities may exacerbate the impact of O_2 demands on O_2 concentration. It should also be noted that lowered interstitial flow velocities may also reduce natural flushing of harmful metabolic waste products that are excreted by embryos, potentially contributing to mortalities (Burkhalter and Kaya, 1975).

In European water management, the Habitat Directive and Water Framework Directive endorse a move towards the management of watercourses to support biological communities (European Community, 2000). Within this legislation, Atlantic salmon is identified as a species that requires specific management attention. In response, UK government organisations, supported by European funding, have developed broad definitions of physical habitat requirements at different life stages, including incubation. These highlight the importance of low levels of fine sediments within spawning and incubation gravels, and the need to develop measures to prevent excess accumulations of fine sediments. The success of these programmes will be determined by their ability to alleviate the interacting sedimentary-related pressures that contribute to poor incubation survival. Central to the success of these schemes is the availability of information regarding the processes and factors controlling the quality of the incubation environment and the specific mechanisms whereby fine sediments (often derived from the land surface) impact on the survival of incubating salmon progeny.

Previous approaches to investigating the influence of fine sediment accumulation on incubation success have typically focused on defining relationships between survival to emergence and measures of the granular character of the incubation environment (e.g. Peterson and Metcalfe, 1981; Cederholm et al., 1981; McCrimmon and Gots, 1986; Chapman, 1988; Tappel and Bjornn, 1983; Young et al., 1991; Reiser, 1998). However, by focusing on empirical relationships between sediment composition and embryonic survival, these approaches do not provide information on the specific mechanisms affecting O_2 availability, or how these mechanisms may vary within or between systems.

To assist with the development of management strategies that target the specific sediment-related causes of poor incubation success, this paper identifies three specific mechanisms by which fine sediment accumulation restricts O_2 availability and assesses how these factors interact in different UK river systems to influence embryonic survival. The factors investigated are: (i) the impact of fine sediment accumulation on the rate of passage of oxygenated water through the incubation environment; (ii) the intragravel O_2 demands intragravel O_2 concentrations; and (iii) the impact of fine particles (clay) on the exchange of O_2 across the egg membrane (Fig. 1). To supplement these investigations, the links between fine sediment supply and accumulation within spawning gravels over the incubation period are discussed. Finally, an overview of the implications of the research findings for the effective management of UK salmon rivers is presented. It should be noted that the paper focuses on O_2 deficiency-related mortalities and does not describe the impact of fine sediment accumulation on the emergence of fry from the incubation zone.

2. Field sites and methods

A complimentary set of field and laboratory experiments were undertaken to investigate the relationships between fine sediment and embryonic survival. Five specific research objectives were identified:

(1) Acquisition of a dataset describing subsurface O_2 fluxes, granular properties of incubation environment and embryonic survival.
(2) Establish the existence of a direct correlation between fine sediment accumulation within salmon redds and the velocity of the interstitial water.
(3) Quantification of the magnitude of the O_2 demand imposed by materials infiltrating the incubation gravels.

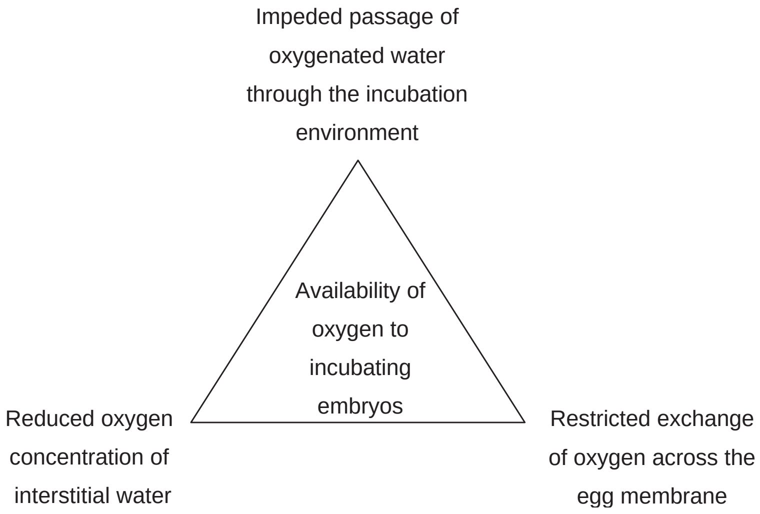

Fig. 1. Summary of factors influencing the availability of oxygen to incubating embryos.

(4) Assessment of the impact of clay particles on the exchange of O_2 across the egg membrane.
(5) Determination of the relationship between sediment supply and the rate of accumulation of fines within the redd environment.

Objectives (1)–(4) were undertaken in the field, while objective (5) was explored under controlled laboratory conditions.

In total, four field sites were monitored over two field seasons (spawning and incubation periods). The field sites selected and study years were: the River Test, Hampshire (groundwater-dominated) (2001–2002), River Blackwater, Hampshire (lowland freshet) (2002–2003), River Ithon, Powys, Wales (upland freshet) (2001–2002), River Aran, Powys, Wales (upland freshet) (2002–2003) (Fig. 2, Table 1). The field sites were selected to represent (i) the two dominant salmonid UK river types (freshet and groundwater-dominated), (ii) a range of potential levels of habitat quality and (iii) a variety of distinct physical features that would potentially influence O_2 availability and incubation success (Table 1).

The field-monitoring programme centred on the use of artificial redds to study the characteristics of the incubation environment and factors effecting incubation success. At each field site, several artificial redds were created and monitored for a variety of environmental parameters (Fig. 3a and b), including sediment accumulation, intragravel O_2 concentrations and temperatures, interstitial flow velocities and embryonic survival. In view of the number of parameters

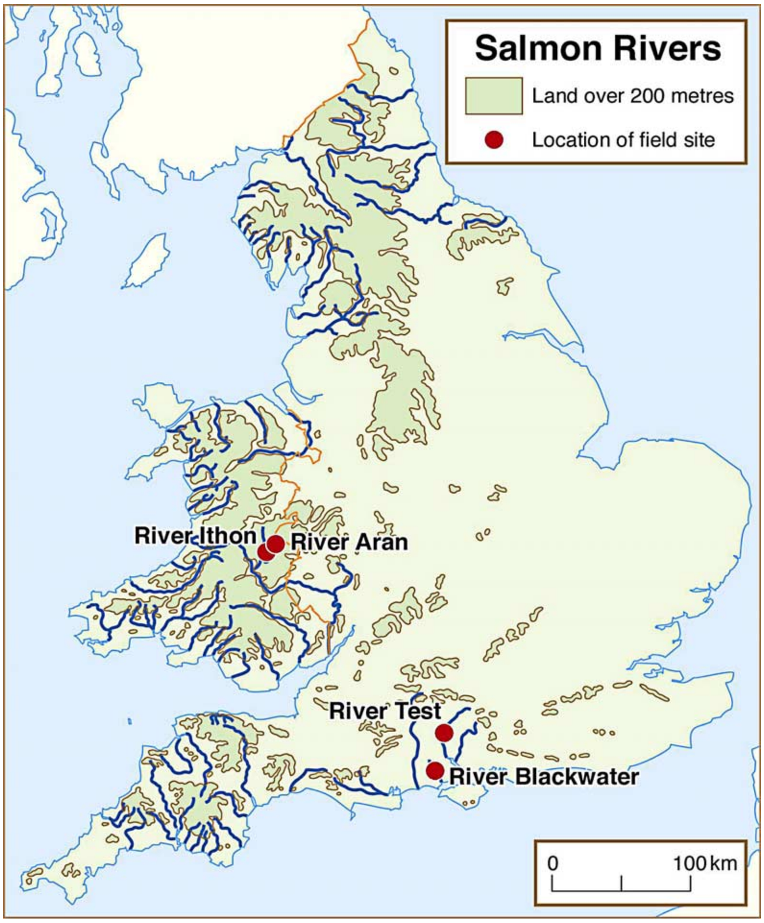

Fig. 2. Location of the four field sites and source of eggs used in this study.

Table 1
Summary of conditions represented at each field site

	Level of habitat modification High ← Low			
	Test	Ithon	Aran	Blackwater
Excess fine sediment	✓	✓	✓	
Excess organic detritus	✓			
Excessive nutrients		✓	✓	
Controlled hydrological regime	✓			
Flashy hydrological regime		✓	✓	✓
Significant groundwater inputs	✓			

under consideration, it was deemed inappropriate to attempt to study all parameters in each individual redd. The principal concern relating to excessive disturbance to the incubation environment, however, space requirements were also a concern. In response to this concern, three types of redds were constructed to address different monitoring objectives. Each redd contained sampling equipment related to the monitoring objectives associate with that redd (Fig. 3b). Redds were grouped such that one of each monitoring objective were present at each riffle (in practice within 3–5 m of each other per riffle).

A two-stage particle size analysis was performed on all sediment samples (details of specific sediment are sampling given in results section). For particles greater than 710 μm, dried samples were sorted on a mechanical shaker at 1/2 phi intervals and the samples retained on each sieve were weighed. For particles below 710 μm, subsamples of between 3 and 8 g were taken for Coulter analysis (Coulter Counter™ LS

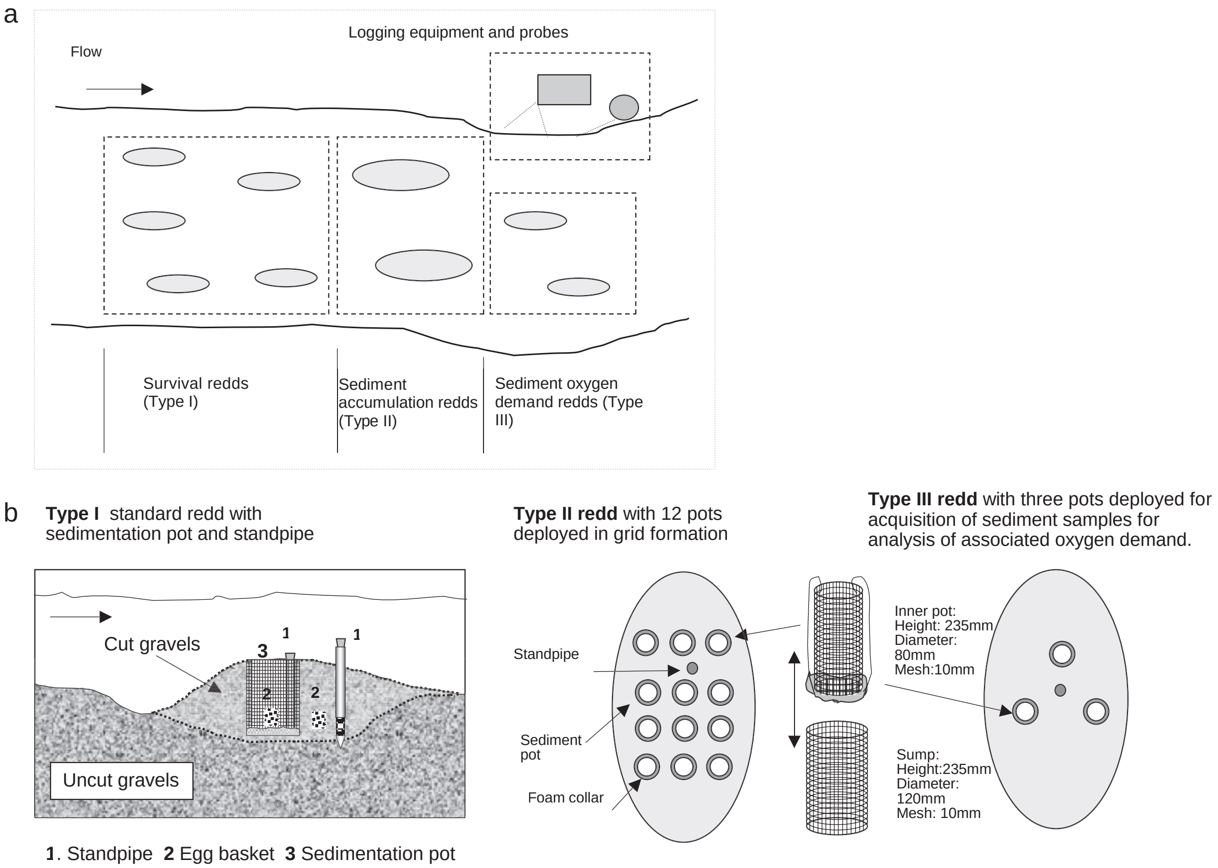

Fig. 3. (a) Schematic of monitoring set-up deployed at each field site. (b) Schematic of the different artificial redd experiments deployed at each field site.

100). Samples of fine sediment were also retained for laboratory analysis of associated O_2 demands (Greig et al., in press). Long term (25-day) O_2 demands of sedimentary material were carried out using a Biochemical Oxygen Demand Oxitop control system in association with an Oxitop OC 110 controller (WTW instruments). Nitrogen (N) demands of samples taken from the River Test and River Ithon were assessed following the same procedure, but with the addition of a N inhibitor. All incubations were carried out at 20 °C. Ignition analyses (450 °C) of sediment subsamples were performed to determine the organic content of sediments at each field site.

Egg survival was determined using eyed North Tyne salmon eggs from the Kielder Hatchery. The eggs were placed in each sedimentation pot and in adjacent cut gravels using a new technique that permits insertion of cylindrical Harris-type boxes directly into the spawning gravels or artificial redds (Greig, 2004). An important element of this technique is the ability to place the Harris-type boxes at the start of the incubation period, remove them for egg insertion at eyed stage and redeploy them within the same location without disturbance to the surrounding gravel. A control batch of eggs was retained at a hatchery close to each field site, which utilised water of similar quality and thermal characteristics.

Information on river discharge, suspended sediment concentration and bedload were logged at each study site at a resolution of 10 min throughout the incubation period. Discharge was either recorded at a nearby Environment Agency gauging station, or via a rating relationship developed for the site. Suspended sediment load was determined from a Partech IR400 turbidity probe (NTU) located 0.05 m above the stream bed and locally calibrated against daily pump samples of suspended sediment concentration (Hicks and Gomez, 2003). Bedload was recorded at each site using a calibrated load-cell pit trap (Sear et al., 2000). Dissolved O_2 and interstitial flow velocity were determined at weekly (Ithon and Test) and once every 2-week (Aran and Blackwater) intervals during low discharges via access through permanent standpipes (see Carling and Boole, 1986) located in all sedimentation baskets and (as a control) in adjacent cut gravels. Dissolved O_2 and water temperature within the standpipes was measured using a YSI 250™ O_2 probe. Interstitial flow was measured using a conductiometric technique (Greig et al., in submission b).

The laboratory experiment was undertaken to provide information pertaining to factors influencing O_2 availability that could not be assessed in the field. This involved investigation of embryonic O_2 consumption and the impact of clay particles on the exchange of O_2 across the egg chorion. Salmon egg respiration rates were measured within an incubation chamber composed of a Digital Model 10 Respirometer in conjunction with a 50 ml Perspex electrode cell (Rank Brothers). Dissolved O_2 concentrations were continuously recorded using a dual channel Model BD112 chart recorder. A magnetic stirrer ensured complete mixing within the incubation chamber and reduced the potential for zones of O_2 depletion to develop around respiring eggs. Temperature control was maintained via a Grant LTC6-40 cooled thermocirculator. All tests were carried out on hatchery reared Atlantic salmon eggs. Borehole water at 100% dissolved O_2 saturation was used as the incubation medium. Consumption rates were determined for eggs in the final stages of embryonic development, thereby providing an estimate of maximum O_2 requirements (Greig et al., in press).

3. Results

3.1. Physical conditions during the field season

The field seasons were characterised by above-average flows at the River Ithon, and below average flows at the River Aran and River Blackwater (Fig. 4). The River Test's flow regime is moderated by the influence of groundwater inputs, and therefore displays less variation between years (Acornley and Sear, 1999). Based on an analysis of thermal profiles, hydraulic head and subsurface conductivity, the local influence of groundwater was not detected at any of monitoring locations within each field site. Thus, the influence of a variable groundwater table on subsurface O_2 concentrations was not considered a significant control over egg survival (Soulsby and Malcolm, 2001; Malcolm et al., 2003).

Sediment transport was highly variable within and between the field sites (Fig. 4). The River Ithon

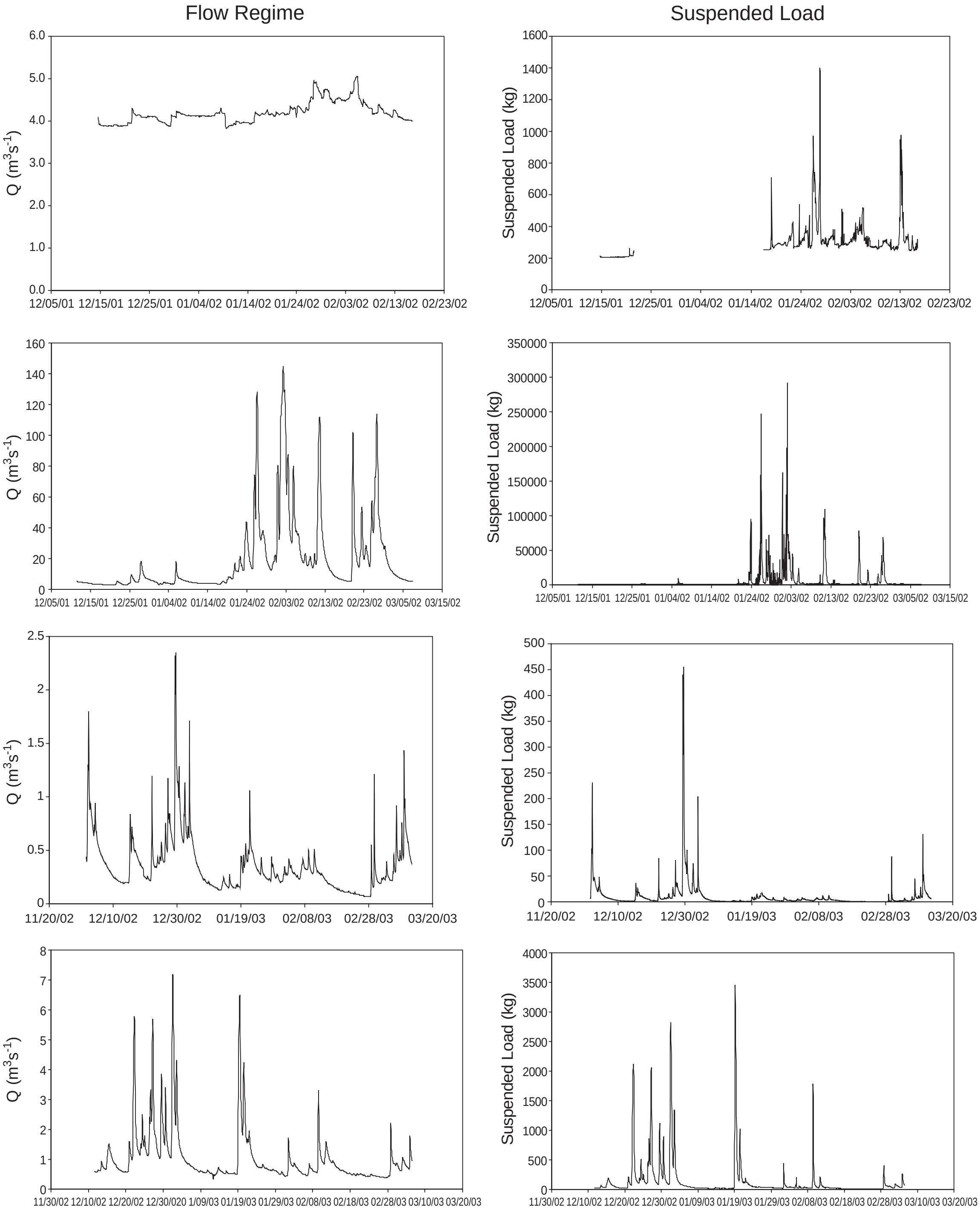

Fig. 4. Flow (*Q*) and suspended sediment transport conditions recorded over the incubation period at the four field sites.

exhibited the largest sediment loads, with both bedload and suspended load associated with above average discharge. The River Blackwater site was characterised by relatively frequent bedload transport and a low suspended load. The flow conditions at the Aran and Test produced minimal bed load transport and bed disturbance and, therefore, relatively low suspended sediment loads (Table 2).

Sediment accumulation rates over the study periods were variable between and within sites. Final levels of fine sediment accumulation are shown as a percentage value for grainsizes less than 2 mm diameter (Table 3). A 2 mm grainsize was chosen as the upper limit to the size-range of sediments usually infiltrating the gravel bed (Reiser, 1998). Comparison with other sedimentation studies reveal similar levels to those reported in this study (Frostick et al., 1984; Carling and McCahon, 1987; Sear, 1993; Walling and Amos, 1999; Acornley and Sear, 1999; Soulsby and Malcolm, 2001), suggesting that the conditions monitored are broadly consistent with those found in other streams. Overall, the River Ithon recorded the highest total accumulation of fine sediments (<2 mm) within the sedimentation pots followed by the River Aran, River Blackwater and River Test. The organic component of the accumulated fine sediment was also variable between the field sites, with the River Test (in common with other chalk streams) recording the highest percentage organic matter content (19.7%) followed by the Aran (7.5%), Ithon (5.3%) and Blackwater (3.4%).

3.2. Egg survival and oxygen supply

Egg survival varied between sampling locations at each field site (Table 4). Minimum survival was zero at all sites. Maximum survival at the River Test, Blackwater, Ithon and Aran was 35%, 100%, 97% and 91%, respectively. Mean survival was 22% at the River Ithon, 8.7% at the River Test, 71% at the River Blackwater and 28% at the River Aran.

Table 2
Sediment loads recorded over the incubation period based on hourly data

River	Suspended load (tonnes)	Bed material load (tonnes)	% Bed material load
Blackwater	273	3.7	1.34
Aran	24	0.4	1.64
Ithon	9995	91	0.91
Test	350	0.0	0.00

Table 3
Comparative values for the percentage <2 mm diameter particles recorded at the end of the field experiments and for other similar accumulation studies

Study	% Fine sediment <2 mm accumulated within gravels	Source
Newmills Burn	23.1	Soulsby and Malcolm (2001)
North Tyne	11.0	Sear (1993)
Gt Eggleshope Beck	10.0	Carling and McCahon (1987)
Turkey Brook	31.0	Frostick et al. (1984)
*River Test (Bossington)	24.5	Acornley and Sear (1999)
*Wallop Brook	17.0	Acornley and Sear (1999)
*River Piddle	22.6	Walling and Amos (1999)
*River Test (Horsebridge)	10.0	This study
River Blackwater	12.2	This study
River Ithon	28.9	This study
River Aran	15.7	This study

Based on the stage of embryonic development and the condition of the expired eggs, the probable timing of mortality at each site was assessed. Dead eggs in the River Test were either in the latter stages of development, or in the process of hatching, suggesting that mortalities had occurred directly prior to or during hatching. At the River Blackwater, the few observed mortalities were deemed to have occurred a number of days prior to egg removal. At the River Ithon and Aran, spatial variability in the timing of expiry was recorded: ranging from during hatching up to a number of weeks prior to the estimated hatching date.

An assessment of the ability of measures of O_2 availability to delineate survival to hatching was performed. This analysis was divided into two stages. First, the data from each field site were collated and a Pearson correlation analysis was performed to determine the strength of the relationship between measures of O_2 availability and survival. Second, to identify inter-site difference in the performance of measures of O_2 availability to describe embryonic survival, a site-specific analysis was performed.

Table 4
Rates of survival recorded within artificial redds

Location	Total percent survival		Location	Total percent survival	
	Test	Ithon		Blackwater	Aran
Redd 1 (front)	0	2	Redd 1 (right)	68	0
Redd 1 (rear)	9	18	Redd 1 (left)	100	21
Redd 2 (front)	2	–	Redd 2 (right)	0	12
Redd 2 (rear)	23	4	Redd 2 (left)	92	45
Redd 3 (front)	37	93	Redd 3 (right)	31	24
Redd 3 (rear)	4	15	Redd 3 (left)	96	0
Redd 4 (front)	6	0	Redd 4 (right)	79	4
Redd 4 (rear)	0	0	Redd 4 (left)	0	0
Redd 5 (front)	0	19	Redd 5 (right)	68	91
Redd 5 (rear)	–	–	Redd 5 (left)	88	14
Redd 6 (front)	6	48			
Redd 6 (rear)	–	–			

Data omissions result from problems encountered during sampling.

The results of a Pearson correlation analysis on the information collated for all field sites indicated that O_2 concentration, interstitial flow velocity and O_2 flux performed similarly as measures of incubation success, with correlation coefficients ranging from 0.64 (interstitial flow velocity) to 0.74 (O_2 concentration). However, the site specific analysis (Table 5) suggested inter-site variations in the strength of the correlations between embryonic survival and measures of O_2 availability. The results of the analysis indicated that O_2 supply was the best determinant of survival (significant at the 5% confidence limit) at the River Test, Ithon and Aran field sites. This was followed by interstitial flow velocity, which was also statistically significant at these field sites. Oxygen concentration at these field sites was the poorest predictor of survival. Conversely, at the River Blackwater, O_2 flux and interstitial flow velocity were poorer determinants of survival than O_2 concentration, which was statistically significant at the 5% confidence limit. This poor correlation was affected by two factors, first the lack of variability between most redds and second the presence of an outlier value associated with one redd that recorded zero survival.

3.3. Correlations between granular properties of the incubation environment and embryonic survival

Previous studies have proposed a variety of grainsize-based measures of incubation success (e.g. Chapman, 1988). The sedimentary data gathered in each field site were used to test the performance of previously proposed grainsize-based measures of incubation success. Generally, grainsize-based measures of survival were poor descriptors of incubation success (Table 6). Furthermore, in many instances, the direction of the correlations opposes those reported in other studies (McNeil and Ahnell, 1964; Lotspeich and Everset, 2001; Chapman, 1988; Young et al., 1991).

Table 5
Pearson correlation coefficients between egg survival and measures of oxygen availability

Variable	River Test	River Blackwater	River Ithon	River Aran	All sites
Final oxygen concentration	0.53	0.82[a]	0.3	0.55	0.75
Minimum oxygen concentration	0.37	0.49	0.61	0.57	0.51
Final intragravel flow velocity	0.84[a]	0.5	0.84[a]	0.85[a]	0.63
Final oxygen flux	0.80[a]	0.56	0.89[a]	0.82	0.68

[a] Significant at the 5% confidence limit.

3.4. Impact of fine sediment on interstitial flow velocity

At the Rivers Aran and Blackwater, trends in sediment accumulation were shown to be closely related to flow over the monitoring period, with greater deposition occurring during higher flow events (Fig. 5). Additionally, a strong relationship between interstitial flow velocities and sediment accumulation is apparent (Fig. 5). A Pearson correlation analysis of sediment accumulation and interstitial flow velocity was undertaken to investigate the strength of the relationship between these parameters. Four measures

Table 6
Pearson correlation coefficients for the relationships between egg survival and commonly applied measures of grainsize characteristics

	D_{50}	Dg	Fi	%, <4 mm	%, <1 mm	%, <0.067 mm
Sediment pots	−0.18	−0.17	−0.12	0.11	0.14	−0.09
Freeze cores	0.13	−0.07	−0.02	−0.31	−0.08	0.5

D_{50}=50th percentile grainsize diameter (mm), Dg=geometric mean grainsize $[(D84)(D16^{0.5})]$, Fi=Fedle Index (Dg/So—where So=$\sqrt{(D75/D25)}$.

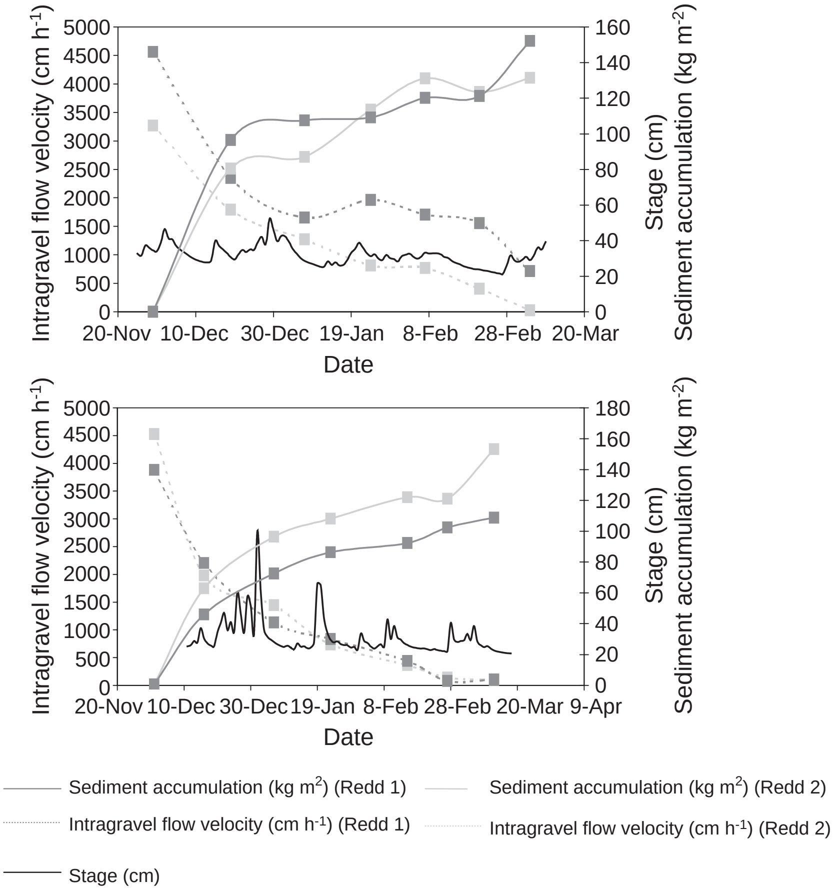

Fig. 5. Relationship between flow, fine sediment (<2 mm) accumulation and interstitial flow velocity at (a) River Blackwater and (b) River Aran.

describing gravel composition were analysed: % fine sediment <4 mm, % fine sediment <1 mm, geometric mean and D_{50}. With the exception of median particle diameter (D_{50}), granular descriptors were significantly correlated with interstitial flow velocity (99% confidence limit) at all sampling locations. However, spatial variations in sedimentary composition and hydraulic gradient dictated that the relationships were site specific (Freeze and Cherry, 1979; Chevalier and Carson, 1984).

In addition to the influence of inorganic sediments on interstitial flow velocities, the probable impact of organic sediments was also identified. As with inorganic sediment, organic material will block interstitial pore spaces and reduce gravel permeability. However, organic material also promotes the growth of biofilms, which may exacerbate this effect (Chen and Li, 1999). A sharp decline in interstitial flow velocities was recorded at the River Test. However, inspection of the sedimentary recorded indicated that low levels of fine sediment were recorded within the redd gravels at this site (Table 5).

3.5. Impact of infiltrated materials on oxygen concentrations within the incubation environment

The sedimentary O_2 demand data recovered at each field site is shown in Fig. 6. Oxygen demand values are reported in mg of O_2 per gram of organic material (dry weight) (mg O_2 g^{-1}). It should be noted that this value relates to the total O_2 demand induced by organic material and does not delineate between carbon (BOD)- and nitrogen (NOD)-based demands. Furthermore, the contribution of inorganic

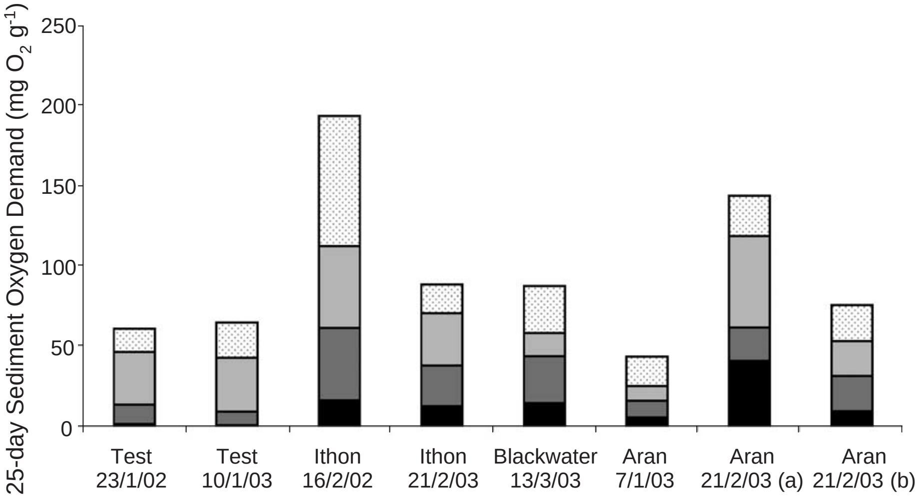

Fig. 6. Stacked column chart outlining temporal trends in oxygen demand for infiltrated fine sediments (<710 μm) recovered from the four field sites.

or dissolved substances to the overall O_2 demand has not been defined. The O_2 demand values display spatial (intra- and inter-site) and temporal variability. In broad terms, the River Test recorded the lowest demand. Furthermore, the demand recorded in successive years remained constant. Infiltrated material at the River Ithon recorded the highest O_2 demand. However, this system also recorded the highest temporal variability, with O_2 demand values obtained over the 2001–2002 monitoring season being less than half those recorded in the previous monitoring period. In addition to assessing total O_2 demands, an assessment of the relative contribution of carbon-based and N-based demands was undertaken. The results of this analysis indicated that carbon-based O_2 demands were dominant in the River Test, whereas at the River Aran N demands composed a significant proportion (50%) of the total O_2 demand. Potential sources of N compounds in this system include organic and inorganic fertilisers, animal faeces and agricultural waste (e.g. silage liquor/barn washings, etc.).

3.6. Impact of clay particles on oxygen consumption

In the laboratory experiment, the introduction of clay particles and the subsequent development of a thin film of sediment across the egg surface reduced rates of embryonic O_2 consumption (Fig. 7). The clay ranged between 5 and 11 phi with a modal value of 9 phi. The clay was heated at 450 °C for 2 h to burn off any volatiles. Tests were conducted with Borehole water at 100% saturation and with the addition of 0.1 to 0.5 g clay. These resulted in no detectable change in O_2 consumption and the clay was therefore considered to be inert with respect to O_2 consumption. The tests were repeated with 10 Atlantic salmon eggs. A 0.3 g sample of clay (equivalent concentration 6000 mg l^{-1}) was introduced to the water. Egg O_2 consumption was reduced to between 0.00129 mg O_2 egg^{-1} h^{-1} and 0.00139 mg O_2 egg^{-1} h^{-1}. This equates to an average reduction in consumption of 41%. The addition of a further 0.2 g of sediment (giving 0.5 g in total and a concentration of 10,000 mg l^{-1}) resulted in a total drop in consumption of 96% compared to sediment free conditions. The differences in consumption recorded between the addition of 0.3 g and 0.5 g of sediment are conjectured to result from differences in sediment coverage and thickness across the egg surface. The addition of 0.3 g of sediment left a small portion of the egg surface free from sediment, which may have allowed the egg to continue consuming O_2 at a slightly greater

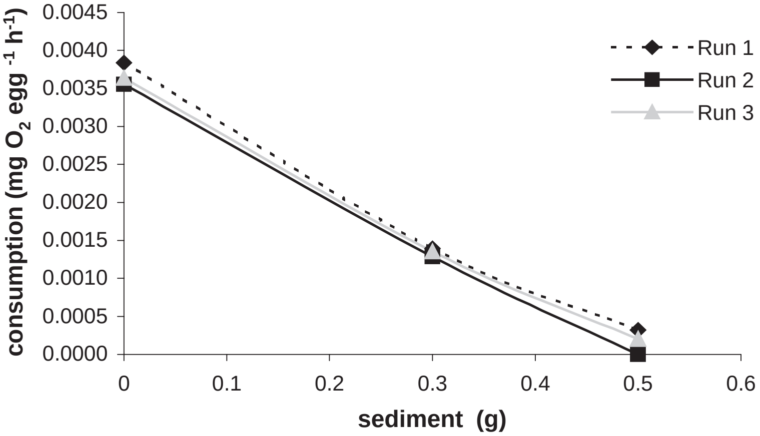

Fig. 7. Decline in egg oxygen consumption with the addition of inert clay particles. Volume of sample was 50 ml in all cases.

rate than under conditions of complete surface coverage.

To ensure that the amount of clay sediment introduced to the incubation chamber was representative of typical values of clay sediment recorded in the egg zone of salmon redds, the equivalent percentage weight of clay within a sediment–water mixture was calculated. These values were estimated by assuming that the entire volume of the incubation chamber was filled with a sediment–water mixture with a porosity value (0.35) typical of that reported in spawning gravels (Lisle and Lewis, 1992). Based on this assumption, 0.3 g and 0.5 g of clay sediment equates to a percentage weight of clay of 0.65% and 1.2%, respectively, which is representative of field observations of percentage clay in salmon redds found in this and other published studies (Crisp and Carling, 1989).

Two explanations for the recorded drop in consumption are proposed. First, the clay particles created a zone of low O_2 supply around the eggs, thereby reducing O_2 availability and restricting O_2 consumption by incubating embryos. This zone was caused by the reduction in permeability provided by the clay film. Secondly, the clay particles physically blocked the pore canals in the egg chorion, thereby restricting the transport of O_2 across the egg's chorion. The chorion, or cell wall, is composed of tough ichthulokeratin perforated by mircopore canals that permit O_2 to diffuse through the eggs tough outer shell. Micrographs of the egg surface suggest that the total area of canals is roughly one tenth the total egg surface area and that the pore canals are between 0.5 and 1.5 μm in diameter (Bell et al., 1969). A comparison of the size of pore canals with the size of clay particles introduced to the incubation chamber indicated that the clay material potentially contained particles, which were less than or equal to the size of the pore canals (Greig et al., in press).

3.7. Relationship between suspended sediment and infiltration

Based on data derived from the sediment accumulation pots and the flux of near-bed suspended sediment, the relationship between suspended sediment load and the accumulation of sediment in the spawning and incubation gravels was assessed. This analysis was based on the assumption that there is minimal flushing of fines from the gravels once material has been accumulated. This is probably a valid assumption for the River Test and River Aran, where bed disturbance was negligible, but less reliable for the River Blackwater and River Ithon study sites. Loads in kg m^{-1} were derived from the 10-min suspended sediment and discharge data, and aggregated for the period between sediment pot sampling to provide a total near-bed fine sediment load per m^2 (Sear, 1993). The results (in kg m^{-2}) show that the proportion of total load contributing to the measured sediment accumulation varies over time and between rivers, but are characteristically low; ranging between

0.003% and 0.13%, with averages ranging between 0.01% and 0.05% depending on the study site.

4. Discussion

4.1. Relationship between oxygen availability and embryonic survival

The strength of the relationships between O_2 availability and embryonic survival are in agreement with previous studies and suggest that measures of O_2 concentration, interstitial flow velocity and O_2 flux can be applied to assess potential rates of embryonic survival (Turnpenny and Williams, 1980; Chapman, 1988; Maret et al., 1993; Ingendahl, 2001). However, site specific inspections of these relationships indicated inter-site variability in the performance of these variables. Although this site specificity may be partly explained by the impact of inadequate data points on the strength of the statistical analysis, it may also be indicative of variations in the specific causes of O_2-related mortalities at the field sites (Greig et al., in submission a,b,c). Furthermore, although the relationships developed are statistically valid, the effective use of statistical correlations requires knowledge of the processes linking variables under investigation and awareness of additional factors affecting the variables under consideration, for example, temporally variable conditions within the incubation zone and threshold responses. The results of the field-monitoring programme indicated that threshold responses may have influenced the causes of embryonic mortalities, for instance, at a number of locations, O_2 concentrations within the range considered critical to survival (2–7 mg l^{-1}) were recorded (Shumway et al., 1964; Davis, 1975). In response to these observations, the principals of cutaneous O_2 consumption (Daykin, 1965) were used to identify the potential causes of O_2-related mortalities at each field site (Table 7).

4.2. Impact of fine sediment accumulation on oxygen availability

The results of the field investigation also revealed the complexity of factors influencing O_2 availability, and demonstrated how the composite of these factors varies within and between rivers. The factors influencing O_2 availability operate contemporaneously and over a variety of spatial and temporal scales. Therefore, awareness of environmental conditions that will result in O_2 deficiencies within spawning gravels requires identification of potentially harmful factors and awareness of how these factors interact to influence O_2 availability (Fig. 1). Limiting conditions will be determined by physical and biological characteristics of the river and its surrounding catchment. Consequently, the precise factors influencing O_2 availability may vary significantly between and within river systems. For instance, in agricultural catchments, excessive sedimentation may be coupled with inputs of organic and nutrient rich material associated with over-grazing or poorly managed fertiliser and waste application. These materials may reduce interstitial flow velocities, exacerbating the impact of O_2 demands. Similarly, the infiltration of a small amount of clay post-redd creation may promote the development of a sedimentary seal around incubating embryos that restricts O_2 consumption. Finally, if the infiltration of inorganic and organic material results in interstitial flow velocities that are inadequate to supply O_2 at a rate sufficient to support respiratory requirements, mortalities may ensue.

4.3. Management implications

These observations have important implications for management strategies that aim to enhance the productivity of salmon spawning and incubation gravels through the reduction of fine sediment loads within the river network. Grainsize measures are frequently applied to assess the quality of salmon spawning gravels. Such measures typically include some estimate of the percent sediment below an empirically determined size fraction, or else some moment measure that reflects the influence of the finer sediment on the overall population of particles. However, although potentially providing a statistically significant relationship with pre-hatching success, bulk measures of fine sediment accumulation cannot be linked directly to embryonic survival. Rather it is the impact of the sediment on the supply of O_2 to the incubating embryos that influences survival. This distinction is important because considerable expenditure and reliance is placed by fisheries management

Table 7
Summary of factors contributing to the mortality of salmon eggs at each field site

Field site	Factors potentially influencing survival
River Test	*Cause of mortalities:* (i) Oxygen deficient resulting from combination of lowered oxygen concentrations and intragravel flow velocities. (ii) Accumulation of metabolic waste resulting from low intragravel flow velocities. *Factors contributing to reduced oxygen availability:* (i) The accumulation of fine sediments, although it should be noted that fine sediment <1 mm was <10%. (ii) However, high percentage organic material (20%) further reduced intragravel pore space, resulting in low intragravel flow velocities. (iii) The presence of high levels of organic material may have promoted the growth of biofilms further reducing pore space and lowering intragravel flow velocities. (iv) Sedimentary oxygen demand, induced by high organic content, lowered intragravel oxygen concentrations. *Critical factors:* (i) High organic content. (ii) Potential increase in levels of fine material accumulating in spawning gravels. (iii) Limited bed mobility has reduced the potential cleansing action of scour events.
River Blackwater	*Causes of mortalities:* (i) Exceptional survival recorded. *Factors contributing to reduced oxygen availability:* (i) Low levels of fine sediment (<4 mm) accumulation. (ii) Low levels of organic material.
River Ithon	*Cause of mortalities:* (i) Oxygen deficient resulting from combination of lowered oxygen concentrations and intragravel flow velocities. (ii) Sublethal oxygen concentrations. *Factors contributing to reduced oxygen availability:* (i) High levels of fine sediment ((<4 mm) accumulation (>30%). (ii) High sedimentary oxygen demands. (iii) Long periods of low flow resulting in reduced surface–subsurface exchange of oxygenated water. *Critical factors:* (i) Compound of all factors.
River Aran	*Cause of mortalities:* (i) Oxygen deficient resulting from combination of lowered oxygen concentrations and intragravel flow velocities. (ii) Sublethal oxygen concentrations. *Factors contributing to reduced oxygen availability:* (i) High levels of fine sediment ((<4 mm) accumulation (>30%). (ii) High sedimentary oxygen demands. *Critical factors:* (i) Compound of all factors.

agencies on the validity of these measures, and they form the basis of the condition assessments required under the Habitat Directive. Thus, it can be argued that, while the former appear to provide a relatively simple measure of the quality of the incubation environment, in the light of the model of O_2 supply advanced above (Fig. 1), the interpretation of these correlations remain problematic. Furthermore, although these grainsize measures can be obtained fairly easily in the field using freeze coring techniques, the redd cutting action of the hen salmon substantially modifies the bed texture (Kondolf et al., 1993) and hence the value of these measures of grainsize distributions and porosity are changed. Consequently, unless artificial or natural redds are assessed at times coincident with hatching or emergence, conceptually, the measurements of the grainsize of spawning beds alone are difficult to justify.

Regarding the relationship between sediment availability and accumulation, the results of this study agree with those of previous studies, which indicate that sediment accumulation in gravels is strongly correlated with the availability of fine sediment in the water column (Carling, 1984; Sear, 1993). This relationship provides river managers with one method for controlling the accumulation of fine sediment in spawning gravels, and hence increasing the productivity of spawning gravels. Thus, if through some form of river or land management (depending on the source of fine sediments), it is possible to reduce sediment loads, then the quantity of fine sediment stored within the redds will decrease. Current water management practices are reducing the delivery of fine sediment from the catchment via bank erosion control, riparian buffer practices and modified land use practices (Summers et al., 1996; Crisp, 2000; SEPA, 2002). More recently, recognition of the role that fine sediments play in delivering sediment-bound nutrients (phosphorous in particular) and pollutants to aquatic ecosystems has resulted in a new impetus to reduce fine sediment inputs from catchments (Defra, 2002). However, this study has also demonstrated that in the presence of high organic matter loads even relatively small rates of accumulation can have disproportionate impacts on spawning habitats. Similarly, the laboratory experiment supports that view that a small quantity of clay, can have a disproportionately large impact on the productivity of incubation gravels. With regard to the scale of the reductions in fine sediment inputs required to improve incubation success, the results of this study suggest that in some systems, a dramatic decline in sediment input may be required to effect a major improvement in productivity although model studies have reported increases in the time above critical O_2 levels with decreasing silt levels (Theurer et al., 1998). Nevertheless, this study casts doubt on the ability of current sediment management methods to reduce the delivery of fine sediment sufficiently to result in significant improvements in spawning gravels.

Fig. 8 reproduces a conceptual diagram of the factors influencing the accumulation of fine sediments within rivers. Four elements are involved: (1) catchment sources, (2) sediment delivery, (3) the ability of the river network to trap this material (providing channel sources) and (4) the composition and structure of the spawning gravels, which influence the trapping and retention of fines in the river bed. Current management practices attempt to treat the sources through land management or, in some cases, by altering the channel structure to reduce trapping potential, thereby, increasing the flushing of fines from the stream bed. In the UK, these two treatments are typically undertaken in isolation of each other, risking the increase in fine sediment loading on the river bed by restoring more storage opportunities for

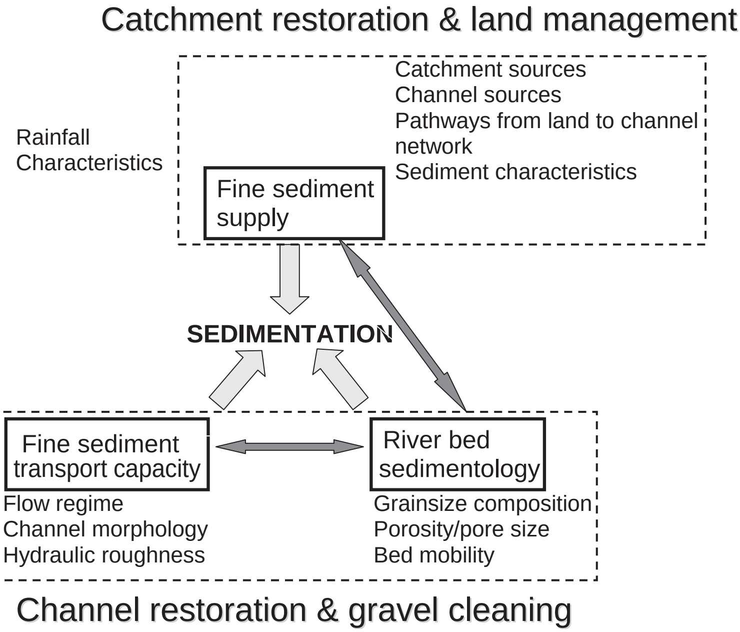

Fig. 8. Conceptual diagram of the fine sediment system of a river emphasizing the need to manage both source and storage elements on the catchment land surface as well as within the river network and spawning beds.

fine sediment (Kondolf et al., 2003). First identifying the cause of the poor productivity, and then applying a range of treatments designed to alleviate that cause will reduce fine sediment delivery to spawning beds. However, macrophyte vegetation provide a source of organic detritus and inputs of organic material contribute to the low interstitial flow velocities recorded over the incubation period. Subsequently, management strategies should aim to treat the sources and pathway of inorganic sediments and high O_2 demanding material, much of which are derived from the catchment surface and agricultural practice; for instance, fertiliser application, animal faeces and agricultural waste.

5. Conclusion

A study of the factors influencing the survival of incubating salmonid eggs within natural river gravels has demonstrated the importance of O_2 supply rates. Field and laboratory experiments have quantified the multiple impacts of fine sediment accumulation on the supply of oxygenated water to the incubating salmon embryos. These effects are threefold: (i) the impact of organic and inorganic sediment accumulation on gravel permeability and interstitial flow velocities, (ii) the impact of O_2 demands associated with infiltrated materials on intragravel O_2 concentrations and (iii) the impact of fine particles (clay) on the exchange of O_2 across the egg membrane.

European river management agencies are discussing the delivery of new habitat legislation for the protection of Atlantic salmon and, more widely, the quality of river ecosystems (European Community, 2000). One of the issues under consideration is the identification of ecologically appropriate targets for nutrients, river flows and fine sediments in watercourses. The present study has defined a complex set of processes and factors influencing incubation survival, which are not adequately described by simple fine sediment targets, at least in UK watercourses. It is suggested that, in order to provide effective treatments of sediment-related pressures, such targets must reflect the specific river, catchment and site-level factors influencing sediment accumulation. Consideration should also be given to the potential O_2 demand associated with accumulated sediment. In a dynamic environment, these factors are likely to be temporally variable, further complicating the identification of fine sediment thresholds. Finally, the results of this study, which indicate that the accumulation of fines within artificial salmon redds involves less than 0.1% of the available load, raises concerns regarding the effectiveness of current land management practices to reduce the impact of fine sediments on spawning and incubation gravels. This research suggests that much larger reductions in sediment runoff from the land surface and in-channel stored will be required. These might be achieved through targeted application of effective soil erosion control from agricultural land coupled with treatment of the sediment pathways into the river network. Such treatments will need to recognise not only the inorganic but also organic components of the wash load to streams. Underpinning such treatments is a need to research the sources and pathways of organic sediment from catchment to the salmon redd.

Acknowledgements

This research was made possible through the support of Defra Grant SF0225 awarded to P.A. Carling and D.A. Sear. Dr. Les Whitcombe is thanked for his support in undertaking fieldwork. Dr. David Smallman is thanked for his assistance in setting up the sediment oxygen demand and clay experiments. The improvements of two anonymous referees are gratefully acknowledged.

References

Acornley RM, Sear DA. Sediment transport and sedimentation of Brown trout (*Salmo trutta* L) spawning gravels in chalk steams. Hydrol Process 1999;13:447–58.

Alonso CV, Theurer FD, Zachmann DW. Technical Report No. 5-Tucannon River offsite study: sediment intrusion and dissolved oxygen transport model. USDA-Agricultural Research Service, National Sedimentation Laboratory, PO Box 1157, Oxford MS 38655 1996; 400pp.

Bell GR, Hoskins GE, Bagshaw JW. On the structure and enzymatic degradation of the external membrane of the salmon egg. Can J Zool 1969;47:146–8.

Bjorn TC, Reiser DW. Habitat requirements of salmonids in streams. In: Meehan WR, editor. Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats.

Special Publication, vol. 19. Bethesda, Maryland: American Fisheries Society; 1991.

Burkhalter DE, Kaya CM. Effects of prolonged exposure to ammonia on fertilised eggs and sac fry of Rainbow trout (*salmo gairdneri*). Trans Am Fish Soc 1975;106:470–5.

Carling PA. Deposition of fine and coarse sand in an open-work gravel bed. Can J Fish Aquat Sci 1984;41:263–70.

Carling PA, Boole P. An improved conductiometric standpipe technique for measuring interstitial seepage velocities. Hydrobiologia 1986;135:3–8.

Carling PA, McCahon CP. Natural Sedimentation of Brown Trout (*Salmo Trutta* L) Spawning Gravels during Low-Flow Conditions Regulated Streams. Plenum Publishing Corp; 1987.

Cederholm CJ, Reid LM, Salo EO. Cumulative effects of logging road sediment on salmonid populations in the Clearwater River, Jefferson County, Washington. Proceedings from the Conference on Salmon Spawning Gravel: A Renewable Resource in the Pacific Northwest. Washington Water Research Centre, Report, vol. 39. Pullman: Washington State University; 1981. p. 38–74.

Chapman DW. Critical review of variables used to define effects of fines in redds of large salmonids. Trans Am Fish Soc 1988;117:1–21.

Chen B, Li Y. Numerical modelling of biofilm growth at the pore scale. Proceedings of the 1999 Conference on Hazardous Waste Research. WRC; 1999. p. 112–8.

Chevalier BE, Carson C. Modelling the transfer of oxygen between the stream and the stream substrate with application to the survival rates of salmonid embryos. Colorado State University, Department of Agriculture and Chemical Engineering ARS Report No. 5602 20813-008A; 1984. 99p.

Crisp TD. Trout and Salmon: Ecology Conservation and Rehabilitation. Oxford: Fishing News Books; 2000.

Crisp DT, Carling PA. Observations on siting, dimensions and structure of salmonid redds. J Fish Biol 1989;34:119–34.

Davis JC. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. Can J Fish Aquat Sci 1975;32:2295–332.

Daykin P. Application of mass transport theory to the problem of respiration of fish eggs. J Fish Res Board Can 1965;22:159–70.

DEFRA (Department of Environment, Food and Rural Affairs). The government's strategic review of diffuse water pollution from agriculture in England: Paper 1. Agriculture and water: a diffuse pollution review; 2002.

European Commission. Directive 2000/60/EC of the European Parliament and of the Council of 23rd October 2000: establishing a framework for community action in the field of water policy. Off J Eur Communities L 2000;327:1–72.

Freeze RA, Cherry JA. Groundwater. Upper Saddle River (NJ): Prentice-Hall; 1979. 604 pp.

Frostick LE, Lucas PM, Reid L. The infiltration of fine matrices into coarse grained alluvial sediments and its implication for stratigraphical interpretation. J Geol Soc 1984;141:955–65.

Greig SM. Factors influencing the supply of oxygen to incubating salmon embryo: a field study, Unpublished PhD thesis, School of Geography, University of Southampton; 2004. 330 pp.

Greig SM, Sear DA, Carling PA. Review of factors influencing the availability of dissolved oxygen to incubating salmon embryos. North Am J Fish Manage in submission a.

Greig SM, Carling PA, Sear DA. Refinement and re-calibration of a conductiometric standpipe method of assessing interstitial flow velocities. Hydrobiologia in submission b.

Greig SM, Sear PA, Carling PA. A field-based assessment of oxygen supply to incubating Atlantic salmon embryos. Can J Fish Aquat Sci in submission c.

Greig SM, Sear DA, Smallman D, Carling PA. Impact of clay particles on cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs. J Fish Biol in press.

Haygarth PM, Condron LM, Heathwaite AL, Turner BL, Harris GP. The phosphorus transfer continuum: linking source to impact with an interdisciplinary and multi-scale approach. Sci Total Environ this volume.

Heaney SI, Foy RH, Kennedy GJA, Crozier WW, O'Connor WCK. Impacts of agriculture on aquatic systems: lesson learnt and new unknowns in Northern Ireland. Mar Freshw Res 2001;52:151–63.

Hicks DM, Gomez B. Sediment transport. In: Kondolf GM, Piegay H, editors. Tools in Fluvial Geomorphology. Chichester (UK): J. Wiley and Sons; 2003. p. 425–61.

Huntington CW, Nehlsen W, Bowers JK. A survey of healthy native stocks of anadromous salmonids in the Pacific Northwest and California. Fisheries 1996;21(3);6–14.

Ingendahl D. Dissolved oxygen concentration and emergence of sea trout fry from artificial redds in tributaries of the River Rhine. J Fish Biol 2001;58:325–41.

Kondolf GM, Sale MJ, Wolman MG. Modification of fluvial gravel size by spawning salmonids. Water Resour Res 1993;29(7); 2265–74.

Kondolf GM, Piegay H, Sear DA. Integrating geomorphological tools in ecological and management studies. In: Kondolf GM, Piegay H, editors. Tools in Fluvial Geomorphology. Chichester (UK): J. Wiley and Sons; 2003. p. 633–60.

Lisle TE, Lewis J. Effects of sediment transport on survival of salmonid embryos in a natural stream, A simulation approach. Can J Fish Aquat Sci 1992;49:2337–44.

Lotspeich FB, Everset FH. A new method for reporting and interpreting textural composition of spawning gravel. US Department of Agriculture Research Note PNW-369; 2001.

Malcolm IA, Soulsby C, Youngson A, Petry J. Heterogeneity in ground water surface water interactions in the hyporheic zone of a salmonid spawning stream: towards integrating hydrometric and tracer approaches. Hydrol Process 2003;17:601–17.

Maret TR, Burton TQ, Harvey GW, Clark WH. Field testing new monitoring protocols to assess Brown trout spawning habitat in an Idaho stream. North Am J Fish Manage 1993;13:567–80.

McCrimmon HR, Gots BL. Laboratory observations on emergent patterns of juvenile rainbow trout, *Salmo gairdneri*, relative to test substrate composition. In: Miller JC, Arway JA, Carline RF, editors. Proceedings of the Fifth Trout and Stream Habitat Improvement Workshop. Harisburg: Pennsylvania State Fish Commission; 1986. p. 69–73.

McMellin G, Walling DE, Nicholls D. Land Use and Fisheries, Report W2-046/TR1. Bristol (UK): Environment Agency; 2002. 59 pp.

McNeil WJ, Ahnell WH. Success of pink salmon spawning relative to size of spawning bed materials. Spec Sci Rep, Fish, vol. 469. Washington (DC): U.S. Fish and Wildlife service; 1964. 15 pp.

Peterson RH, Metcalfe JL. Emergence of Atlantic salmon fry from gravels of varying composition: a laboratory study. Can Tech Rep Fish Aquat Sci, vol. 1020. St. Andrews, New Brunswick: Department of Fisheries and Oceans, Biological Station; 1981. 15 pp.

Reiser DW. Sediment gravel bed rivers: ecological and biological considerations. Gravel-bed rivers in the environment; 1998. p. 199–228.

Scottish Environment Protection Agency (SEPA) managing river habitats for fisheries: a guide to best practice. SEPA, Fisheries Research Services, Scottish Natural Heritage, Scottish Executive Joint Publication, Edinburgh; 2002.

Sear DA. Fine sediment infiltration into gravel spawning within a regulated river experiencing floods: ecological implications for salmonids. Regul Rivers Res Manage 1993;8:373–90.

Sear DA, Damon W, Booker DJ, Anderson D. A load-cell based continuous recording bedload trap. Earth Surf Processes Landf 2000;25:659–73.

Shea K, Mangel M. Detection of population trends in threatened Coho salmon (*Oncorhynchus kisutch*). Can J Fish Aquat Sci 2001;58(2);375–85.

Shumway SJ, Warren CE, Doudoroff P. Influence of oxygen concentration and water movement on the growth of steelhead trout and chinook salmon embryos at different water velocities. Trans Am Fish Soc 1964;93:342–56.

Silver SJ, Warren CE, Doudoroff P. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different velocities. Trans Am Fish Soc 1963;92(4);327–43.

Soulsby C, Malcolm IA. Fine sediment influence on spawning habitat in a lowland regulated stream: a preliminary assessment. Sci Total Environ 2001;265:295–307.

Štĕrba O, Uvira V, Mathur P, Rulik M. Variations in the hyporheic zone through a riffle in the R Moriva, Chechoslovakia. Regul Rivers Res Manage 1992;7:31–44.

Summers DW, Giles N, Willis DJ. Restoration of riverine trout habitats: a guidance manual, Fisheries Technical Manual 1. R&D: Technical Report W18, Environment Agency, Bristol 1996.

Tappel PD, Bjornn TC. A new way of relating size of spawning gravel to salmonid embryo survival. North Am J Fish Manage 1983;3:123–35.

Theurer FD, Harrod TR, Theurer M. Sedimentation and Salmonids in England and Wales Report P2-103. Bristol: Environment Agency; 1998. 70 pp.

Turnpenny AWH, Williams R. Effects of sedimentation on the gravels of an industrial river system. J Fish Biol 1980;17: 681–93.

Walling DE. Tracing suspended sediment sources in catchments and river systems. Sci Total Environ this volume.

Walling DE, Amos CM. Source, storage and mobilisation of fine sediment in a chalk stream system. Hydrol Process 1999; 13(3);323–40.

Walling DE, Collins AL, McMellin GK. Provenance of Insterstitial Sediment Retrieved from Salmonid Spawning Gravels in England and Wales, Report W2-046/TR3. Bristol: Environment Agency; 2001. 43 pp.

Whitman RL, Clark WJ. Availability of dissolved oxygen in interstitial waters of a Sandy Creek. Hydrobiologica 1982;92: 651–8.

Wickett WP. Mass transfer theory and the culture of fish eggs. In: Adams W, editor. Chemistry and Physics of Aqueous Gas Solutions. Princeton: The Electro Chemical Society; 1975 521 pp.

World Wildlife Fund (WWF) The status of wild Atlantic salmon: a river by river assessment. WWF-US, Washington; WWF-Norway, Oslo; WWF European Freshwater Programme, Copenhagen 2001 [Online.www.panda.org/endangeredseas/salmon2.pdf].

Young MK, Hubert WA, Wesche TA. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. North Am J Fish Manage 1991;11:339–46.

Youngson AF, MacLean JC, Fryer RJ. Declining trends in the abundance of early running two-sea-winter Atlantic salmon, *Salmo salar*, in Scottish rivers. ICES J Mar Sci 2002;59: 836–49.