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Physical controls on salmon spawning habitat quality and embryo fitness: An integrated analysis

by

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ABSTRACT

FACULTY OF SOCIAL AND HUMAN SCIENCES
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PHYSICAL CONTROLS ON SALMON SPAWNING HABITAT QUALITY AND EMBRYO FITNESS: AN INTEGRATED ANALYSIS

by Niamh Sarah Burke

The research focusses on the river Lugg – a cross-border catchment and major tributary of the river Wye, the most important Atlantic salmon river in England and Wales.

The problem of declining Atlantic salmon populations in the catchment is addressed through investigating recruitment from egg fertilization to the emergent life stage and beyond using multiple field-based and laboratory techniques. The approach adopted is multidisciplinary and addresses the need for holistic approaches to habitat degradation which is increasingly recognised as systemic in nature; often with multiple stressors acting interactively.

The initial premise of deleterious fine sediment infiltration into spawning gravels was addressed by a sediment fingerprinting study to ascertain the provenance of infiltrated redd sediment from a range of land-use types. In addition, nine artificial redd sites were constructed and assessed for fine sediment infiltration, intragravel dissolved oxygen levels, intragravel flow velocity and other hyporheic pore water characteristics, in relation to survival to emergence over two field seasons. A study examining the quality of emergent fry was also carried out using fitness tests and individual stress levels. Additionally, a study on long-residence groundwater infiltration into the incubation environment was carried out.

The main fine sediment contributor was derived from agricultural sources, particularly during wetter periods. The average contribution of fine sediment from agricultural sources was 60%.

Survival ranged from 12% to 70% during the 2008 flood season and from 76% - 93% during the 2009 dry season. Fine sediment mass as a stand-alone index was only weakly correlated with survival but is thought to influence other factors; medium strength correlations of survival with dissolved oxygen, intragravel flow velocity and oxygen supply in particular were observed.

Evidence of groundwater-surface water interactions were detected at two of three sites investigated and is proposed as an additional controlling mechanism for embryonic survival in the catchment.

Sublethal fitness tests demonstrated variations between cohorts in the 2009 period despite a relatively small range of oxygen concentrations. The results highlight both temporal and spatial variations in spawning habitat quality, which influence not only survival to hatch but also post-hatch fitness.

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DECLARATION OF AUTHORSHIP

I, Niamh Sarah Burke, declare that the thesis entitled '**Physical controls on salmon spawning habitat quality and embryo fitness: an integrated analysis'** and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- none of this work has been published before submission

Signed: ……………………………………………………………………..

Date:…21/12/2011…………………………………………………………….

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Dedicated to my father, whose love of nature inspired my own
And to my mother, who encouraged all her children to strive for their goals.

Chapter 1 Introduction

1.1 Project overview

This PhD has been undertaken with the support of the Environment Agency Wales and aims to address the problems affecting salmonid spawning habitat quality in a representative catchment affected by high sedimentation and siltation loads.

The approach taken is through a number of interrelated studies which look at the potential drivers of habitat degradation and salmonid incubation success, initially addressing the premise of sedimentation as the main driver, but additionally investigating other potential drivers influencing incubation success and highlighting some of the possible connections and interactions between these drivers.

Catchment sediment sources were investigated in order to define the main contributing components and with a view to informing catchment management efforts in sediment reduction.

Responses to environmental drivers were measured through field studies which assessed survival success relative to a range of environmental variables, temporally and spatially. Additionally, tests for sub-lethal effects of environmental conditions on salmonid progeny were carried out, which highlighted the future viability of salmonid fry and served as a higher resolution measure of recruitment; providing a more robust measure of response than survival indices alone.

1.2 Research Background

Research into salmonid incubation success originated early last century with observations by fishery biologists that salmon fry survival was low in gravels with high proportions of fine sediment (Harrison 1923, Hobbs 1937).

Lab-based research into fine sediment and reduced water velocities were associated with lowered survival (Krough 1941, Hayes 1951) and field observations by Wicket (1954) and Cooper (1965) lent support to this; attesting that fine sediment lowered survival success in the wild.

Interest in the role of intragravel flow velocities in incubation habitat quality led to investigation into the oxygen demands of developing embryonic salmon and the delivery of oxygen within the redd environment. Studies in this field were divided between lab-based experiments and theoretical approaches. Lab studies involved the investigation of oxygen consumption rates of embryos and concluded that below threshold concentrations of oxygen, respiratory demands of embryo were unmet (Alderdice et al 1958, Silver 1963, Shumway et al 1964, Hamor and Garside 1976). Theoretical approaches to the problem of supply and demand involved the development of models of oxygen consumption using diffuse oxygen exchange equations coupled with the application of mass transport theory to represent the exchange of oxygen from the stream water to the embryo, and relate this to embryonic demands (Hayes 1951, Wickett 1954, Daykin 1965, Wickett 1975, Chevalier and Carson 1985).

In the field of sedimentology, physical scientists investigated the characteristics and dynamics of sediment deposition in river beds. Field and flume studies yielded observations of fine sediment infiltration associated with the porosity of the framework bed material, and gave insight into the dynamics of deposition with in the redd zone. The association of the very fine sediment portion with the rate of water flow in the redd zone was an important finding in predictions of incubation success, and the observation that sand-sized particles tended to form surface ‘seals’ at the stream-gravel interface, was important in understanding the emergence success of young fry (Einstein 1968, Beschta and Jackson 1979, Carling 1984).

Research on incubation success experienced renewed interest in the mid-late 1980s in response to rapidly declining salmon stocks and the partial attribution of incubation success to this population decline. Some researchers worked from the premise of physical parameters as determinants of incubation success through development of indices of habitat quality based on granular determinants such as the geometric mean, fredle index, permeability measurements, and percentage fines (Koski 1975, Lotspeich and Everest 1981).

Other studies looked more specifically at interstitial oxygen concentrations as the clearest determinant of incubation success (Turnpenny and Williams 1980, Rubin and Gilmsater 1996, Ingendahl 2001). Intragravel flow was also recognised as an important factor influencing oxygen availability within the redd zone, but due mainly to sampling difficulties, in-situ measurements of intragravel flow were not widely carried out and few studies report this parameter relative to survival (Cooper 1965, Turnpenny and Williams 1980, Grieg 2005).

In more recent years, other aspects of potential controls on spawning habitat quality have been addressed and developed from a variety of disciplines, such as the impacts of groundwater-surface water interactions on the incubation environment (Soulsby 2001, Malcolm et al 2003, 2005), and the effects of stream bed topography on the flow characteristics of stream water into the redd zone (Thibodeaux and Boyle 1987). The impacts of the oxygen demands of organic and inorganic matter on the incubation environment have been pinpointed as a factor of concern in some rivers (Chevalier et al 1984, Grieg 2005). Additional factors raised have been water temperature (Chadwick 1982), scour and mechanical shock (De Vries 1997, Lapointe 2000). Water quality measures, such as pH (Sayer et al 1993), the effect of metabolic waste products (Chapman 1988, Meehan 1991, Crisp 2000) and of chemical pollutants from both urban and agricultural environments are also areas of concern (Finn 2007). The impact of biofilms on sediment, interstitial flow and oxygen exchange within the redd is an emerging topic which deserves attention (Claret et al 1998, Battin and Sengschmitt 1999, Petticrew 2003).

So, while the original problem of sedimentary impacts on spawning gravel remains a key factor in assessing habitat quality, and previous studies have considered the pertinence of oxygen availability in relation to larval salmonid survival (Silver 1969, Malcolm et al 2003) while others have looked at larval survival in relation to oxygen and the infiltration of sediment (Koski 1966, Tappel and Bjornn 1983, Lisle 1989; Zimmerman and Lapointe 2006, Julien and Bergeron 2006), there is a growing recognition that other drivers may be at work within the hyporheic zone and affecting incubation habitat quality - in addition to the single metrics studied previously (Chapman 1988, Reiser 1998, Wu 2000, Crisp 2000, Greig et al 2005).

However, few studies have addressed the complex interaction of factors within the hyporheic zone that may be contributing to a decline in quality of the incubation environment. More recent studies have shown the need to address this complex environment as just that, and look holistically at the suite of interactions affecting the incubation zone during embryonic and larval development (Chapman 1988, Alonso 1996, Wu 2000, Malcolm et al 2003, Greig et al 2005). In recent years, Malcolm et al highlighted concerns about the impact of the upwelling of groundwater of low oxygen concentration on developing larvae, and Greig et al (2005) advocated the need to approach the problem from a holistic perspective, taking into account the multiple interactions between processes.

In his study on the effects of sediment on the survival of Atlantic salmon to hatching, Grieg (2004) addresses sediment infiltration in relation not only to oxygen concentration in the redd zone but calculates the net oxygen ‘flux’ available to the eggs through the integration of the interstitial flow rate within the egg zone. This value was then matched with the oxygen demand of eggs throughout the stages of incubation to find if critical levels of oxygen supply were being achieved or not. Further laboratory studies investigated the effect of clay particles on the respiratory abilities of incubating eggs.

There is a growing trend in river research and management to look at rivers as whole ecosystems. This requires that all aspects of a river’s physical, geomorphological, hydrological, chemical and biological qualities be considered and the relationships between these areas defined. In turn, this demands an approach which encompasses inter-disciplinary knowledge and expertise. The need for this new approach has been addressed recently in the literature and the emergent approach termed variously - including eco-geomorphology (Thoms and Parsons 2002), eco-hydromorphology (Vaughan et al 2007) geobiology and biogeomorphology. Pickett et al (1994) advocate the need to move towards the integration of disciplines via a scale-sensitive approach, and identify some consequences of uni-disciplinary research:

1. Gaps in understanding appear at the interface between disciplines

2. Disciplines focus on specific scales or levels of organization

3. As subdisciplines become rich in detail, they develop their own view points, assumptions, definitions, lexicons and methods.

Vaughan et al (2007) state the need to focus on the development of eco-hydromorphology at the interface between ecology, hydrology and fluvial geomorphology via integrated approaches which will lead to an improved capacity to solve river management problems in an effective way. In their 2007 paper they state the need to understand how eco-hydromorphic processes generate observed patterns and in turn how those patterns influence processes. One example of this kind of feedback is the interaction between vegetation and sediment and how they together influence river channel shape and flow characteristics and in turn vegetation recruitment and sediment transport.

In their call for an interdisciplinary approach to river science, Thoms and Parsons (2002) state that the emerging field of eco-geomorphology has the potential to bring about fresh solutions to environmental problems in river systems when all contributing disciplines are matched in a spatial and temporal context that considers key hierarchical links at specific scales.

Using an approach which integrates multiple factors and linkages can elucidate heretofore separate problems and highlight the systemic nature of hyporrheic interactions. By looking at other disciplines' approaches to related problems – even those with initially different research interests, new ways of measuring and explaining all the interacting variables may be brought to light.

Related studies have shown that oxygen supply to eggs can be further depleted if oxygen-consuming substances form part of this sediment influx – such as respiring/ decaying organic fractions (Chevalier and Carson 1984, Grieg 2005). Additionally, organic fractions can also facilitate the development of 'biofilms' - algal and bacterial communities which cleave to sediment particles and form a cohesive mass. Biofilms may further block pore space and reduce permeability and interstitial flow velocity (Chen and Li 1999, Battin et al 2003) with knock-on effects for the flushing of metabolic waste products from the incubation zone which can independently be harmful to embryos (Grieg et al 2005). The incidence of feedback effects such as outlined above may be more common than previously considered and are worthy of further research in the context of assessments of spawning habitat quality.

Additionally, toxicity studies have shown that a variety of compounds, from metabolic waste products such as ammonia and nitrite (Vedel et al 1998) to sediment-bound toxins of anthropogenic origin (Strmac et al 2002) may affect the survival and health of developing embryos and larvae.

Studies investigating spawning gravels have with few exceptions used survival as an endpoint for demonstrating the quality of the habitat in question. However, there is growing evidence that emergent alevins may be stunted (Silver et al 1963, Argent and Flebbe 1999) or morphologically abnormal (Malcolm et al 2003, Youngson et al 2004) when exposed to poor incubation habitat conditions. Sublethal effects such as these are liable to compromise the fitness and future viability of the individual and so should be taken into account when assessing habitat quality in studies looking at recruitment and the future viability of populations.

Research into health and survival of fish larvae in aquaculture has used challenge tests such as swimming performance and reactivity to stimuli as a measurement of the health of developing young in fisheries (Cada et al 2003, Portz et al 2006). Biochemical and physiological research into effects of stressors such as hypoxia, elevated temperature and a variety of chemical compounds on fish survival health and stress, has used metabolite and hormone levels as indicators of the health and stress levels of fish in captivity (Feist and Schreck 2002, Ellis et al 2004, Finn 2007).

1.3. PhD context and aims

By embracing and integrating approaches used in other disciplines we can hope to gain an insight into the complexity of the interactions within the hyporheic zone and their effects on alevins survival and long term health. This approach also ensures that we are aware of advances made in different but related fields of salmonid research and facilitates the exchange of methods, approaches and new knowledge gained in any one specific discipline.

This study intends to bring this holistic perspective further by embracing additional potential variables affecting spawning habitat than previously collectively considered and through adopting approaches that originate in other disciplines.

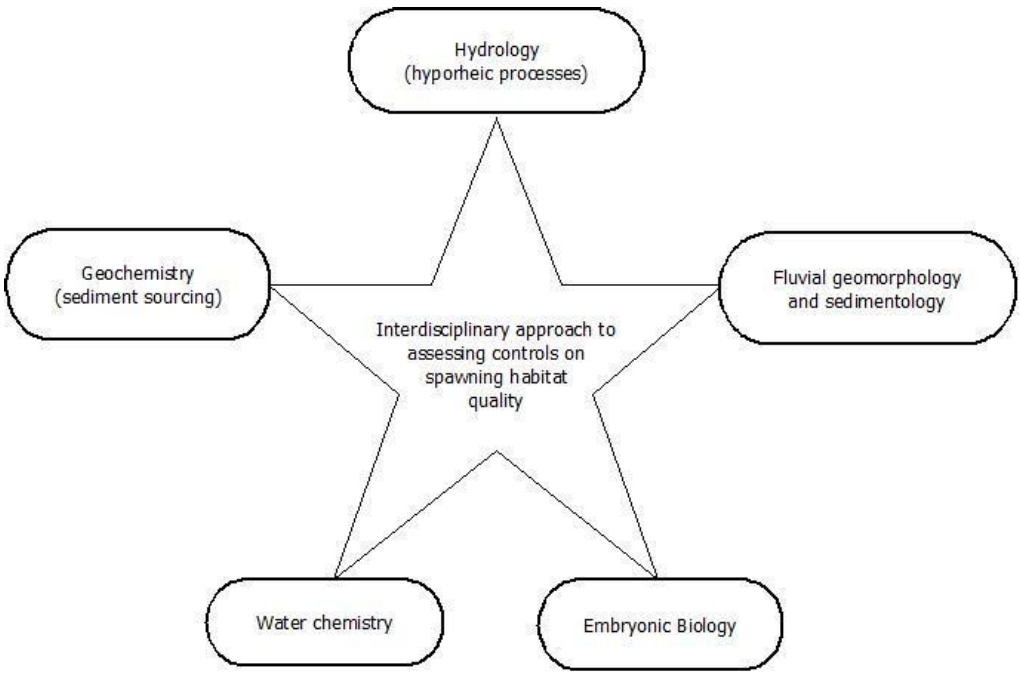


Figure 1.1. Schematic illustrating the thesis research context, highlighting the main disciplines from which the conceptual framework of the main studies are derived.

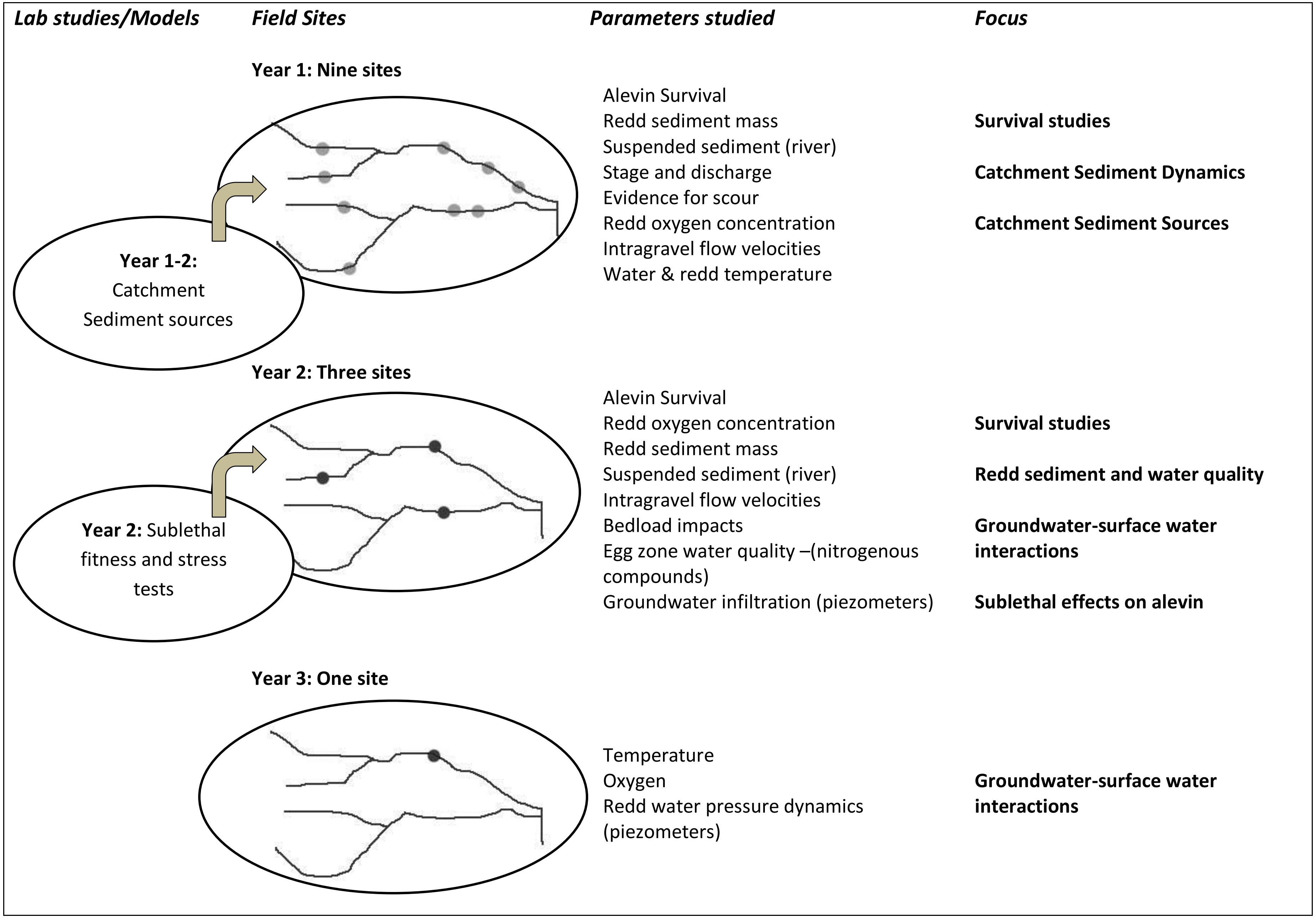


Figure 1.2: Outline of methodology used during the study, highlighting the field sites, the key study focus and main parameters investigated during each year.

A conceptual diagram (figure 1.2 opposite) illustrates the timeline and key foci of the studies carried out during the course of the PhD.

The sediment sourcing study is most related to the sedimentology aspects of the investigations. The other main 'drivers' investigated in the field besides the sedimentary impacts on survival include water quality analysis, evidence for upwelling and physical parameters such as scour and bedload movement. The response variables are survival and sublethal effects-which reflects the most sensitive aspect of the response variables studied.

While the field study served as the initial basis of the project, additional laboratory analyses of field samples and biological tests on alevin were part of the project evolution, and involved collaboration with the Departments of Biosciences and Civil Engineering and Environmental Science at the University of Southampton and use of their facilities to achieve the depth of detail needed to complete the sublethal effects focus.

Geochemical analysis provided the means to carry out a study into the source apportionment of land-derived sediment from varying land-use types and in-channel sources from throughout the catchment. Sediment fingerprinting studies of this kind have found practical application in catchment management in the past decade, but few studies have looked at tracing salmonid redd sediment back to land-derived sources.

1.4 Limitations of the study

The project was initially approached using the dominant controls previously reported in the literature, as the basis for assessing spawning habitat quality. Sediment interactions and oxygen concentrations in relation to intragravel flow over the course of two field seasons thus formed the preliminary research query. Other potential drivers such as groundwater-surface water interactions were then incorporated into the investigation. This is an area which is inherently related to oxygen as dominant driver, but with theoretically different causative factors. Additionally, physical influences such as bedload movement and scour and tests for metabolic waste products (ammonia) were incorporated into the study.

The interdisciplinary approach and multi-level perspective taken, required that certain boundaries be drawn regarding either the degree of depth achieved or the breadth that could be encompassed, within the time and resources limits of the project.

Firstly, certain aspects of the subject that have been recently brought to light in the literature as pertinent have not been addressed and secondly, in some of the studies where an aspect has been dealt with in depth, it is recognized that further study over longer timescales and spatial replications would yield a more consolidated picture of catchment drivers and responses. These limitations are explained further below.

Some studies have recently focussed on the toxicological aspect of the catchments influence on spawning gravel – chiefly in areas of urban influence and the degree of sediment-bound pollutants that may have harmful effects on embryos (Finn 2007, Evans 2009). Although testing for metabolic waste products was carried out, the information available on the water quality of the Lugg in general did not indicate pollutants as a potential factor and so a toxicological testing strategy was not included in the scope of the project.

Other studies have highlighted the importance of the sediment oxygen demand of the intruded sediment and the effects that this may bear on the oxygen supply reaching the developing young (Chevalier and Carson 1984, Mohamed 2003, Greig 2007). Investigation into this aspect of the incubation environment was not possible within the limitations of the project and was ruled out partly due the low organic content of the redd sediment in this catchment in general.

The effect of biofilms have been shown to have both biological and mechanical effects on the oxygen content and hydraulic characteristics of the redd zone (Battin 2000, Petticrew 2003, Koutny et al 2007), and is an area that warrants further study in relevant catchments. However, due to time and budgetary constraints it was not possible to include an analysis in the scope of this project. Additionally it was thought that since seasonal fluctuations in biofilm growth meant their lowest occurrence coincided with the salmonid spawning season in the UK, it may not be a dominant factor influencing the incubation habitat at that time (Claret et al 1998).

The scope of some of the studies could be further verified by wider investigation – some parameters investigated, in particular the high resolution studies which assessed oxygen fluctuations and upwelling groundwater were limited to one or two sites and could benefit from consolidation of evidence both spatially and temporally. Time and budgetary restraints however limited the amount of work that could be achieved within the time span allowed.

1.5 Summary

In summary, the overarching aim of the study is to further understanding of the factors controlling embryo survival and fitness in spawning habitats through promoting an integrative approach to the subject. Previous studies have looked at lone parameter indicators of mortality / habitat degradation, but this study addresses the need for multi-parameter and interdisciplinary studies to be carried out.

The study encompasses multiple environmental parameters - grainsize and sediment accumulation and characteristics – inorganic and organic, as well as groundwater intrusion into egg zone and related this to survival. In the thesis, I address not only survival indices of habitat quality but also look at the problem on a finer resolution scale by addressing potential sublethal effects of environmental influence on the organism.

1.6 Thesis Aims

1. Review current approaches to spawning habitat research in the context of river conservation and management and identify key areas for further research.

2. Determine the sedimentation sources in the study catchment and the key contributors to riverine siltation/sedimentation.

3. Evaluate the key drivers of spawning habitat success in the study catchment and investigate interactions between these drivers.

4. Assess the biological responses to the drivers in terms of survival and sublethal effects, and explain the spatial and temporal variability experienced throughout the catchment.

Chapter 2 Literature Review

2.1 Atlantic Salmon in the UK: A population under pressure

Salmon of all species (Pacific and Atlantic) have experienced a range of pressures since industrial times; exploitation by humans for food being the first major impact encountered (Montgomery, 2003). Other ongoing pressures include pollution of river water, siltation of river beds, channelization and changes in river flow regime, introduction of non-native species and disease. The impact of hatcheries on wild populations has also been cited as a detrimental factor (Whelan 1993, Mongomery, 2003). Climate change has also been implicated as a potential influence on salmonid habitat quality with potential future scenarios exhibiting higher summer water temperatures and lower flows which could reduce the overall area of optimal salmonid habitat available - salmon preferring specific water depths and cooler temperatures. Additionally, under climate change, increased flood severity with associated sediment delivery could affect salmonid habitat in several ways, including scouring out of spawning gravels and washing juveniles from nursery reaches, and through increased sediment delivery from the land surface in susceptible catchments (Walsh & Kilsby 2007, Wilby et al 2006).

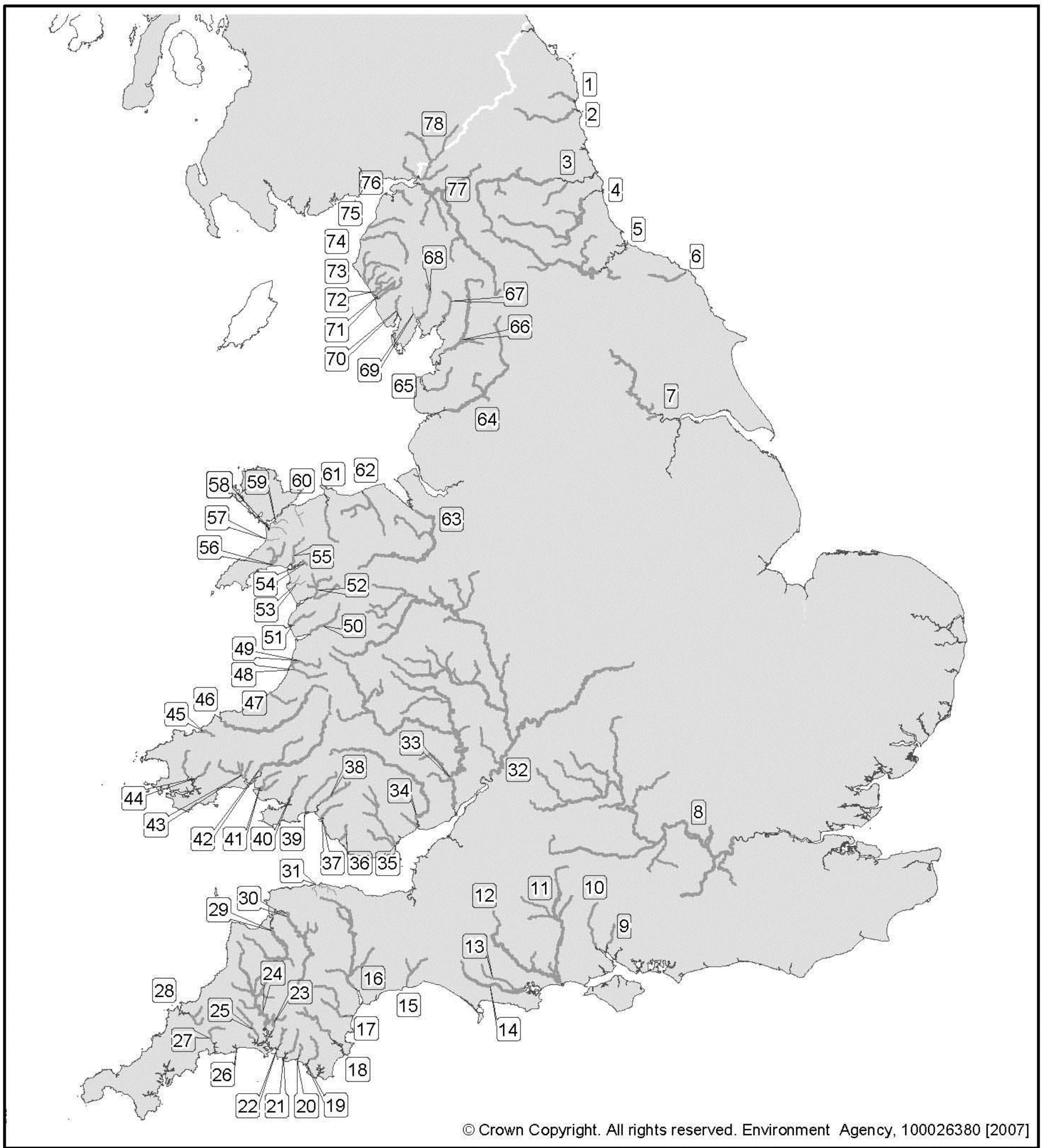
In the oceanic context, it has been suggested that climactic conditions may be contributing to lower population numbers during the adult life stage. A higher average NAO (North Atlantic Oscillation) index since the 1960s has brought warmer waters further north, so effectively reducing the area of potential feeding grounds available to salmon (Friedland 1998, Dickson et al 2000) which are essentially a cold water species. In a European context, two studies of returning 1SW (1 Sea-winter) adult salmon over a 14-year time period indicated that physiological condition had fallen as the Sea Surface Temperature (SST) anomaly in the NE Atlantic has risen, and for each year class, the midwinter (January) SST anomalies they experienced at sea correlated negatively with their final condition on migratory return (Todd et al 2008).

However, it is likely that multiple factors affecting all life stages of the Atlantic salmon (oceanic and freshwater) are responsible for its demise.

Atlantic salmon populations have been lost entirely in the southern part of the former distribution range in the United States, and are currently only found as an endangered status population in the northern State of Maine. On the European continent today, remnant populations are found in a few rivers of France and on the northern coast of Spain, and previously thriving populations on some major European rivers including the Rhine, Elbe and many principal rivers of the Baltic countries are now extinct (WWF 2001).

Marked declines in salmon stocks have also been observed in UK rivers over the past few decades (WWF 2001). The total pre-fishery abundance (PFA) of salmon (the number of salmon alive on 1st Jan of their first sea winter) from English and Welsh rivers is estimated to have declined from over 350,000 in the 1970s to around 150,000 over the past 10 years, despite substantial reductions in exploitation both in national and distant water fisheries. It is thought that, in the same timeframe, spawning escapement (the numbers of mature fish returning to spawn) also suffered a decline, but this decline has been buffered by the reduction in exploitation and increasingly effective catch-and release practices in recent times (NASCO 2008).

Figure 2.1 below shows the UK main river systems with salmon populations and highlights those with Salmon Action Plans – local salmon management schemes under the national salmon management strategy as required by the NASCO Implementation Plan for UK (England & Wales) 2006-11.



1 Aln
2 Coquet*
3 Tyne*
4 Wear*
5 Tees*
6 Esk (Yorkshire)*
7 Ouse
8 Thames*
9 Itchen*$
10 Test*
11 Avon (Hants)*$
12 Stour (Dorset)*
13 Piddle*
14 Frome*
15 Axe*
16 Exe*
17 Teign*$
18 Dart*$
19 Avon (Devon)*
20 Erme*$
21 Yealm*$
22 Plym*
23 Tavy*$
24 Tamar*
25 Lynher*
26 Looe
27 Fowey*
28 Camel*$
29 Torridge*
30 Taw*$
31 Lyn*
32 Severn*
33 Wye*$
34 Usk*$
35 Taff*
36 Ogmore*
37 Afan*
38 Neath
39 Tawe*
40 Loughor*
41 Gwendraeth Fawr
42 Tywi*
43 Taf*
44 E & W Cleddau*
45 Nevern*
46 Teifi*$
47 Aeron
48 Ystwyth
49 Rheidol*
50 Dyfi*
51 Dysynni*
52 Mawddach*$ & Wnion*
53 Artro
54 Dwyryd*
55 Glaslyn*
56 Dwyfach & Dwyfawr*
57 Llyfni
58 Gwyrfai$
59 Seiont*
60 Ogwen*
61 Conwy*
62 Clwyd*
63 Dee*$
64 Ribble*
65 Wyre*
66 Lune*
67 Kent*
68 Leven*
69 Crake*
70 Duddon*
71 Esk (Cumbria)*
72 Irt*
73 Ehen & Calder*$
74 Derwent*$
75 Ellen
76 Wampool
77 Eden*$
78 Esk (Border)*

** River with Salmon Action Plan; $ River designated as a Special Area of Conservation*

Figure 2.1: Map of England and Wales showing the main salmon rivers and denoting those with Salmon Action Plans (*) and those designated as Special Areas of Conservation ($) in which salmon must be maintained or restored to favorable conservation status. (Environment Agency, 2008).

A national assessment of the status of the salmon resource in England and Wales is undertaken annually, using the Pre-fishery Abundance and National Conservation Limit Models (Potter et al 2004).

The Conservation Limits for individual river systems (CL) are set at a stock size below which a further decline in spawner numbers is likely to result in significant reductions in the number of juvenile fish produced in the next generation. Two relationships are used to derive the CL: (i) a stock-recruitment curve – defining, for the freshwater phase of the life cycle, the relationship between the number of eggs produced by spawning adults (stock) and the number of smolts resulting from those eggs (recruits). (ii) a replacement line – converting the smolts emigrating from freshwater to surviving adults (or their egg equivalents) as they enter marine homewaters. This relationship requires an estimate of the survival rate at sea. The model used by the Environment Agency to derive a stock-recruitment curve for each river assumes that juvenile production is at a 'pristine' level for that river type (i.e. is not affected by adverse water quality, degraded physical habitat, etc). Recently, the model has been adjusted to account for the lower observed proportions of MSW and 1SW returns (now 15 and 11% respectively).

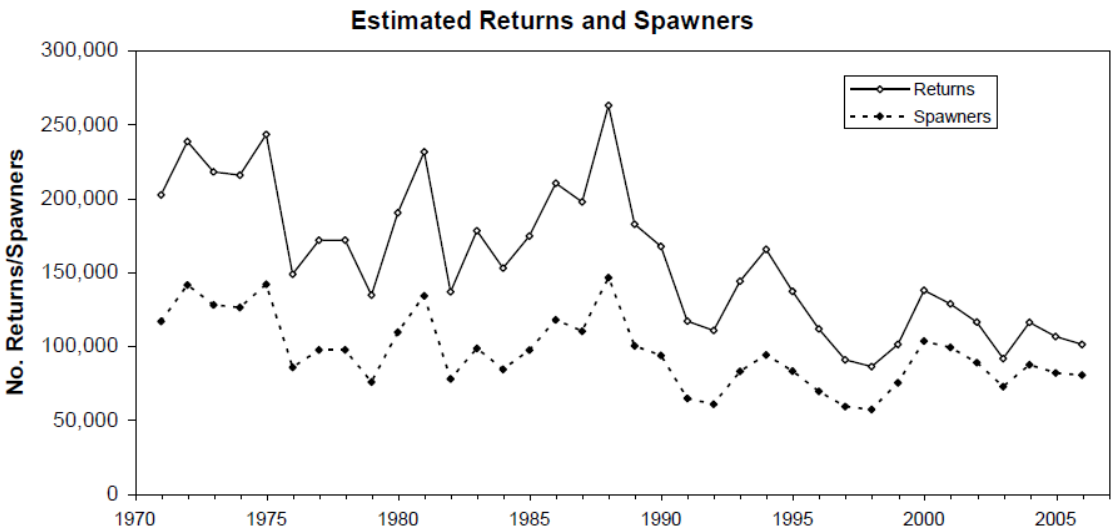


Figure 2.2 Estimated numbers of returns and spawners for rivers in England and Wales 1971 -2006 (Source: NASCO 2008)

In terms of trends in age composition of populations seen, studies of the relative proportions of MSW fish and grilse have been undertaken since 1999 and have shown that despite overall falling trend in fish numbers, the relative proportions of MSW and grilse have remained stable in in most rivers. However, a declining trend in the size of migrating smolt has been observed in recent years (Russel et al 2012). Smolt in UK rivers in recent years tend to be smaller and migrate earlier than before (Clews et al 2010, Russel et al 2012). Over the same period, smolt run-timing across the geographic range has been earlier, at an average rate of almost 3 d per decade. It is thought that climatic influences may be instrumental in these trends with faster growth rates in fry and parr leading to earlier smoltification. However, freshwater factors such as water quality/ contaminants and other factors operating in freshwater also impact smolt quality with adverse consequences for their physiological readiness for life at sea. From a management perspective, where there is limited ability to influence the broad scale factors affecting salmon survival at sea, it is vital that freshwater habitats are managed to both maximize the smolt output and to minimize the impact of factors acting in freshwater that may compromise salmon once they migrate to sea.

In the freshwater habitat, monitoring of parr and fry densities have been undertaken in England and Wales since 2001 as required by ICES and NASCO and the Environment Agency have carried out monitoring programs on salmon rivers to help assess riverine habitat quality. While it is difficult to discern individual population within individual river systems, it is thought that populations will be spatially or even temporally separated – with varying return and spawning times. These data will be used to monitor the year-on-year freshwater spawning environment and as part of the wider monitoring strategy using returns and fisheries data to assess stocks and population dynamics.

Egg deposition requirements have been derived for each of the 64 main salmon rivers in England and Wales, and estimated deposition each year can be compared with these values. Overall, there was a slight decrease in the proportion of stocks meeting their conservation limits over the period 1993 to 2003, but there has been a slight improvement in the years since 2004 (NASCO 2008).

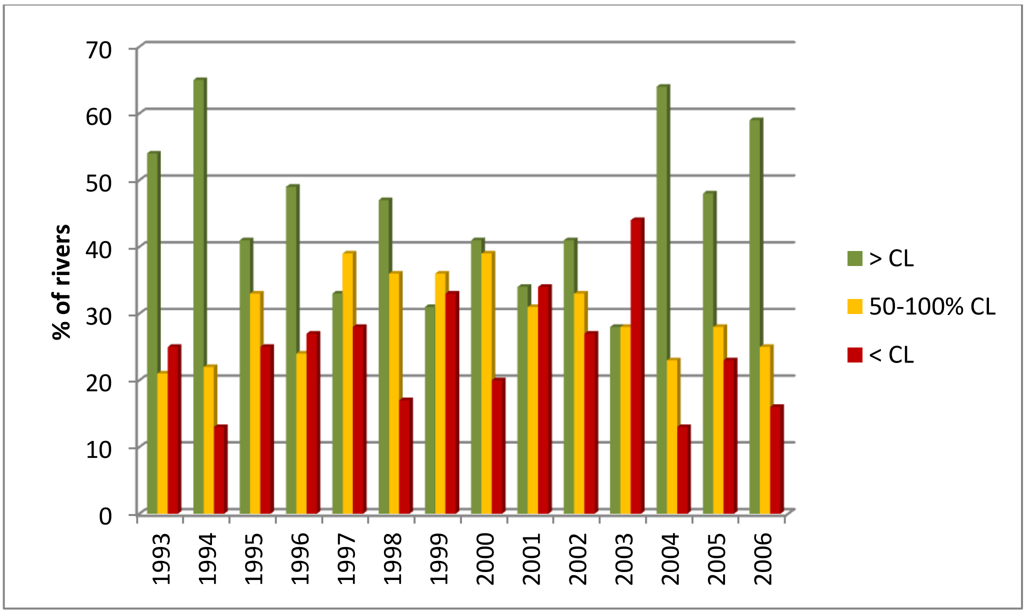


Figure 2.3 Summary of the number and percentage of rivers above their Conservation Limits (CL), between 50% and 100% of the CL, and less than 50% of the CL, from 1993 to 2006.

In the context of the Wye catchment, Environment agency method of salmon stock assessment reports that it remains within the 'at risk' category, which encompasses those rivers with a less than a 5% estimated probability of meeting the catchment management objectives by the 2014 forecast.

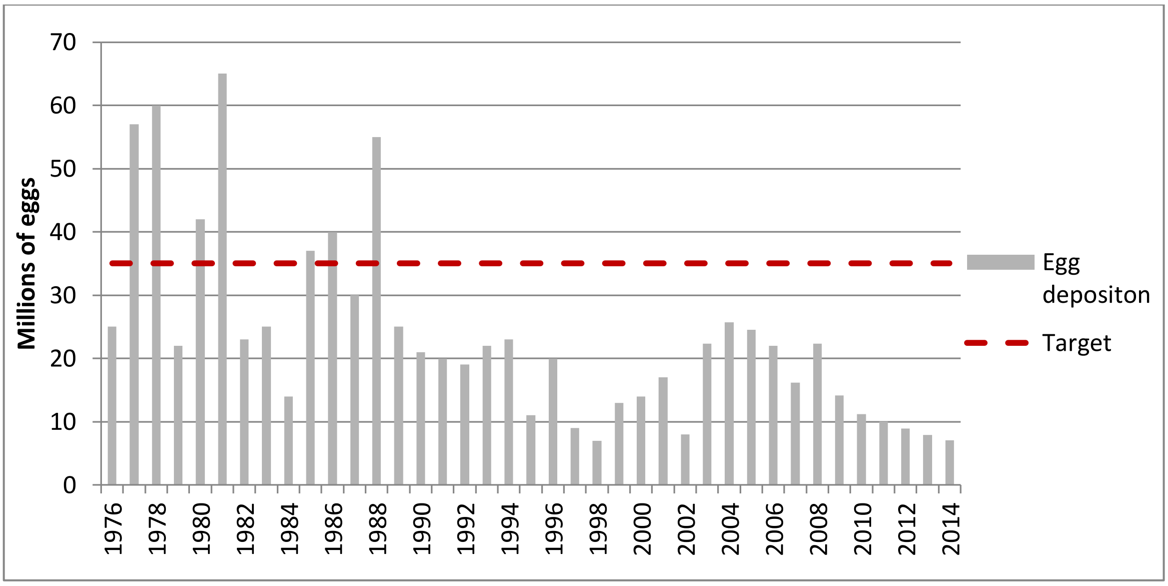


Figure 2.4 Trend in estimated salmon egg deposition on the Wye river catchment since 1976.

The above diagram shows how egg deposition is in long term decline and has fallen below the population conservation limit since the late 1980s. The conservation limit equates to 34.5 million eggs and is partially dependent on the quality and amount of spawning habitat. (E.A. River Wye Salmon Action Plan, 2003, 2011).

In the UK, the major freshwater pressures currently experienced by Atlantic salmon are related to channel construction works, forestry, land-use / drainage and mining.

Channelization and river regulation which cause changes in the natural hydrological regime of a river and low flows (which may occur naturally) can be exacerbated by river regulation or artificial land drainage schemes. Extremely low flows may result in higher summer water temperatures, de-oxygenation and salmon mortality. Regulation of watercourses can also result in a decreased discharge which might otherwise naturally wash gravels of fine sediment and re-oxygenate the interstitial pore water of river bed gravels during spate events. In the absence or reduction of these spate events, low oxygen and increased accumulation of fine sediments may persist (Sear 1993, Meyer 2003).

High flows - a frequent result of both channelization and land-use practices, can cause increased erosion of spawning beds; washing eggs and alevins downstream with resultant high mortality (Crisp 1995). Higher flows have also coarsened stream-bed gravels in some rivers rendering them less suitable to spawning. Additionally, higher flows can result in lateral bank erosion releasing increased amounts of fine sediment which can infiltrate spawning gravels (Hey 1986).

A further hazard to salmon – particularly spawning adults, are weirs and other barriers to migration that can often limit salmon runs to the lower reaches of a river (Lucas and Baras 2001).

A change in hydrological regime may also cause changes in the temperature of the interstitial pore spaces in the gravel bed. The temperature of salmon spawning beds is influenced by the porosity and the hydraulic conductivity of the gravel, so impacts on the porosity - including compaction and long term changes in flow regime, can result in changes of temperature on which developing salmon embryos are highly dependent

(Crisp 1981, Acornley 1999). This then can influence emergence time which may or may not be advantageous to salmon fry - depending on timing and availability of food (Webb and Walling 1993, Crisp 1995).

Riparian land use is an issue that not only affects the hydrographic regime of a river but may entrain increased amounts of sediment from the land. A lack of sufficient buffering vegetation between land and river can result in poor consolidation of soil and premature collapse of banks into the river channel. Again; this increase in sediment flux can result in siltation of salmon spawning areas (Kondolf and Wolman 1993). Additionally, land-use practices of leaving fields fallow during the winter period following harvest can result in large amounts of sediment flowing into river channels via efficient field drainage systems (EA Fisheries Technical Manual 1997).

An additional hazard which directly affects salmon is the use of chemical substances used in agriculture and forestry; in particular, nitrate and phosphate fertilizers which are released from the land during tree-felling in the case of forestry practices and during high rainfall in both cases (Binkley, 1993). Organic sediment influx from the land can increase the biochemical oxygen demand (BOD) in a river through the action of aerobic organisms which require oxygen to break down organic material. Decay of organic matter by bacteria, ammonia oxidation by nitrifiers, algal respiration and flux of oxygen into the sediment all increase oxygen demand (Walker and Snodgrass, 1986). More specifically, sediment oxygen demand (SOD) is comprised of biological sediment oxygen demand (BSOD) and chemical sediment oxygen demand (CSOD). SOD creates oxygen deficits in water bodies by reducing the amount of available oxygen in the water column (Hatcher, 1950, Seiki et al, 1994). SOD can be a significant percentage of the total oxygen uptake in aquatic systems (Caldwell and Doyle 1995, Rounds and Doyle 1997). Measurements of SOD give indications about decomposition rates of settling detritus and regeneration rates of nutrients from the sediment (remineralization) (Seiki et al 1994). SOD rates also serve as proxies for the effects of pollution and other environmental factors on the biological activity of the benthic community. A nutrient loaded system often has an increased demand for oxygen (Natural Resource Council, 2000). This demand on oxygen within the sediment can thus compromise the high oxygen requirement of both spawning salmon (Binkley and Brown 1995) and developing young in the gravel beds (Greig et al 2005).

One of the most worrying pollution impacts on salmonid streams in recent years is the effect of inadequate disposal of the comparatively new synthetic pyrethroid (SP) sheep dips on stream invertebrates. SP sheep dips are many times more toxic than the organophosphate (OP) products previously used. Recent evidence from the Environment Agency suggests that inadequate disposal has seriously affected several thousand kilometres of upland stream in England and Wales, sometimes wiping out invertebrate populations over several kilometres during each incident, leaving little or no food for juvenile salmonids (Millbrand 1997).

Another topic that is of increasing concern is the future impact of climate change on the hydrological regime of UK rivers and the associated impacts on water quality that this may bring. As mentioned above, apart from the direct effects of higher temperatures to which salmonids are intrinsically more sensitive (Taylor and Soloman 1979), there are other secondary factors which are likely to impact upon salmon habitat health with a change in climactic conditions as predicted by the UKCIP02 climate change scenarios 2007 – 2100. Higher temperatures may result in increased eutrophication – potentially affecting dissolved oxygen levels in streams, and more intense rainfall and flooding could result in increased suspended solids, sediment yields and associated contaminant metal fluxes (Moss et al 2010).

A study by Whitehead et al (2008), combined climate models with river catchment models to predict the potential impact of climate change on the water quality of rivers, suggested that in the longer term (c.2100) lower minimum flows may result in less discharge volume to dilute any anthropogenic input to stream waters. The same study predicted that increased storm events could cause more frequent incidences of sewer overflow as well as the potential dislodging of salmonid spawning gravels as discussed above. In a study by Walsh and Kilsby (2007), a SHETRAN model applied to the Eden catchment in North West England predicted longer term peak flows to increase by up to 1.5%, but that a greater impact due to decreasing summer flows was predicted, with current Q95 flows becoming the predicted Q85 flows. The same model predicted that areas hosting suitable flow depths for catchment spawning activity would be reduced by 6%.

Clew et al (2010) looked at climate mediated effects on juveniles on the river Wye catchment and found that altered summer flows coupled with increased summer temperatures were likely to have highest impact on recruitment of parr and fry; they advocate increased stream shading and catchment abstraction management as potential mitigation measures.

2.2 Life Cycle and Evolution

The life cycle of the Atlantic salmon is split into a freshwater embryonic to juvenile stage, followed by a marine adult stage, through which the cycle is closed when the mature fish return to their native rivers to spawn. The marine adult stage is the main feeding phase where rapid growth is achieved. The term 'anadromous' refers to this dichotomy of environments in the salmons' lifecycle (Mills 1989).

After emergence, when the fry emerge from the spawning gravels to feed, they develop into juvenile 'parr' and feed on macro-invertebrates such as stonefly and mayfly nymphs. Once parr have attained a length of approximately 10cm, they begin to migrate downstream and go through series of physiological changes including body shape and colour (they attain the silver colouring typical of adult salmon), osmoregulatory functions (salt tolerance), energy storage, drinking and urination patterns, and behavior (McCormack et al 1987, 1998, Quinn, 2005). At this stage, they are referred to as 'smolts' - a transitional phase during which they prepare for life in a marine environment. In British rivers, this time to 'smolting' varies between 1 and 5 years before moving out to sea (Mills, 1989). Once at sea, they travel to feeding grounds in the North Atlantic; near the Faroe Islands, the Norwegian Sea and the waters off west Greenland consuming small crustaceans and fish thereby rapidly increasing in body mass (Mills 2000). The total life-cycle ranges from four to eight years. (WWF 2001).

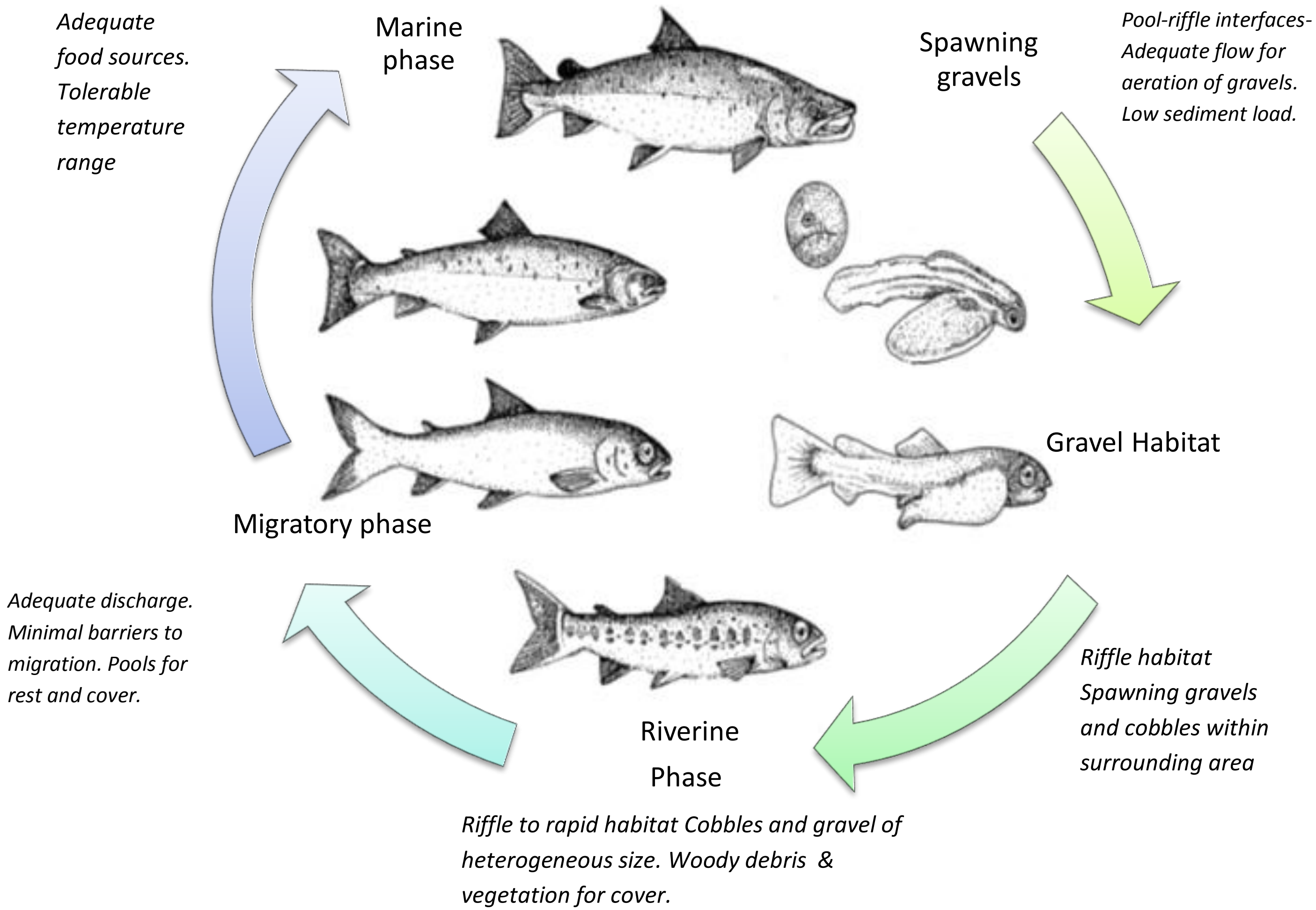


Figure 2.5: The Life cycle of the Atlantic Salmon with habitat preferences for each life stage.

The Atlantic salmon *(Salmo salar)* is an anadromous species which evolved from a smelt-like ancestor common to trout, Pacific salmon, char, grayling and whitefish –all of which branched off at earlier points along an evolutionary line that can be traced back approximately 100 million years. *Salmo salar* has existed as a distinct species for around 10 million years. (Nelson 1984)

Genetic isolation of European from American Atlantic salmon around 600,000 years ago resulted in sub-species status: *Salmo salar europaeus and Salmo salar americanus.*

During the ice-age of 100,000 -70,000 ya, the European sub-species split into two distinct strains: the Celtic strain in the south-west, which survived the ice-age in refugia off the Iberian peninsula, and the Boreal strain which survived in an ice-free lake that is now the North Sea basin. (Greenhalgh 2005)

Since the end of the last ice-age, the population of the Boreal strain living in the Baltic Sea became isolated and then genetically distinct. Recent genetic fingerprinting has indicated some interbreeding between the Celtic and Boreal strains in northern France, eastern Britain and Fenno-Scandia, while the only European example of interbreeding between European and American Atlantic salmon is found in Russia's Kola Peninsula (Verspoor et al 2007).

The Atlantic salmons' navigational and orienteering abilities have contributed to the genetic isolation and evolution of populations, as they will preferentially return to their native rivers to spawn (Quinn 1980, Youngson 1997).

It has been proposed that the homing instinct of Salmon has resulted in genetic isolation between river systems and so to local adaptations to those specific systems, such as variances in spawning times, incubation requirements, and freshwater residence times. (Bjorn and Reiser 1991). This variation between river catchments has been thought to maximize the chances of fry survival in the specific river catchments (Wilson 1997) by influencing the timing of emergence with favourable flow conditions, temperature and food supply (Jenson et al 1991).

Figure 2.6 below shows the results of a study by Verspoor et al (2005) which looked at the genetic diversity and isolation of European populations of *Salmo salar.* They found that, based on examination of the frequency of 12 polymorphic alleles, there was significant genetic isolation of most of these geographically separate populations. It is generally assumed that genetic drift is the main causal factor at work in these populations (Jordan et al 1994), but is recognized that not all detectable variation is due simply to drift and selection pressures may also be at work (Verspoor et al 2007).

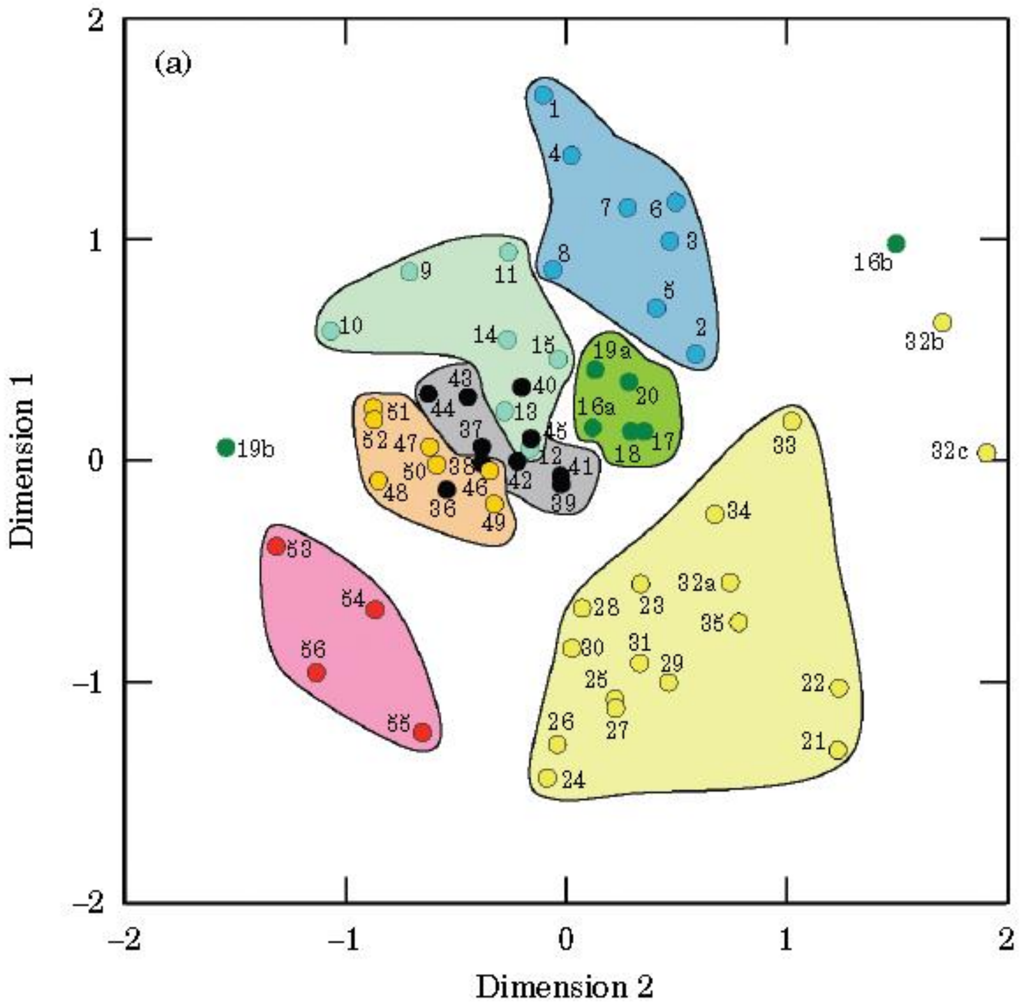


Figure 2.6 : An MDS (Multi-dimensional scaling) plot for European river samples based on genetic distance (From Verspoor et al., 2005). Lines enclose regional geographic groups: ***Iceland/Greenland*** , ***Northern Russia/Norway*** , ***Baltic*** , ***Southern Norway/Western Sweden*** , ***Northern British Isles*** , ***Southern France/Spain*** , ***Southern British Isles/Northern France).***

A U.K. - based study on genetic variation in populations of salmon in the rivers Teifi, Usk and Wye in Wales was carried out by O'Connell et al (1995) using mitochondrial DNA and allozyme analysis. They concluded that there was a significant degree of genetic isolation between salmon populations, both within and between catchments, with only a small proportion of genetic migrants or strays (approximately 3%).

In another study, a high degree of accurate homing was reported for approximately 50% of adults entering the Girnock Burn in Scotland on the basis of tagging experiments carried out in 1986–1988 (Youngson et al 1994).

In the U.K., spawning generally tends to occur during November/December in northern rivers and January/February in southern rivers since embryonic development is heavily influenced by temperature (Crisp 2000).

However, whether all observed inter-catchment variation is due to local adaptations based purely on genetic differences/drift or to phenotypic differences with an element of plasticity, remains uncertain.

Nevertheless, because many salmon home with high precision, they are at least potentially capable of restricting gene flow between breeding locations to the low levels that might foster population differentiation (Youngson et al 2003).

Behavioural, morphological and ecological variations have been observed between populations within the U.K. and some of the characteristics which were points of interest of various studies of are cited in Table 2.1 below.

Characteristic	Reference
Embryo development	Berg and Moen (1999)
Hatching success	Donaghy and Verspoor (1997)
Juvenile behaviour	Hensleigh and Hendry (1998)
Juvenile performance	McGinnity et al. (1997), Palm and Ryman (1999), Rikardsen and Elliott (2000)
Growth capacity	Conover (1990), Nicieza et al. (1994), McGinnity et al. (1997)
Body morphology	Riddell et al. (1981), Hard et al. (1999)
Habitat preference	Hesthagen et al. (1995)
Timing of smolt migration	Orciari and Leonard (1996)
Migratory behaviour	Jonsson (1982), Svardson and Fagerstrom (1982), Jonsson et al. (1994)
Age at sexual maturity	Hutchings and Jones (1998)
Homing behaviour	Bams (1976), McIsaac and Quinn (1988), Candy and Beacham (2000)
Seasonal run-timing	Saunders (1967), Hansen and Jonsson (1991), Laughton and Smith (1992)
Adult size	Schaffer and Elson (1975), Jonsson et al. (1991)
Timing of spawning	Heggberget (1988), Webb and McLay (1996), Hendry et al. (1999), Sakamoto et al. (1999)
Resistance to the parasite, *Gyrodactylus salaris*	Bakke et al. (1990), Bakke (1991)

Table 2.1: (From Youngson et al 2003) Performance characteristics reported to vary among populations or larger geographical groupings of salmonids.

Some studies found that variation within a river catchment - both ecologically and genetic, may be due to several different genotypes of ‘equal fitness’ (Youngson et al 2003), i.e. genetic polymorphisms for specific traits within the same population. The population within a single catchment would then consist of a number of ‘options of equal strength’: individuals with differing genotypes for certain traits but similar levels of average fitness.

However, some studies have found that the genetic component is supported by evidence of a reduction in fitness (i.e. outbreeding depression) when stocks are transferred from native rivers to other salmonid rivers and found that they were out-competed by the native populations there (Einum and Fleming 1997, Mc Ginnity et al 2003).

Therefore, when considering management of salmonid rivers in the UK, a best practice of using morphological, ecological, physiological and behavioural features of populations, against a background knowledge of patterns of explicitly genetic variation may be the optimum approach.

2.2.1 Geographic distribution and temperature range

European geographical distribution of the Atlantic Salmon ranges from Portugal's river Douro in the south (41°N), to the river Tana on Norway's northern cape - eastwards towards the Pekhora and Kara rivers in Russia's Barents sea (70°N, 83°E) and west to Iceland's Straumfjarðará river (66°N). Previous wild population existed in the Rhine and Elbe rivers which drain to the North Sea but are now exinct. The species is also extinct or endangered in many major rivers in France, Spain and Portugal (Verspoor et al 2007). River temperature ranges for Atlantic salmon runs range from 0°C to 27.8°C (Elliot 1991, Crisp 1996). This temperature range refers to adult salmon tolerances, but the lethal limit for developing embryos and alevins is thought to be within a smaller range - typically between 2° and 12°C. (Gunnes 1979, Takle et al 2005). At temperatures between 0°C and 2°C development is arrested and this state can be tolerated for only a short period (Danner 2008).

2.3 Salmon Freshwater Habitat Preferences

The physical habitat requirements of Atlantic salmon vary according to the life-stage concerned. River typology is relevant to salmon habitat preference in that a river must contain sufficient areas of suitable habitat relevant to each life stage of the salmon during its freshwater residence period.

In terms of scales of resolution used to identify habitat and fluvial influences on salmon, table 2.2 below defines the various levels that define a river and the features affecting salmon life stages found within.

Waterways defined by Topography (Highland/ Lowland)
↓
Waterways defined by Lithology (Underlying geology – chalk, limestone, sandstone, clays)
↓
Channel characteristics – (Morphology and Flow type)
↓
Meso-Habitats / Channel Features (Pools, Riffles, Meanders, Rapids, Rock-steps, Waterfalls)

Table 2.2. Scales of resolution used to identify fluvial influences on Salmon. (From Environment Agency R&D Technical Report W44)

As well as anthropogenic influences, the above habitat and fluvial influences will also affect water chemistry and oxygenation levels of a stream, to which salmon are extremely sensitive.

The adult feeding stage is marine and holds unique metabolic requirements and as such is set apart. We will address here the habitat preferences of the freshwater stages of the salmon life-cycle – namely the returning mature adults, the juvenile stage and the spawning and incubation stages.

Regarding the adult freshwater stage, the main factors influencing their upstream migration to spawning grounds will be barriers to migration, adequate areas of holding pools and cover for rest periods, flow velocity/ stream discharge, temperature and water quality.

The presence of barriers to migration such as waterfalls, debris dams and man-made structures such as weirs can prove to be a challenge during the upstream journey of adult salmon. Reiser and Peacock (1985) mention the leaping ability of steelhead which can reach up to 3 vertical metres. A study by Eiserman (1975) showed that the ideal ratio of fall height to pool depth as 1:1.25. This ensures that the standing wave created by the falling water is at a proximal distance to the obstacle and is useful as a launching area with extra upward thrust for salmonids.

Cover for salmon waiting to migrate upstream is of importance to migrating salmon as protection from predators and shade from bright sunlight (Crisp 1996). Overhanging vegetation, undercut banks, tree roots, woody debris, rocks, deep pools and turbulence can all serve this function. Bjorn and Reiser (1991) suggest that proximity to cover may play a part in spawning location choice. The availability of deep holding pools is also important (Kennedy 1984), since the fish spend a good proportion of their time during the migration resting in these pools before continuing their onward journey, and may spend up to 3 months in any given pool (Webb 1989). The proximity of spawning grounds to pools may also be important. This aspect was reported in a study where the carrying capacity of the holding areas was increased if the spawning areas were less than 800m away (Moreau and Moring 1993 from Bardonnet and Bagliniere 2000).

Stream discharge was a delaying factor in the migration of salmonids in studies by Clarke et al (1991) where low flows delayed entry into a river system. Hendry et al (2003) reported an approach by the former Lancashire River Authority where studies on fish movement derived from counters were used to conclude that upstream migration of salmon commenced when the flow reached $0.084m^3\ s^{-1}\ m^{-1}$ of channel width, peaking at a flow of $0.20m^3\ s^{-1}\ m^{-1}$ width. This data however was derived from spate rivers in North West England, and may not be applicable to other river types.

Water temperatures which were either higher or lower than seasonal norms have been seen to affect migration patterns. In studies on Pacific Salmon, delays in migration were observed in response to warm stream temperatures (Major and Mighell 1966, Hallock et al 1970; cited in Bjornn and Reiser 1991) and for Atlantic Salmon similar observations were made by Alabaster (1990). The rate of upstream migration of Atlantic salmon was seen to be impaired by warmer temperatures in a study by Gowans et al (1999) and Pacific anadromous trout were reported as waiting for tributaries to warm up before entering their spawning grounds (Rheingold 1968 from Bjornn and Reiser 1991).

In terms of water quality, the level of turbidity in rivers has been found to affect whether salmon will delay migrating up a river with high silt loads (Bjornn and Reiser 1991) and low dissolved oxygen levels may elicit avoidance reactions (Whitmor et al 1960) and halt migration. Migration was observed to cease when DO fell below 4.5mgl (Hallock et al 1970).

During the nursery life stage, Atlantic salmon fry emerge onto substrate that also corresponds to their needs as young juveniles, and generally settle on gravel/ cobble substrate relatively close to the redds from which they emerge (Bardonnet and Bagliniere 2000). In a study by Beall (1994) the majority of the fry population settled at a distance of less than 200m (usually downstream) from the redd. A second phase of dispersal may then occur approximately 1 month after emergence (Gustafson-Greenwood and Moring 1990). Young-of-year (YOY) salmon tend to settle on these riffles near the spawning site but PYOY (Post young-of-year) have higher water velocity preferences and can be found in rapids as well. Juveniles may also be found in runs but rarely in pools (Caron and Talbot 1993).

YOY are generally found in water depths of around 20cm whereas PYOY are found in deeper water – up to 50cm (E.A. R&D Technical report 2003). These respective habitats correspond to characteristic velocities – or 'nose velocities' with a range of 10-60cm s^{-1} with YOY being found at the lower range of these velocities (Heggenes 1990, Tremblay et al 1993). Substrate will provide cover for the juvenile stages and usage by YOY of larger cobbles and boulders as cover was seen in one study to be 45% during daytime surveys and for PYOY to be only 10% (Gries and Juanes 1998).

Nocturnal activity tends to be more exploratory with a trend for upwards movement in the water column, especially during the winter months. Seasonal variation is also a feature of habitat usage with juveniles occupying slower-flowing reaches in winter months than summer months (Metcalfe et al 1997) and a higher proportion of diurnal time spent sheltering in the substratum as temperatures declined (Heggenes 1993, Mitchel et al 1998). It is thought that snout velocity plays a part in choice of habitat during the colder months with velocities in the substratum nearing 0 ms $^{-1}$ (Cunjak 1988). A study by Rimmer (1984) found that all ages of juvenile using snout velocities of <10ms $^{-1}$ during the autumn.

Salmon have evolved a strategy to ensure improved survival of their progeny by means of burial of their fertilized eggs in deep gravel nests (redds) in the river bed. Within the redds, they are protected from stream flow, predators and light. However embryo survival depends on oxygen availability within the redd and the corresponding substrate size that can help achieve optimum survival. These topics are discussed in more detail in the following sections.

2.3.1 Spawning Habitat Characteristics

The Salmon spawning season is characterized by female competition for suitable gravel matrices in which to build their nests, and by male competition for females (Fleming and Reynolds 2004).

The female or hen salmon constructs the egg nest or 'redd' from the gravel substrate in the natal river to which she has returned. To create the redd, she turns on her side and through a series of vertical paddling motions with her tail, creates a hollow in the gravel bed (Chambers et al 1954, Jones and Ball 1954). Turbulence, as well a direct physical contact with the substrate carries the smaller fractions downstream and out of the redd area and the larger fractions adjacent to the hollow accumulate in a mound called the 'tailspin' (Jones and Ball 1954).

The female salmon will lay her eggs in the gravel pocket she has excavated which the male will fertilize simultaneously. The female salmon will 'infill' the egg pocket by shifting gravels from just upstream of the redd causing them to be deposited onto the fertilized eggs. She then moves upstream to construct a further redd via the same process. A hen salmon will typically create between 2 to 4 separate redds during a spawning season and the number of redds built per female can range from 1 to 9 (Jonsson and Fleming 1993, Lura et al 1993, Barlaup et al 1994).

The location where salmon preferentially spawn has been identified as usually occurring on pool-riffle interfaces near the top of the riffle (Jones 1959, Mills 1989). This location is thought to benefit from downwelling along a hydraulic gradient where stream water is forced into the convex redd gravels, thereby improving intragravel flow velocity and optimizing oxygen transport within the redd (Cooper 1965, Chapman 1988, Crisp and Carling 1989, Kondolf 2000).

According to Crisp (2000) and Armstrong et al (2003) the present evidence points to depth, water velocity and substrate size, as the most important instream variables in determining the spawning habitat selection of salmonids.

It seems also that gravel size is physically related to water depth and velocity, so determining which of these critieria is the most important in spawning site selection is difficult (Quinn 2005).

Investigations into preferred flow velocities of spawning salmon have found a range of velocities at spawning sites that vary from site to site. Moir et al (2004) from their investigations at two Scottish upland streams found spawning site velocities of 0.5-4.5 times the median discharge at one site but only 0.8 to 1 times the median discharge at another site.

In one study, lower water velocity was limited to the range 15–20 cm s−1 below which salmonids of all sizes preferred not to spawn. The upper velocity limit was correlated to fish size (Crisp and Carling 1989). This upper velocity was estimated by Crisp (1993) to be approximately two female body lengths per second.

In terms of water depth over spawning gravels, a minimum depth of the individual fishes' body depth has been proposed (Armstrong et al 2003) and had been upheld through observation. However there has been variation in the maximum depth of spawning gravels observed with major differences between rivers – up to 10 metres for some Pacific salmon (Haggerty 2007) and varying between sites in studies undertaken by Moir et al (2002). It has been suggested that spawning site choice involves an interactive quality of both velocity and depth and that this may be more accurately explained by the Froude no. which is a function of both velocity and depth such that:

$$v/(gd)0.5 \ = \text{mean Froude number} \qquad (1)$$

where *v* is flow velocity,

d is flow depth and

g = gravitational acceleration – (9.81 m s–1 s–1)

This measure has been shown to correlate more effectively with spawning site choice but it has also been observed that Froude number correlates closely with gravel-size (Moir et al 2006), so more attention should perhaps be given to geomorphologic influences in spawning site choice.

In terms of substrate size, according to Kondolf and Wolman (1993), larger fish can construct redds in coarser substrate and in more powerful currents than smaller fish, so there may be a spectral range of suitable substrate depending on fish size.

A review paper by Louhi et al collates substrate size data from several studies to form a generalized suitability curve for substrate sizes used by Atlantic Salmon, as shown below.

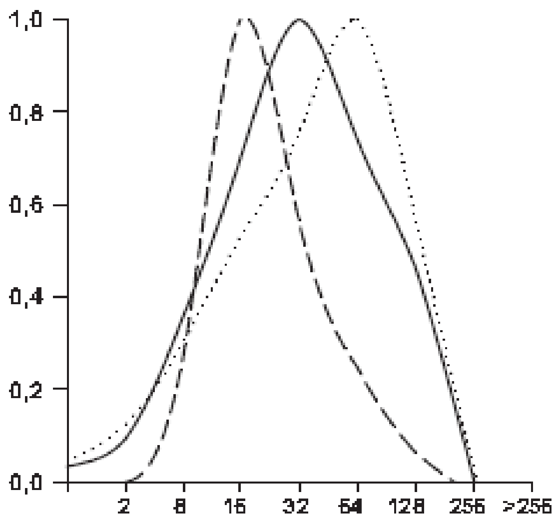


Figure 2.7 Generalized suitability curve for substratum composition in spawning sites of Atlantic Salmon: X-axis: Substrate size values in mm; Y-axis: proportion of total substrate at X-values. (———, data combined; – – –, river with discharge < $10m^3s^{-1}$; ····· , river with discharge > $10m^3s^{-1}$) – from Louhi et al. 2008.

The main effect of redd building in a spawning reach is the ejection of fine sediments and the average increase in gravel particle size due to the hen salmon's activity (Chapman 1988, Kondolf et al 1993).This change in particle size is generally thought to help improve intragravel flow and aid oxygenation of the redd during incubation of the eggs.

The gravel substrate from which the female salmon builds her redd and lays her eggs is the environment in which the young will develop over the next few months – a period that is variable with stream temperature. The conditions that the eggs and larvae encounter there will influence their health and development over this vulnerable period; of the entire salmonid life cycle, survival is generally lowest during the intragravel period (MacKenzie and Moring 1988).

2.4 Morphological influences on Hydrology

At a given point in time, river discharge interacts with the channel to determine where, within the catchment, suitable hydraulic conditions for spawning occur (Gibbins et al 2008).

It has been found that the topography of the redd form will influence the flow of water over and within the redd itself. Localized pressure differentials caused by the redd bed-form will affect flow patterns such that the increase in height caused by the redd structure will locally create hydraulic head upstream of the redd and a 'downwelling' current into the redd gravels (Chapman 1988, Thibodeaux and Boyle 1987, Carling 1999). The downstream side of the redd will be in an effective hydraulic shadow, and so an upwelling current will occur as flow is directed towards the lower pressure water at the stream surface.

Dye-tracing laboratory techniques have shown this basic (2-dimensional) 'pumping flow' pattern to be downwelling on the upstream side of the redd and upwelling on the downstream side (Cooper 1965, Carling 2006).

This is illustrated in figure 2.8 below where dye tube flow paths are seen to travel in an arc-like shape downward into the redd and upwards to emerge on the other side.

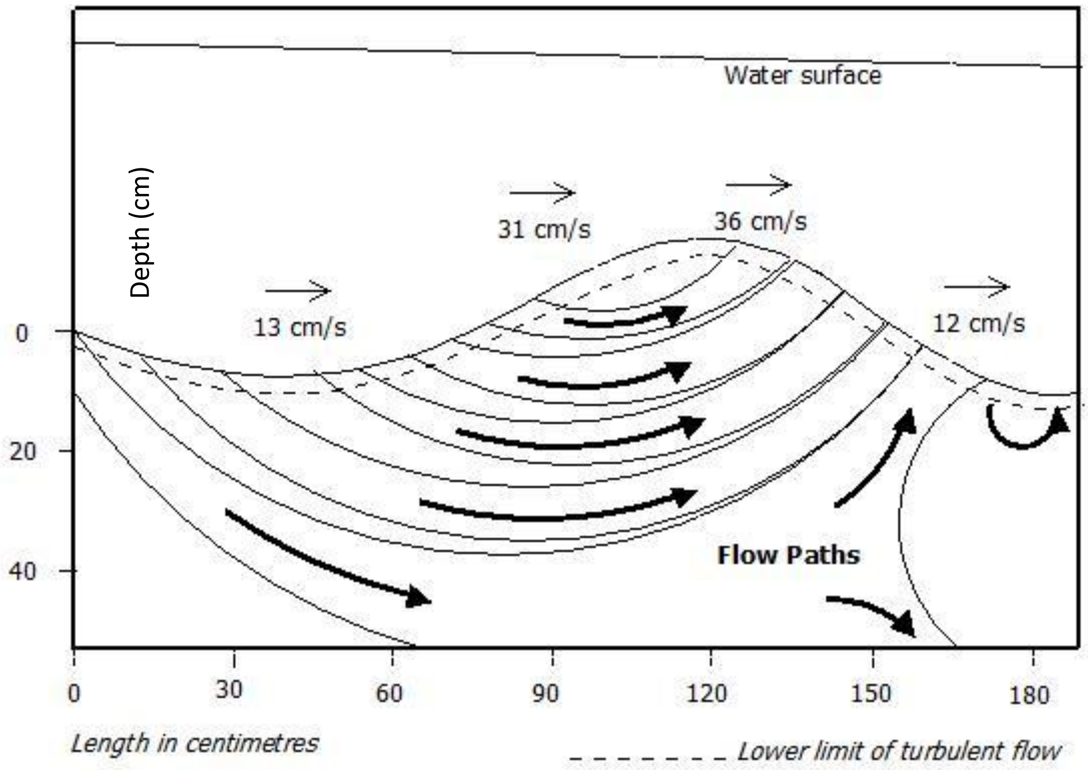


Figure 2.8 Illustration of flow paths within a redd structure (adapted from Cooper, 1965, Taylor 2002). Stream velocities are seen to vary close to the gravel surface with lows occurring the topographical troughs and highs towards the mound of the redd.

Comparison studies of pool-riffle channels with and without redds, show that the act of redd formation changes the river hydraulics and the local areas of upwelling and downwelling, thereby enhancing the flow velocity and dissolved oxygen content through the redd egg pocket. This could potentially enhance the survival of salmonids incubating within the streambed gravels (Tonina 2005).

At a similar same scale as pumping flow, but in the absence of a bedform, redd-scale flow can also occur. This is driven by the downstream hydraulic head drop associated with the drop in water surface over the redd cell as shown below.

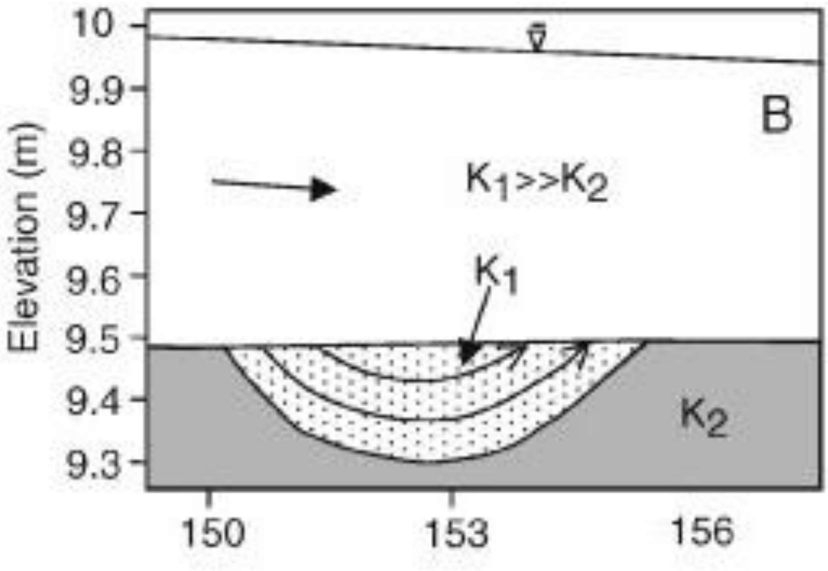


Figure 2.7. Redd-scale flow due to drop in water depth over downstream side of redd. (From Savant et al. 1987)

This redd-scale flow accompanied by the pumping-induced flow may be a significant factor when permeability caused by flushing of fines during the salmonids construction of the redd is much increased in comparison to surrounding gravel substrate. Redd-scale flow may dominate when the redd substrate is much more permeable than the surrounding, undisturbed riffle gravels. Both instances would follow Darcy's law which states that the rate of groundwater flow (or Darcy velocity, *V)* is the product of the permeability (or hydraulic conductivity, *K)* and the hydraulic gradient *dh/dl.*

Because water is forced into the redd gravels, the flow velocities within the egg zone and tail of the redd are increased. These can be up to twice as fast as interstitial flow elsewhere in the riverbed (Sear et al 2005).

At larger spatial scales, interstitial flow at the riffle scale occurs when stream water flows into riffle gravel at the tail of the upstream pool and emerges at the head of the downstream pool. (Zimmerman and Lapointe 2005). Riffle-scale flow is thus driven by the concentrated drop in water surface level across riffles, from pool to pool, and is significant except during the highest flow stages.

At an even larger spatial scale; intragravel flow through redds can also be driven by local groundwater input as discharge out of the stream bottom. Flow at this scale is driven by differences in head (elevation and pressure potentials) between the water under valley sides and stream bed; these differences are affected by infiltration, runoff and evaporation patterns, depth to bedrock, hydraulic conductivities and consequent variations in the storage of groundwater across the whole valley (Harvey et al 1996, Malcolm et al 2003).

In a study by Tonina (2005) the 3- dimensional flow through the redd gravel matrix was modelled in an attempt to look at the lateral extent of flow within this hyporheic zone, which was seen to spread widely and more extensively than in the vertical sense.

The downwelling current forces stream water into the hyporheic zone - a horizontally inclined zone where a variable amount of mixing of surface water and groundwater occur along a vertical geochemical concentration gradient. Downwelling fluxes have multiple effects: they bring high concentrations of dissolved oxygen and nutrients into the sediment (Findlay et al 1993, Triska et al 1993), while the sediment and benthic species living in the streambed filter the water, reducing the biological and chemical loads (BOD, COD, P, C, NOx, etc.)(Triska et al 1993). In contrast, upwelling flow brings reduced elements and transformed solutes from the hyporheic environment into the river (Nagaoka and Ohgaki 1990, Triska et al 1993). Upwelling fluxes also remove waste products of the hyporheic fauna from the sediment and bring filtered water to the river (Tonina and Buffington 2007). Hyporheic flow can also be a source of nutrients and algal cells to streams that are recovering after flood events (Valett et al 1994). Riparian vegetation is responsive to patterns of hyporheic exchange and nutrient-rich upwelling areas (Harner and Stanford 2003, NRC 2002). Riparian processes can in turn have an effect on these flows – such as upwelling areas caused by tree roots which draw in hyporheic water (Duke et al 2007), and the chemistry of hyporheic water affected during seasonal flooding onto riparian zones (Tonina and Buffington 2006).

2.5 Hydrological and Hyporheic influences on spawning gravels

Salmonid spawning gravels consist mainly of cobble and pebble–sized clasts that form an open framework which supports the weight of the deposit and also encloses areas of pore space. Some of this space is occupied by smaller particles; the rest being filled by hyporheic water which flows through the deposit at a rate dependent on the permeability of the gravel matrix. This permeability together with the local hydraulic pressure gradient, determines the rate of hyporheic flow. Permeability can vary spatially and temporally especially over the vertical plane (Peterson and Quinn 1996). The quality of water within the hyporheic zone is of increasing interest and may be described as '*the saturated interstitial area beneath and adjacent the streambed that comprises some proportion of channel water or that has been altered by channel water'* (White 1993).

Equations predicting egg to alevin survival as a function of gravel size have been developed (e.g. Tappel and Bjorn 1983) and some rules of thumb regarding sediment size have also been employed - such as the Fredle index gravel descriptor developed by Lotspeich and Everest (1981). Other parameters such as % fine sediment below an arbitrary threshold, D50, D16/D10, and Geometric mean have been used as prognostic indices of survival (Koski 1966, Phillips 1975, Petersen and Metcalfe 1981, Tappel and Bjorn 1983, Platts et al 1983, Young et al 1991). However, other studies have shown that while sedimentary character and fine sediment may be instrumental in defining the incubation success, it is the secondary effects produced due to the presence of the sediment, which may impact survival more directly (Chapman 1988, Chevalier and

Murphy 1985, Greig et al 2005). More recent studies testing the transferability of these indices to a wider context i.e. applying gravelometric indices and survival data from other catchments, has proved inconsistent. For example, In their study on survival to emergence of natural redds, Peterson and Quinn (1996) did not find a significant correlation between dissolved oxygen in egg pockets of chum salmon and the quantity of fines in freeze cores. Similarly, Ingendahl (2001) found a significant correlation between a series of sediment parameters investigated (Dg, D50, Fredle index) but no relation of these to dissolved oxygen levels within the redds.

The impact of fine sediment particles on intragravel flow has been demonstrated to depend on the size of the framework of the gravel bed matrix. Typically, the smaller the infiltrated sediment size the more negative its effect on permeability and intragravel flow. (Kondolf 2000, Julien and Bergeron 2006, Greig et al 2007).

Permeability varies inversely with the amount of fine sediment, and some studies have suggested that percentage of sediment of less than 1 mm diameter should compose less than 10 % of the gravel bed substrate to be suitable for incubation purposes (Crisp 1996, Kondolf 2000, Milan 2000). Particles between 1 and 10 mm (sand-sized) have also been proposed as deleterious through a different mechanism; it is thought that these particle may form a ‘sand seal’ near the surface (gravel bed - stream interface) and may thus hinder the movement of alevins through the gravel as they seek to emerge (e.g., Bjorn 1969). In their review of salmon spawning habitat criteria, using depth velocity and substrate size parameters only, Louhi et al (2008) compiled a table of studies reporting ‘critical amounts’ of sediment below an arbitrary size threshold which affected survival negatively. This is shown in table 2.3 below.

Table III. The particle size (mm) and proportion (%) of critical sediments in substrata of salmonid spawning sites

Critical sediment (mm)	Critical sediment (%)	Species	Reference
<2.2	n/a	*S. salar*	Peterson (1978)
<2.0	>10	*S. trutta*	Ottaway *et al.* (1981)
<9.2	n/a	*S. trutta*	Witzel and MacCrimmon (1983b)
<4.8	n/a	*S. trutta*	Olsson and Persson (1986)
<15.0	n/a	*S. trutta*	Rubin and Glimsäter (1996)
<1.0	>15	Salmo sp.	Crisp (1996)
<15.0	n/a	*S. trutta*	Rubin (1998)
<1.0	>10	*S. salar*	O'Connor and Andrew (1998)
<10.0	n/a	Salmo sp.	Kondolf (2000)
<1.0	>14	*S. trutta*	Milan *et al.* (2000)
<2.0	>23	Salmo sp.	Soulsby *et al.* (2001)
<0.063	>1.5	*S. salar*	Lapointe *et al.* (2004)
<0.125	>0.2	*S. salar*	Levasseur *et al.* (2006)
<0.063	>0.4	*S. salar*	Julien and Bergeron (2006)

n/a: information not available.

Table 2.3. A review of the particle size and critical percentage mass of fine sediment reported in the literature relative to embryonic salmonid survival (From Louhi et al. 2008).

The model PHABSIM was developed in the late 1970s to assess "microhabitat" variables: depth, velocity, and substrate size (Bovee 1978). However, hyporheic conditions - except for estimates of sediment size are not addressed by PHABSIM. More recently, attention has shifted back to subsurface or hyporheic flow and the geomorphic context of spawning habitat (Geist et al 2002, Merz et al 2004, Greig et al 2007).

The dissolved oxygen requirements for successful incubation of embryos and the emergence of fry is reliant on intragravel oxygen supply which generally act as a function of many interacting chemical, physical and hydrological variables. Among these variables are: the DO of the overlying stream water, the water temperature, the substrate size and porosity, the sediment oxygen demand as well as biochemical oxygen demand (BOD) of the intragravel water, the stream velocity and gradient and finally, the channel configuration and the depth of the stream where the redds are located.

Of the factors mentioned above, the hydraulic controls on a river system are the broadest influencing factors on the quality of spawning gravels. Fine sediment build-up in redds is thought to reduce the intra-gravel flow by reducing the hydraulic conductivity of the gravels (Sear 2007). Biofilms, bacterial mats created by organisms cleaving to particle surfaces in the interstitial spaces, can simultaneously create a BOD and physically block the pore spaces reducing intragravel velocity (Greig et al 2007).

Work by Youngson et al (2004) and Malcolm et al (2008) on hyporheic exchange of oxygen and other solutes between surface water and groundwater, highlights some examples of biogeochemical influences on oxygen availability in spawning gravels. Dissolved oxygen concentration was found to vary spatially and may reflect the degree of ground water-surface water interaction. Studies focussing on upwelling areas of long-residence groundwater, which were depleted in dissolved oxygen, were found to have a deleterious effects on salmonid incubation (Malcolm et al 2004, Malcolm et al 2006).

Studies have also shown that characterization of groundwater is possible in that its electrical conductivity, alkalinity, calcium and sulphate levels are generally higher than surface water, and its dissolved oxygen content, lower (Soulsby et al 2001, Malcolm et al 2004).

Infiltrating sediments also contain a portion of organic content, the breakdown of which may contribute to oxygen consumption and nutrient mineralization. (Malcolm et al 2004, Grieg et al 2004).

In addition to the pathways that oxidize dissolved and particulate organic matter, there are important biogeochemical pathways that oxidize selected nutrients and elements. For example, nitrification, methane oxidation, sulphide oxidation, manganese oxidation and iron oxidation are key oxidative pathways occurring within waters of the riparian ecotone, particularly at the interfaces between anaerobic and aerobic waters and exchange points between groundwaters and surface waters (e.g. Dahm et al 1987, Triska et al 1990). However, the anaerobic phase interactions are less likely to occur at the depths where salmonid redds are generally located (Chevalier 1984, Grieg et al. 2005).

Marmonier et al (1992) showed that nitrate and sulphate contents in interstitial water in an abandoned channel had very different seasonal dynamics, according to the origin of the interstitial water and the grain size characteristics of bottom sediments. Dahm et al

(1998) also showed that availability of electron donors for biogeochemical processes within the interactive surface water-groundwater (SW/GW) ecotone was spatially variable in the large rivers they studied.

In terms of hydrological influences, a study by Claret and Boulton (2008), showed that low hydraulic conductivity, tended to create steeper gradients in biogeochemistry and microbial activity along hyporheic flowpaths than where hydraulic conductivity was high, due to a larger and deeper influx of surface water to the hyporheic zone.

Another hydrological factor that must be considered when looking at alevin survival is the risk of scour during high flow events. This, for Atlantic salmon is a real risk since their burial time in the gravels coincides with winter rain and storm events. Scour may excavate eggs that are buried to a depth within the gravel scour or mobilization depth. (De Vries 2008). Another risk associated with scour events are the physical impacts experienced due to mobilization of the gravel and to which early-stage salmonid embryos are extremely sensitive (Gibbons 2008). In addition, scour can facilitate fine sediment intrusion deep into the gravel matrix and so become an additional hazard for incubating eggs (Sear et al 2008). Redd de-watering may also be a potential mortality factor for eggs and alevins – especially in streams with modified flow regimes (Ames and Beecher 2001). Dewatering is more likely to cause mortality at the alevin stage due to the need for gill respiration (Becker et al from Gibbins et al 2008).

Factors controlling the oxygen availability in salmonid redds are thus multiple and act over a range of temporal and spatial scales. Thus, the precise factors influencing spawning gravels may vary significantly between reaches and river systems depending on the dominant influences at work (Greig et al 2007).

2.6 Infiltration and accumulation of sediment in river bed gravels

The process of fine-sediment infiltration and accumulation is of great interest to those trying to improve salmon spawning habitat, as it is at this scale that the major changes in the redd gravel size and porosity of the substrate can occur, on a time-scale relevant to the incubation period. This can affect the interstitial oxygen levels by reducing the supply of oxygenated stream water to developing embryos. This reduction in oxygen supply is possibly compounded by further demands due to the increased biological oxygen demand (BOD) of organic matter that has also infiltrated the interstitial spaces, and by sluggish flow through redds impeding the passage of potentially toxic respiratory waste products (Grieg et al 2005).

The process of infiltration of fine sediment into the redd matrix is controlled by a number of factors including gravitational forces, turbulence, fluid velocity and the individual characteristics of the infiltrating grains versus the gravel-bed matrix. Also, gravel-bed disturbance during high flows affects the structure of infiltrated sediment.

In a situation where all particles are perfectly spherical, it has been shown that larger particles will drop out of suspension first, and the smallest last. However, most particles are not perfectly spherical, and irregular shapes will have an effect on the rate of settling. Flocculation can occur in finer sediment/ clays causing a number of particles to adhere to each other, thus again causing an unpredictable effect on settling path (Sear et al 2007).

The nature of the accumulation of fine sediment into spawning gravels depends on the supply of inorganic and organic fine sediment into the river, the size-range of the sediment relative to the gravel bed matrix, and the ability of the river system to cleanse the gravels - via scour and entrainment (Sear et al 2007).

Since most flow experienced in streams is turbulent, this plays a part in the path particles take before settling to the gravel bed and possibly infiltrating the framework of the bed.

The dominant forces affecting particle settling have been investigated and found to be gravity and turbulence. Gravity affected the settling of larger particles (D_{50} > 350 μm), while turbulence plays a more important role in the settling of smaller particles (D_{50} < 350 μm), (Roy et al 1996 from Sear 2007).

Infiltration into the river bed matrix, once the particles have settled, is dependant both on gravity, fluid movement and turbulence; but the control of the larger grains of the framework of the river-bed matrix plays a large part in how settling within this environment occurs.

Some research has shown that gravity remains the most important factor in settling of coarser sediment within the bed, and that this portion (<1mm) will settle more quickly in the matrix than the finer portions of sediment (Sear et al 2007 from Hoyal et al 1997).

In some cases, especially during times of lower-flow, smaller sand-size particles are seen to stay relatively close to the bed surface and when settling out, may form a top-heavy 'seal' on the upper surface of the bed without penetrating into the matrix. This shows us that there may be other factors to consider when predicting sediment infiltration patterns; such as the size and shape of the individual grains and their density, as well as the dynamics of bed disturbance during higher flow events which can bring about the reorganization of the infiltrated sediment.

Infiltration into the gravel bed has been found to act via three mechanisms: (1) surface (bridging) filtration where particles accumulate on the surface i.e. the 'sand seal' effect (2) straining filtration - where particles pass into the subsurface spaces and cease travelling only when they reach a pore too small to pass through; and (3) physical-chemical filtration - where small clay-like particles will adhere to one another and to the gravel matrix due to molecular charges (Sear 2007 from Mc Dowell-Boyer et al 1986).

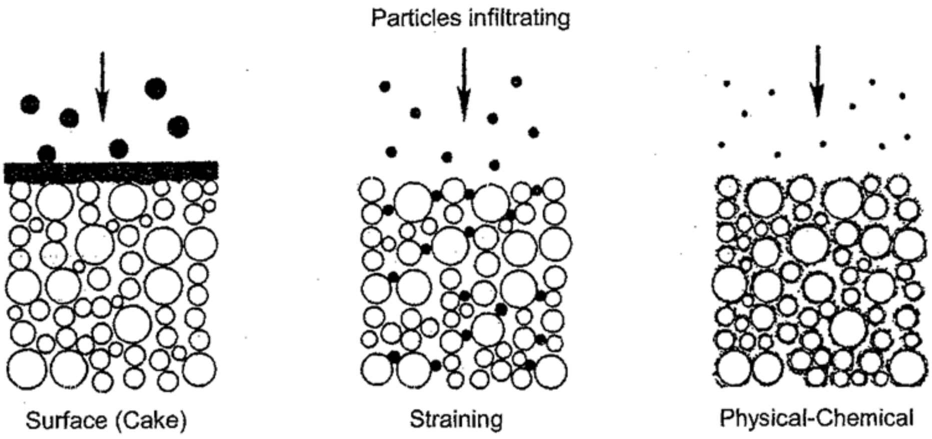


Figure 2.8: Relationship between gravel bed type and infiltrating sediment : Three filtration mechanisms for sediment infiltration into porous gravel beds (from Sear et al 2008).

The rate of infiltration of sediment into redd gravels has been found to have a decaying curve, where increased amounts of infiltrated fines leave less pore-space for subsequent fines to enter and be deposited (Carling, 1984; Sear 1993; Heywood and Walling 2007). So, both the amount and the pattern of sediment infiltration will depend on the particle size composition of the transported sediment and the pore size distribution of the gravels (Frostick *et al.*, 1984; Lisle 1989).
Acornley and Sear (1999) found that the siltation rate of any one redd site tended to be related to the suspended sediment rate of the overlying stream water.

At higher discharge rates, fine sediment tends to fall to the low pressure depression upstream of the redd – the 'pot', leaving less fines to infiltrate the egg pocket. At lower discharges, this effect is lessened (Sear et al. 2008).

Spatial and temporal patterns of sediment infiltration depend on the ability of a flow to penetrate the framework and to transport any fine sediment that is supplied to it. This is variable from site to site and the main influencing factors are: the porosity and permeability of the bed framework, entrainment induced by pressure gradients and flow velocity and turbulence (Sear 2008).

Bed disturbance during high-flow events can also alter the way that sediment infiltrates the matrix. Pore spaces within the gravel 'dilate' due to the increased mobility of the gravel framework, so allowing increased intrusion of sediment to deeper layers within the river bed (Allan and Frostick 1999, Sear et al 2008).

2.7 Incubation requirements

Within the redd environment, a sufficient dissolved oxygen supply from the surrounding pore water is required for healthy development and survival of incubating embryos. Egg development starts with a newly-fertilized 'green' stage and develops to an 'eyed' stage where eyes are distinctly visible through the egg membrane (Robson 2006, Stead and Laird 2002). After a few weeks - depending on water temperature throughout the incubation period, the eyed eggs hatch to produce alevins, which later swim up and emerge through the gravel to begin feeding in the water column (Mills 1989). The dissolved oxygen level must be adequately high in order to diffuse from the thin layer of intragravel water which is in contact with the egg surface - called the boundary layer, across the egg membrane, so ensuring continued respiration and development. The early stages of larval development are wholly dependent on diffusion for satisfying oxygen requirements. Once the circulatory system is functional, oxygen transfer to the embryo becomes more efficient (Bjornn and Reiser 1991 from Wickett 1954).

In terms of studies carried out to investigate the incubation mortality in relation to infiltrated sediment, Phillips and Campbell (1961) found that intragravel dissolved oxygen must average 8 mg/l for embryos and alevins to successfully thrive. Davis (1975) reviewed a number of studies and concluded that DO levels of 9.75mg/l is fully protective of both eggs and alevin, while at levels of 8mg/l the average members of the incubating population will start to exhibit symptoms of stress and at 6.5mg/l, a large proportion of the incubating eggs are likely to be affected.

In a review by Bjornn and Reiser (1991) minimum dissolved oxygen concentration of 5mg/l is suggested as a critical limit, and they state that DO levels should be at or near saturation for successful, stress-free incubation.

In a study by Greig et al (2007) it was found that the broad critical threshold for embryonic survival was around 4mg/l and their linear regression model intercepting at 5mg/l when DO was plotted against survival. In respect to percentage survival to hatching, they performed an analysis of the oxygen concentration, the Interstitial flow velocity and a third combination of these parameters - the oxygen flux (the oxygen availability to the egg itself) which is stated as:

$$O_2\,(flux) = C_o\, v a_{egg} \qquad (2)$$

Where;

C_o is the interstitial oxygen concentration

v is the interstitial flow velocity, and

a_{egg} is the cross-sectional area of an Atlantic salmon egg

Previous studies on tolerated levels of dissolved oxygen have reported a range of DO concentrations as table 2.4 below illustrates:

Researcher	*Embryo -Stage*	*Stress limit*	*Lethal limit*
Alderdice et al. 1958	Green	-	1.4mgl
Silver et al. 1963	Eyed	11.7mgl	1.6mgl
Hayes 1951	Eyed	-	3.1mgl
Wickett et al. 1954	Eyed	-	5mgl
Lindroth 1942	nearly at Hatch	-	5.8mgl
Alderdice et al. 1958	Hatch	-	7.19mgl
Hayes 1951	Hatch	-	7.1mgl
Davis 1975	Hatch	8.1mgl	2 – 5mgl
Phillips and Campbell 1962	Alevin	8mgl	

Table 2.4: Critical and sub-optimal levels of dissolved oxygen (DO) for salmonid embryos at various stages of development.

Suggested reasons for the discrepancy between these studies were differences in water velocity which may improve DO supply to the eggs in higher velocity streams (Cooper 1965, Chapman 1988). Experiments have also shown that sub-optimal (but not lethal) DO levels can affect the development and growth rate of developing embryos (Silver 1963, Shumway 1964, Brannon 1965). Fast and Stober (1984) reported newly hatched alevins' ability to detect oxygen gradients and move towards areas containing higher DO concentrations (From Bjornn and Reiser 1991). Shumway et al (1964) and Cooper (1965) noted that dissolved oxygen and interstitial water velocities were important in determining the lethal limit for developing embryos, and that very low water velocities may be tolerated if DO levels remained high.

Newly fertilised eggs are capable of tolerating complete anoxia for short periods (Ortner et al 1993, Danner 2008). This ability is associated with small stores of glycogen that are rapidly depleted (Finn et al 1995) and this anaerobic capacity is lost during development, as stores deplete and demand for oxygen increases (Hayes et al 1951; Hamor and Garside 1979, Rombough, 1988). Sustained environmental hypoxia can significantly delay development (Hamor and Garside, 1976), or cause precocious hatching (Czerkies et al 2001). A natural convection system exchanges the dissolved gases between the perivitelline space and the boundary layer (O'Brien et al 1978; Rombough 1988b) via diffusion. However, this system can be compromised by deposits of infiltrated fine-grained solids such as clay or silt (Greig et al 2005).

Interstitial flow is also an important factor as it provides a renewed supply of oxygen to the incubation zone and must also be of sufficient velocity to carry the waste products of metabolism (ammonia, CO_2) away from the embryos. Metabolic waste remaining within the egg zone can be detrimental to the embryos (Grieg et al 2005). As discussed in the previous sections, both interstitial flow and oxygen supply are dependent on the permeability of the gravel substrate.

When looking at survival in relation to egg burial depth, growing evidence has shown that redd depth is an important determinant in survival to hatching (Meyer 2003, Greig et al 2005).

The capacity of the interstitial water to hold dissolved oxygen (DO) is dependent on temperature with colder water having a greater capacity – thus DO levels will naturally vary even where all other factors remain stable. The different stages of embryonic and larval development also have varying DO requirements. Thus, the DO levels must be adequate for all variations within these frames of reference during these sensitive stages of development (Silver et al 1963, Turnpenny and Williams 1980). Temperature will also in turn affect the embryos' metabolic rate and therefore rate of oxygen consumption. These factors then are closely linked and embryonic development has been shown to be positively correlated both with oxygen levels and temperature (Hamor and Garside 1977).

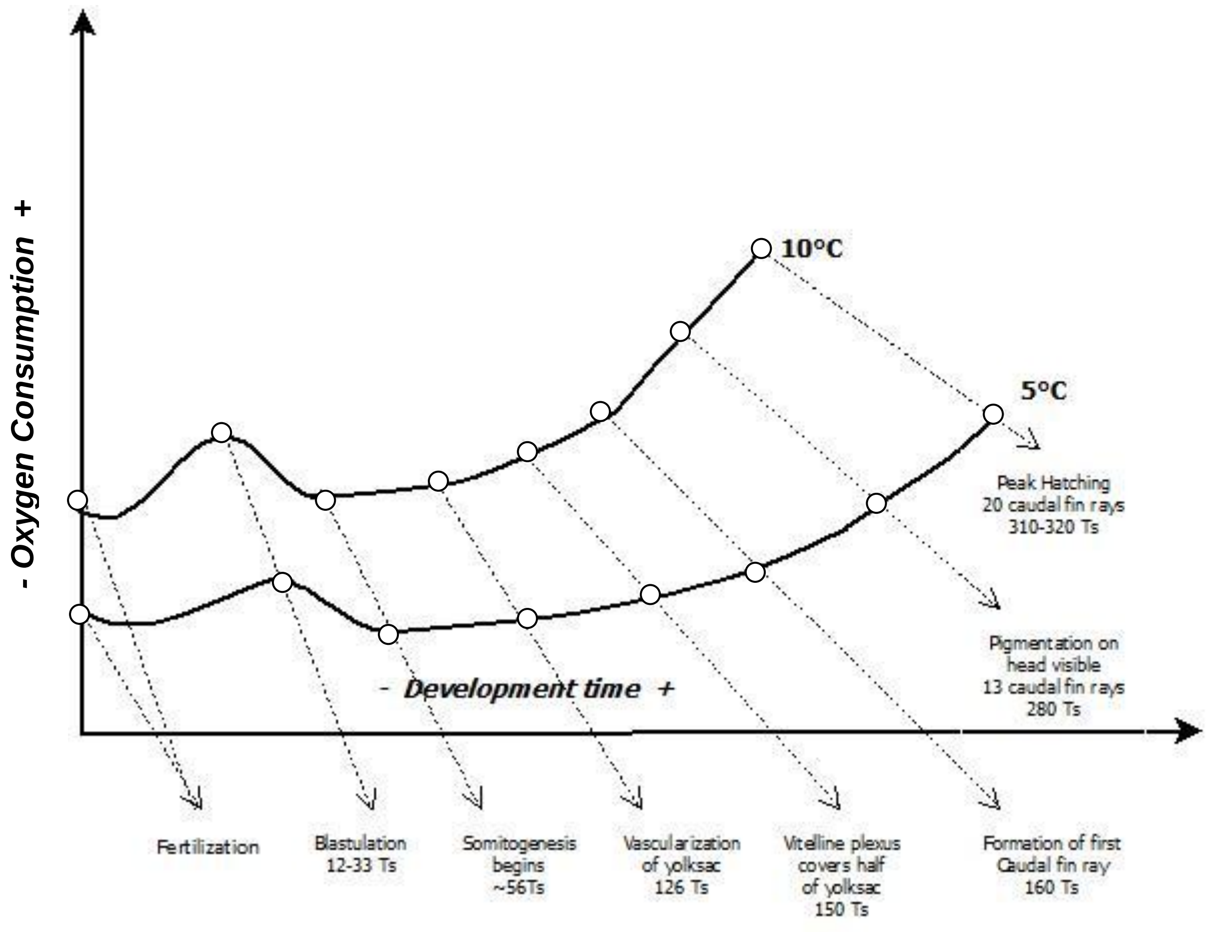


Figure 2.9: Summary of the influence of temperature and stage of development on rates of oxygen consumption (based on Hamor and Garside 1977) with meristic developmental stages as described by Gorodilov (1996)

Gorodilov (1996) described the sequence of changes in morphology, from egg fertilization through to completed yolk absorption, as a set of discrete ‘stages’ or morphological states, as a means of describing developmental progress of the embryo with respect to temperature. A variety of meristic traits were chosen as indicators of specific stages – such as somite pairs in very early ontogeny or caudal fin rays and in the later stages. The relationship between developmental rate and incubation temperature was described as:

$$lg\ N_t = lg\ N_o + (-0.0967 + 0.00207t)\ t, \qquad (3)$$

Where N_o and N_t indicate the time taken to form one somite pair (τ_s) at temperatures of *0* and *t* respectively.

This method – details of which appear in figure 9 above, may serve to define what developmental stage is expected for an alevin with respect to given temperatures and to examine any deviation from this expected trend and which may then be due to other causes.

Another approach used by Beer and Anderson (1997) uses differential equations to model the changing geometric properties of yolk-sac and embryo which in turn describes anabolic and catabolic processes. The model can be used with a variety of temperatures which reflects more accurately field conditions, in comparison to other some previous predictive studies, which only considered embryonic development with respect to a fixed temperature (e.g.: Rombough 1985, Beacham and Murray 1989).

As indicated in figure 9, the oxygen consumption of the embryos peak at times of increased energy expenditure (i.e.: during proliferation of blastodisc and hatching). Reported oxygen consumption values from laboratory experiments vary somewhat; from 0.00104 mg h^{-1} to 0.02 mg h^{-1} for studies carried out on eyed eggs (Hayes et al 1951, Hamor and Garside 1979). This variation may have been due to differences in experimental procedures and sampling techniques, but further studies are required to arrive at a more precise DO consumption figure for Atlantic salmon eggs and larvae.

The physical presence of the egg case and the perivitelline fluid can represent a barrier to efficient oxygen exchange, requiring proportionately more dissolved oxygen availability in the surrounding water during the pre-hatch period (Matschtak et al 1995, Finn 2007).

A study by Berg et al (2001) describes oxygen consumption post-hatching as increasing from an initial 85µl O_2 day and to 290, µl O_2 day^{-l} at emergence - at a temperature of 9.5°C. This agreed with other studies carried out by Boen (1987) and Hayes (1949).

Aside from the aforementioned influences on developmental rate that temperature has on salmonid embryos, sudden changes in, or extremes of temperature may cause increased deformities at hatch (Yamamoto et al 1996, Finn 2007). Several studies have also demonstrated that the early thermal environment has important implications for the specification and recruitment of muscle tissue later in life (Johnston et al 2003; Bjørnevik et al 2003).

Phototoxicity may prove to be a problem in spawning areas where there is insufficient riparian cover and gravels are penetrated by UV irradiation. In particular, UV-B radiation directly damages DNA and may cause death in early-stage embryos exposed to irradiance levels of >50µ Wcm^{-2} (Dey and Damkaer Finn 2007).

An additional factor that may affect incubation success is the risk of physical shock to the eggs during the most vulnerable green to eyed stage (Bardonnet and Bagliniere 2000). High flows during spate events may cause movement of the bedload, delivering impacts to the spawning gravels which may result in mortality.

Dissolved gases may also affect the success of embryonic growth and development. Nitrogen gas is not of biological significance but super-saturation in embryonic tissues can create buoyancy problems and physically damage delicate tissues and membranes. Super-saturation may occur in response to rapid temperature change or denitrification processes by instream bacteria (Danner 2008).

Carbon dioxide is released as a metabolic waste product of most organisms, and if throughflow of water is not sufficient, pockets of water with a low pH may occur due to CO_2 dissolution locally. This may occur especially if the buffering capacity of the intragravel water is low. This acidification may result in disruption of egg development (Grady 1988, Danner 2004).

Stream chemistry has an effect on biological development in salmonid embryos. Some elements act as macro or micro-nutrients that are essential for normal development. Iron, calcium, sodium and potassium are needed for haemoglobin, bone formation, and electrolyte balance respectively (Danner 2008). Streams lacking in these basic nutrients can lead to abnormalities as other elements may be substituted in tissues in place of the required elements and reduce or cancel their biological functionality (Finn 2007, Danner 2008). One example is that of toxic aluminium cations replacing calcium in the gill tissues of developing salmon in streams with a low pH (Evans 1998, Finn 2007).

Heavy metals such as cadmium, chromium, copper, iron, lead, manganese silver and zinc are readily taken up by eggs and larvae (Wedemeyer 1968). These elements may bind to receptor sites normally meant for magnesium or calcium functions, and have been seen to impair growth, metabolism yolk resorption and vertebral column formation (Finn 2007). The egg chorion seems to provide some protection from these metals due to its binding capacity (Wedemeyer 1968). The presence of humic acids, dissolved organic carbon and chloride ions in the stream water can buffer against heavy metal take-up. (Wedemeyer 1968, Hammock 2003). This reduction is associated with the heavy metals binding with organic compounds in the stream water (Finn 2007). Some anthropogenic compounds such as Polynuclear aromatic hydrocarbons (derived from pesticides, detergents, plant or industrial sources) have been found to cause endocrine disruption in developing embryos (Finn 2007).

2.8 Fine sediment and embryonic survival

Fine sediment intrusion into the incubation zone was first thought to physically abrade the embryos (Waters, 1995) and that infiltration of sediment could prevent emergence of fry from the redds (Philips et al 1975). It is now widely thought that the main cause of damage to developing salmonids within spawning gravels is a reduction in oxygen supply to embryos which the accumulation of sediment causes in the redd (Turnpenny and Williams 1980, Rubin and Glimsater 1996).

Sediment intrusion is thought to block the interstitial pore spaces in the redd environment thereby reducing intragravel flow within the incubation zone (Chapman, 1988, Bjorn and Reiser 1991, Acornley and Sear 1996, Theurer et al 1998). This results in a reduced oxygen supply to the redd environment, so impeding uptake by embryos.

In one study, tests carried out to evaluate the effect of intrusion of varying sediment sizes into redds (Beschta and Jackson, 1979) found that fine silts (<0.2mm) moved through the gravel and filled the gravel voids up from the redd bottom. In contrast, the intrusion of sand-sized particles (approx. 0.5mm diameter) became lodged in the upper layers forming a kind of 'sand-seal' that may allow development of embryos but potentially impede the exit of alevins at time of emergence (Alonso et al 1996).

Recent studies have shown that very fine silt and clay portions, (i.e. <63µm) had a disproportionately detrimental effect on embryo survival. Both Julien and Bergeron (2006) and Levasseur et al (2006) found that at low proportions of very fine silts (0.3-04% for Julien and Bergeron and 0.2% for Levasseur et al), they saw a 50% mortality rate of embryos. Both parties suggested that this phenomenon may be explained by recent findings by Greig et al (2005), who observed that clay sized particles physically blocked the micro-pore canals on the egg membrane, thereby restricting oxygen absorption directly.

In a study by Greig, Sear and Carling (2005) it was found that the impact of fine sediments was influenced by the size composition of the infiltrated fine sediments such that as particle size decreased, intragravel flow also decreased. So further investigation into the impact of the complete range of particle sizes found in redds would be useful, rather than simply looking at percentage of fines below an arbitrary minimum threshold size.

If oxygen-consuming substances form part of this sediment influx – such as respiring/ decaying organic fractions then oxygen levels can be further depleted (Chevalier and Carson 1984). Organic fractions can physically block pore spaces within the redd, but can also facilitate the development of 'biofilms' – algal and bacterial communities which cleave to sediment particles and form a cohesive mass which may further reduce permeability and interstitial flow velocity (Chen and Li 1999).

Furthermore, because the sediment and/or biofilms physically block the throughflow of interstitial water in the redd, the flushing of metabolic waste products from the incubation zone is impeded and this can independently be harmful to embryos (Greig et al 2005, Hubner et al – in press).

2.9 Hyporheic zone groundwater-surface water interactions

Some recent research has explored the possibility that variation in dissolved oxygen levels within the redd zone may, in some catchments, be more attributable to groundwater-surface water interactions within the hyporheic zone, and at a depth that may affect incubating salmonid eggs. These investigations originated from the broad research area of hyporheic zone interactions, where the groundwater bodies were found to have differing characteristics, with groundwater often defined by low dissolved oxygen levels (Fowler and Death 2001, Boulton et al 1998). Further investigation into this phenomenon has revealed that the interaction between these two water bodes is seasonal, dependent on discharge patterns and regulated by the upward force of baseflow and the downward force of advecting surface water (Fraser and Williams, Soulsby et al, Malcolm et al). This then provide a means of testing for the presence of the two water bodies and the degree and scale of interaction between them.

Studies on these boundary layer interactions relative to salmonid spawning gravels are few, but have highlighted the detrimental effects of groundwater of depleted oxygen content on developing salmonid embryos (Soulsby et al 2001, Malcolm et al 2003, 2004, 2009, Youngson et al 2004).

This field of research is new but provides potential insights into the possible causes of lowered incubation habitat quality and which may act alongside sedimentary pressures in susceptible catchments.

Below is a diagram of the main factors that are thought to affect salmon embryo and larval stages (From Greig et al 2005).

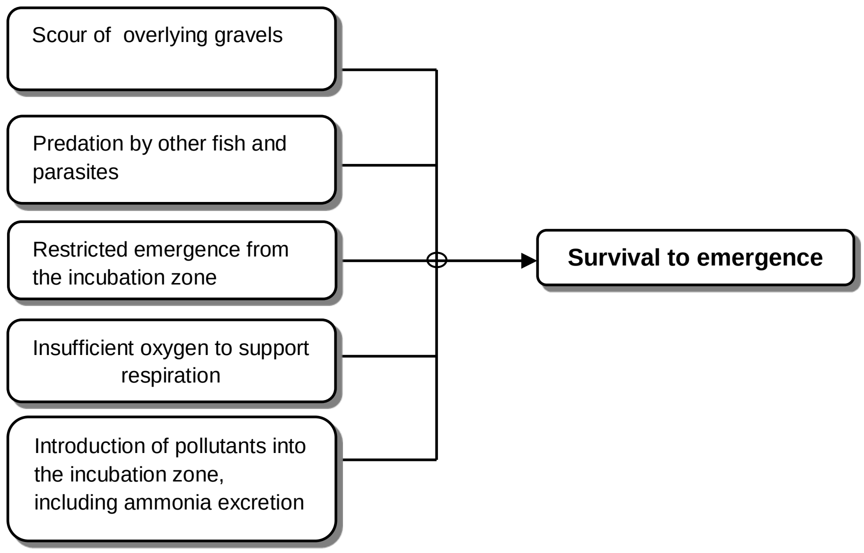


Figure 2.10: Summary of factors reported to influence survival to emergence of salmon progeny (Greig 2005)

2.10 Sublethal effects on embryos

Embryos can survive when dissolved oxygen is below saturation (above a critical level), but development can be affected such that the resultant hatchlings are abnormal (Silver 1963, Bjornn and Reiser 1991).

2.10.1 Hatching

Low dissolved oxygen concentrations can result in premature hatching (Alderdice et al 1975, Rombough 1988, Czerkies et al 2001, Kamler 2002). This may be considered an adaptive response to low oxygen levels, where the shedding of the chorion and perivitelline fluid cause an immediate improvement in respiratory abilities for the larvae (Ciuhandu et al 2005).

2.10.2 Growth

Suboptimal oxygen concentrations can also slow growth and result in fry with a smaller mean weight (Koski 1966, Hamor and Garside 1977, Tappel and Bjornn 1981). Silver et al (1963) reported that oxygen concentrations of less than 11.7 mg/l restricted the growth of Chinook salmon embryos before the 24th day after fertilization.

The mechanism involved in slower growth in hypoxia is thought to involve a series of biological responses such as metabolic depression; where functions serve only more essential metabolic processes, and down-regulation of genes for protein synthesis and locomotion (Wu 2002).

2.10.3 Emergence

Another common result of hypoxic conditions is the delayed emergence of fry from the gravels (Rombough 1988, Roussel 2007). Fry that emerge later and smaller from the gravel may find it more difficult to compete, and are less likely to survive during later life-stages, than fry that emerge on time and/or are larger (Silver et al 1963, Chapman 1988). Evidence shows that larger larval size during early life stages decreases the risk of predation (Fuiman 1994, Kamler 2007), thus this may be one of the most important factors when considering the viability of emergent fry in subsequent life stages. In an experiment carried out under laboratory conditions to measure emergent fry quality against known masses of sediment, it was found that fry weight generally declined as the proportion of fine sediment increased. It was also noted that emergent fry incubated in higher proportions of fine sediment had almost depleted energy stores at emergence (Argent and Flebbe 1999).

2.11 Indicators of sublethal effects

2.11.1 Developmental state

It thus may be possible to use sublethal effects as a higher-resolution gauge of how embryonic development reacts to high sediment loads and correspondingly low dissolved oxygen levels. In terms of the developmental aspects – growth and degree of development, a paper by Gorodilov (1996) looks at the various developmental stages of salmonids. The visible and identifiable physiological changes that are specific to each stage are described and compared to the approximate time-frame of normal development (in degree-days) of salmonid embryos. Thus, by looking at the egg-to fry development in the context of this guide, we can ascertain the degree of deviation from the expected developmental stage, and whether this has correlated to other factors such as oxygen flux, fine sediment proportion, or specific size-fractions of fine sediment.

The problem may also be approached through evaluation of the stress responses (i.e. chemo-physiological changes) of larval fish or fry along with performance at various biological levels, to assess the environmental impact.

2.11.2 Behavioural studies

Behaviour is used as an indicator of the health of an individual since it is an integrated expression of an animal's physiological response to its environment (Murphy et al 2007).

Since the sublethal effect of hypoxia can cause malformation and delays in embryonic fish development as well and deferred timing of emergence, the hypothesis that the subsequent behaviour of the emergent alevins from hypoxic incubation zones may differ from that of those reared in normoxic conditions should also be explored.

Studies on the causality of the links between physiological compromise due to adverse conditions and behaviour in later life are scarce, but evidence from previous studies has shown that a reduction in performance can result from poor environmental conditions (Silver et al 1963, Chapman 1988, Fuiman 1994, Widmer et al 2005, Roussel 2007 Kamler 2007).

Behavioural tests designed to look at sublethal effects should then be designed with a view to evaluating the effects of adverse environment on ecologically significant behaviours and need to determine which survival skills were most informative of larval fishes' viability. Previous studies carried out have looked at quantifying larval/fry performance in terms of startle response time, swimming velocity, angular change, total distance travelled and acceleration – constituting the fishes' escape potential from natural predators (Brewer et al 2001, Fuiman et al 2006, Roussel 2007).

A study by Roussel (2007) found that brown trout alevin that had been incubated in hypoxic conditions exhibited a 20% reduction in swimming activity in the presence of a predator, compared to their normoxic counterparts. In another study, hypoxia-reared fish achieved ~22% slower maximum swimming velocities in comparison to normoxia-reared fish (Widmer et al 2006).

2.11.3 The stress hormone cortisol as a gauge of sublethal effects

The stress response of fish to hypoxic conditions can be measured via assessment of cortisol levels in the blood plasma of fish. Cortisol is the main steroid produced by most teleosts in response to stressful events (Feist and Schreck 2001). This stress response is thought to be the mechanism which enables the organism to cope in the short term to stressful events and recover quickly. However, longer periods of stress and cortisol production can be harmful to the organism (Barton and Iwama 1991, Feist and Shreck 2001). Prolonged periods of high cortisol production can have adverse effects on growth, reproduction, immune function and general fitness (Schreck 1982, McCormick et al 1998).

Primary biological stress responses (in this case production and release of cortisol) can trigger secondary responses, such as increases in plasma glucose concentrations, heart rate, gill blood flow, metabolic rate, and decreases in plasma chloride, sodium, potassium, liver glycogen, and muscle protein in teleosts (Barton et al 2002). Immune function can also be suppressed as a result of increased cortisol levels in the blood (Yin et al 1995, Ortuño et al 2001).

With chronic stress (stress that persists over a long period of time), secondary responses may result in tertiary stress responses, which include decreased growth rate, metabolic activity, disease resistance, and reproductive capacity; as well as altered behaviour and reduced chances of survival (Wedemeyer et al 1990, Barton and Iwama 1991). The extent of tertiary responses is related to the severity and duration of the stressor (Lankford et al 2005).

In one study on the chronic effects of Cortisol on juvenile rainbow trout, chronic plasma cortisol elevation had significant negative effects on individual appetite, growth rate, condition factor, and food conversion efficiency (Gregory et al 1999).

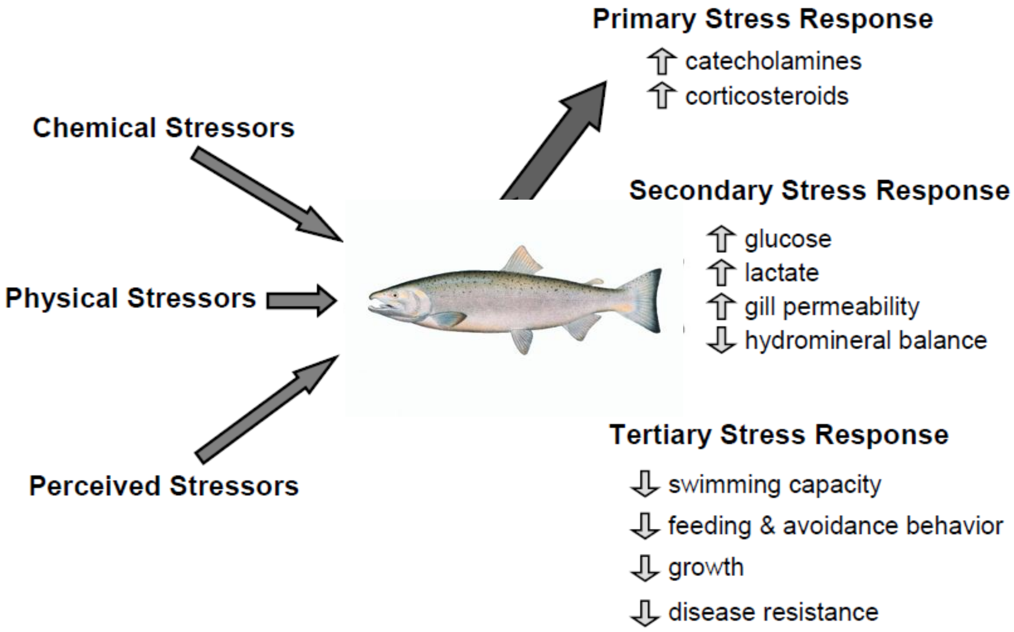


Figure 2.11: Diagram (modified from Barton 2002) of the possible stressors and physiological chain of stress-response reactions that can occur in sub-optimal conditions.

Other approaches to defining sublethal effects in salmonids have been lipid content (Castleberry et al, Mc Farlane and Norton 2002) and selections of different metabolic products that serve as fitness-indicators (Turner et al 2007).

Thus, in terms of chances of survival to subsequent life stages, sublethal effects may indeed play a significant role.

Many field studies have looked at survival to hatch or emergence but studies of sediment infiltration that may allow survival to hatching, but impair survival chances in later life stages - or in effect reduce the 'fitness' of the emerging fry, are relatively few.

2.12 Sediment sources and fingerprinting

The 'fingerprinting' of sediment found in river beds is a relatively new practice that may help to elucidate the sources of the material found in salmonid redds, ascertain whether they are allochthonous or autochthonous in origin, and discover what kind of spatial and temporal variation in sediment content exists between redds in the same river catchment.

Fingerprinting or source-tracing techniques, which began to emerge in the 1970s, initially involved the choice of a physical or chemical property which could differentiate between potential source materials (e.g. arable land and channel banks), and then by comparison of these properties in river bed sediment samples, find which fraction of those source areas contributed to the bed load sediment. The first example of sourcing techniques used geochemical, mineralogical and mineral/magnetic properties to fingerprint sources. However, these first studies could only provide a limited and 'qualitative' indication of the relative contribution of different sources, and a fairly vague discrimination between the potential source types - i.e. surface vs. channel sediments.

Since then, the technique has developed by adding further parameters to potentially improve the discrimination between sediment sources. Plant pollen, isotopic signatures, and fallout radionucleotides were successfully used as distinguishing properties.

Fallout radionucleotides were particularly useful for discriminating between surface and sub-surface sediments as they occur in higher concentrations in surface sediments. They were found also to be useful in distinguishing cultivated soils from uncultivated soils as the actions of ploughing and tilling reduces surface concentrations of the radionucleotides, so acting as a traceable marker when compared to undisturbed soils.

In studies on UK rivers, Collins and Walling have refined the fingerprinting technique and implemented it on several river catchments, which they have been reported on in various papers (Collins and Walling 1997, 2005, 2006, 2007). Their procedure is carried out by means of two separate stages. Firstly, a statistical verification procedure is applied in order to ascertain which individual fingerprint qualities are most indicative of particular sediment types (land-use, etc..) and to define a set of these properties - a 'composite fingerprint', that will successfully differentiate between these 'types', so that they can be easily traced in the river-bed samples. Secondly, application of a multivariate mixing model is used on these composite fingerprints to create quantitative estimates of relative contributions of the discrete sediment source 'types'.

Some results of this procedure used in a study of two Southern English lowland rivers are displayed below.

River	% Woodland	% Pasture	%Cultivation	%Channel bank
Frome	**1 – 6**	**10 – 42**	**44 – 81**	**7 – 19**
Piddle	**1 – 11**	**10 – 28**	**44 – 80**	**7 – 21**

Table 2.5. Comparison of sediment source results from two river channel beds (Collins and Walling 2006)

Other results from studies in Hereford (Gruszowski et al 2003) have indicated that in addition to the relative contributions of arable, pasture, woodland and channel sources, roads may constitute a significant secondary source of material into rivers and that they also may change the chemical signature of sediment that is transported via road surfaces. Their modeling of the river Leadon's suspended sediment samples indicated that around 30% was derived from or transported via roads.

Few studies have looked at the integration of characteristics such as redd flow sediment infiltration with a sediment fingerprinting assessment of the surrounding land use types. An integrative approach may embrace some of the complexity of the land-fluvial-hyporheic system and help to ascertain the linkages within, on a spatial and temporal scale.

2.13 Summary

Thus, as demonstrated in the sections above, the decline in salmon stocks we witness has been found to have multifaceted causes - from overfishing to factors influencing marine survival and freshwater habitat degradation. Many of these factors can be attributed to anthropogenic practices and affect all life stages from adult survival at sea and in freshwater to the riverine juvenile stages. The scope of such an enquiry is huge, so any in-depth study must be limited to a focused investigation into a particular environment influencing survival. Since the freshwater egg to juvenile stage - between spawning and the emergence of fry from the intragravel environment is thought to be the most vulnerable phase of the life cycle during which most population attrition occurs, this study is focused on the factors at play during this stage.

The factors affecting spawning gravels can be defined hierarchically as large scale controls such as the climactic and hydrological influences on a catchment. From this, the sediment yield and discharge effects on the spawning reaches and the hydraulic controls above and within the redd zone will be defined. Smaller scale influences such as hyporheic flow patterns, sediment intrusion, dissolved oxygen gradients, water quality within the redd zone will result.

The form of this study is thus scaled from a study of catchment hydrology in relation to spawning gravels to catchment sediment yield and land-use contributions to spawning reaches in the first chapters. The investigation then looks at the smaller scale relationships between spawning gravels and sediment delivery and the interactive influences of sediment, intragravel flow, dissolved oxygen relative to embryonic survival. Other potential environmental factors affecting redd-scale habitat quality are also considered. Finally, an examination of the sublethal effects of intragravel habitat quality on emergent fry reveals that survival to emergence may not be the most accurate measure of recruitment success in Atlantic salmon. Chapter 3 explains the study approach and methods used.

Chapter 3 Study Sites and Methodology

3.1 Methodological Rationale and Practical Approach

This chapter presents contextual background and information on the catchment area and the field sites addressed in this study and explains the overall field strategy. How these studies link in with further studies in the laboratory and the application of models is also addressed.

By embracing and integrating approaches used in other disciplines and using a 'whole-system approach', the aim is to gain an insight into the complexity of the interactions within the hyporheic zone and their effects on alevin survival and long term health. This approach also ensures awareness of advances made in different, but related, fields of salmonid research and facilitates the exchange of methods, approaches and new knowledge gained in any one specific discipline (Chapman 1988, Vaughan et al 2007, Greig et al 2005).

Greig et al (2004, 2005) recognized the need to address multiple parameters and additional effects that may result from sediment oxygen demand and groundwater interaction in the hyporheic zone. However while this multi-faceted approach accounted for multiple controls on habitat quality, the scope of the study encompassed mainly the effects of sediment on the interactive response of oxygen with intragravel flow velocity in the field, while some assessments of sediment oxygen demand were also made in a separate laboratory study. To date, this is the most expansive and whole system study on the topic.

The present study intends to bring this holistic viewpoint even further by addressing more variables and adopting methodological approaches that originate in other disciplines.

It should also be noted that although the adoption of an holistic approach in terms of the adoption of interdisciplinary methodological techniques and the enquiry into multiple controls on salmonid redd habitat quality, there is a danger in attempting to 'spread the net too widely' and not apply adequate depth of enquiry to any particular control. It was thus decided that physical controls encompass the main part of the enquiry with biological / chemical investigations comprising a supporting role. Another potential limiting factor when designing an holistic investigation is the integration of the different types of data which arise from such a study, and the dearth of current models which are fit to synthesize such holistic datasets. This makes quantification of the individual controls and the proportional impact and degree of synergism between them a challenge. This study has endeavoured to provide insight into the multiple controls that may be active in a given catchment and how these may vary spatially and temporally relative to flow conditions and other environmental parameters.

Other researchers have focused on various aspects of the incubation environment relative to embryonic survival and some of the key studies in this field are listed in table 3.1 below, with descriptions of their main drivers and findings.

Study area & species	Factors investigated	Conclusions	Source
Artificial channels; Chinook, steelhead	Sediment classes: (<9.5mm, <0.85mm) effect on survival	90% of variability in embryo survival correlated with substrate size composition	Tappel & Bjornn (1983)
Artificial channels (4); Chinook, steelhead	Sediment classes: (0.84-4.6mm, <0.84) effect of 6 different loadings on survival	Sediment class <0.84 shown as most detrimental to embryos	Reiser & White (1988)
Artificial streams, Sea trout	Sediment of six values of dg (geometric mean diameter) relative to survival	Correlation of low dg with early emergence and smaller fry	Rubin (1998)
River Rhine, Germany. 11 sites (natural redds), Sea trout	Dissolved oxygen concentration relative to % emergence	Correlation between DO concentration and emerging fry – critical limit of <7mg/l	Ingendahl (2001)
Girnock Burn, Scotland. 3 sites, Atlantic salmon	Hydraulic head, dissolved oxygen, temperature	Low DO effects of hyporheic exchange correlated with reduced survival	Malcolm et al (2003, 2005)
4 different UK sites (England & Wales) 1 site in each; Atlantic salmon	Dissolved oxygen, sediment classes (<4mm,2mm,1mm) suspended sediment, intragravel flow velocity, Sediment oxygen demand	DO supply related to embryo survival via the IGF (intragravel flow velocity) / DO budget	Greig et al (2004, 2005)
Cascapedia river, Canada 4 sites; Atlantic salmon	Sediment infiltration and intergravel flow velocity	Infilling during freshet events can effect survival by reducing IGF velocities	Zimmerman & Lapointe (2005)
St Marguerite river, Canada 6 sites; Atlantic salmon	Sediment classes: <63µm, <500µm relative to embryo survival	Fine sediment portion correlated to reduced survival	Julian & Bergeron (2006)
St Marguerite river, Canada 2 sites; Atlantic salmon	Sediment classes:< 0.125 and <2mm. Percentage relative to survival	Survival correlated to <0.125 size class	Levasseur et al (2006)
Hampshire Avon, UK 14 sites; Atlantic salmon	Dissolved oxygen, sediment classes:<2mm,<1mm, temperature, permeability	DO concentration related to amount of fines, % of both 2mm and 1mm successful predictors of survival	Heywood & Walling (2007)
Review of studies from Pacific salmonid rivers; Chinook, coho, steelhead, chum	Percentage fines of 4 size classes (<0.85, <3.4, <4.8, <6.4) relative to survival	< 0.85 size class most detrimental class in some rivers	Jensen (2009)

Table 3.1 Summary of previous studies on the spawning incubation environment, highlighting the main environmental controls investigated and findings.

With reference to the above table, the factors investigated in this study not only encompass grainsize variables (<63µm, <1mm, <2mm) in relation to dissolved oxygen, intragravel flow and suspended sediment indices, but also extend to other water quality considerations such as upwelling groundwater and nitrogenous compounds. In addition to embracing these factors collectively, the study also uniquely encompasses a sediment-sourcing investigation in order to explain the provenance of the infiltrated sediment, and looks at the potential for bed-load movement and scour in the catchment as a contributory factor.

Another unique aspect within the study is the examination of survival response within the catchment on both spatial and temporal scales, which has obvious relevance to management efforts, and helps give a more complete idea of the breadth of possible responses given variable environmental and climatic stimuli.

Additionally, the use of fitness indices as sensitive indicators of catchment quality is an area which has not previously been used in this context, and borrows methods from the fields of evolutionary biology, endocrinology and behavioural ecology to produce conclusive evidence of habitat quality response on the sublethal scale.

This study differs from previous studies in its aim to encompass not just one main driver focus but a new range of variables and potential drivers within the hyporheic environment. Additionally, by using methods with multidisciplinary roots, the idea of whole-system thinking and integrative science is promoted.

A schematic of the project areas encompassed within the field strategy and accompanying laboratory investigations is displayed in fig 3.1 below, which outlines the new range of variables integrated in to the study, thus distinguishing it from previous studies of this kind.

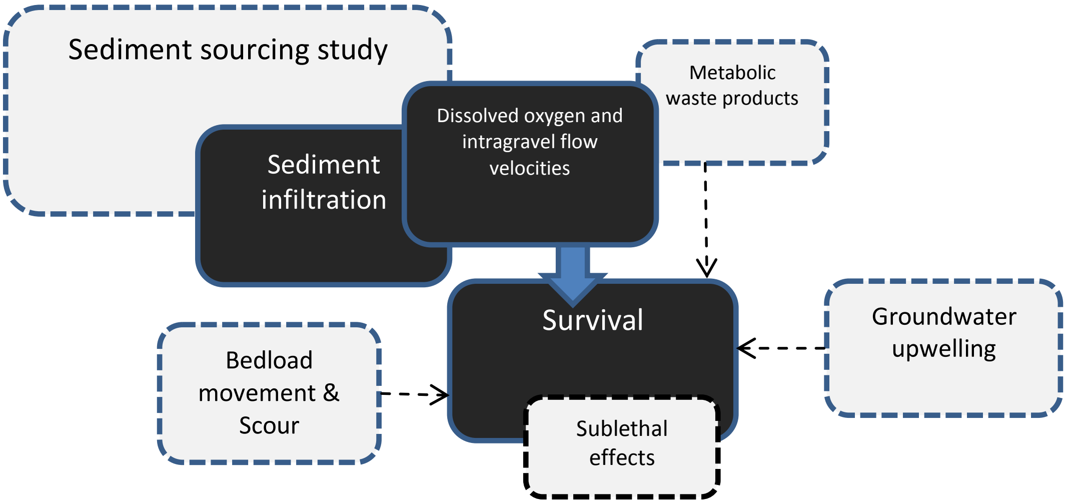


Figure 3.1. Schematic of assessments carried out - illustrating areas encompassed which have previously not been addressed collectively.

In figure 3.1, assessments with a black background are those which have traditionally been examined collectively in previous studies. The panels with dotted perimeters represent those newly added factors which may have been considered separately as driving agents of habitat quality, but have not heretofore been assessed together in this context.

The studies on sublethal effects in larvae were for the most part carried out in the laboratory, as was the geochemical analysis of sediment samples. The geochemical analysis provided the means to carry out a related study into the source apportionment of land-derived sediment from varying land-use types and in-channel sources from throughout the catchment. Sediment fingerprinting studies of this kind have found practical application in catchment management in the past decade, but few studies have looked at tracing salmonid redd sediment back to land-derived sources.

A schematic of the overall structure of the study is shown in Figure 3.2 below.

Figure 3.2 Diagram illustrating the various contributing studies comprising the whole of the Lugg project

In summary, the overarching aim of the study is to better understand the factors controlling embryo survival and fitness in spawning habitats. The methodological approach is integrative and is a new manner of addressing the subject of spawning habitat quality. Previous studies have looked at lone parameter indicators of mortality / habitat degradation, but this study addresses the need for multi-parameter and interdisciplinary studies to be carried out.

The study encompasses multiple environmental parameters - grainsize and sediment accumulation and characteristics, as well as groundwater intrusion into the egg zone and relates these to survival. The study looks not only at survival indices of environmental quality but also investigates at a finer resolution by addressing the sub-lethal effects of environmental parameters on the organism.

3.2 Contextual field site information

3.2.1 Catchment Characterization

The Lugg catchment was pre-specified by the funding body (the Environment Agency) for this study and is one of a series of case study priority catchments nominated via the England Catchment Sensitive Farming Delivery Initiative (ECSFDI), in partnership with the Environment Agency, Natural England, and Defra. The river has also been designated a Special Areas of Conservation under the EU Habitats Directive. The catchment is an important tributary of the river Wye which is a designated area of Outstanding Natural Beauty of ecological importance as a historically abundant salmon fishery (Environment Agency 2002, Jarvie et al 2004).

The Lugg is a cross-border catchment with its source near Pool Hill in Powys, Wales. It flows across the Welsh-English border beyond the town of Presteigne, into the county of Hereford where it flows through Leominster and then southward to its confluence with the river Wye near Mordiford.

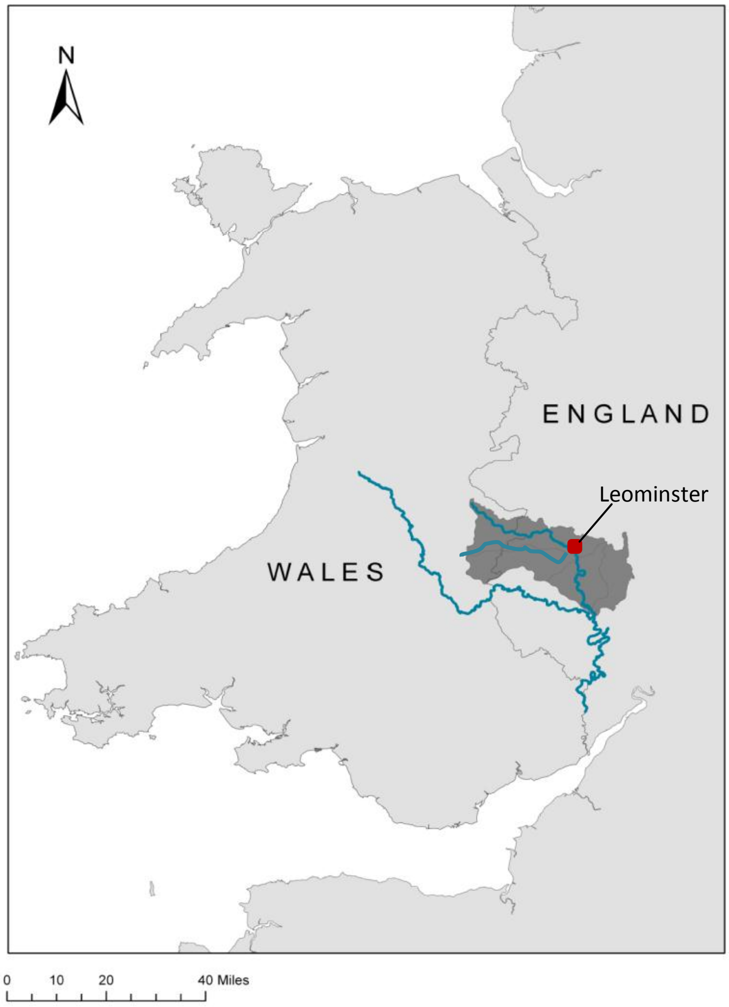


Figure 3.3 The River Lugg catchment location showing its cross border status and relationship to the river Wye.

The river Lugg is the largest tributary of the river Wye and is a 4th order stream to its confluence with the river Arrow where it becomes 5th order. The Arrow is a 4th order stream with its source at Gwaunceste Hill in Powys, Wales.

The Lugg has a catchment area of 1077km^2 to its confluence and is characterized by both upland and lowland river types. The Lugg catchment area upstream of the town of Leominster became the focus of the study due to its importance as potential spawning habitat and to limitations in accessing the lower reaches of the Lugg. The tributary river Arrow was also included in the study area since it provides similar spawning habitat while possessing contrasting soil types and drift geology.

Upstream of Leominster, pool and riffle morphology exists over a gravel/cobble bed whereas downstream the river is deeper and slower over a clay/ silt bed. The river reach type from Mortimer's Cross to Leominster is classed as transitional, having mainly clay river features but with additional coarse substrates.

3.2.1.1 Glaciation History

The river was affected by the last ice age (c. 18k BP), when the Devensian glaciation was active in the region. The actions of the Wye glacier in particular had a dramatic influence on the course of the rivers Lugg and Arrow and on the drift geology that is seen in the area today (Cross 1966). An ice mass escaped from central Wales eastwards and filled the small Lugg, Arrow and Teme valleys to the west. Further south, a large mass of ice from the Wye valley spread over the Hereford basin in an extensive piedmont lobe - now referred to as the Wye glacier (Cross 1966, Luckman 1970).

The Wye glacier extended across the Hereford basin and was enclosed to the north by the Silurian escarpment which marks the northern flank of the Lugg valley today. The limit of the glacier is marked by a large deposits of moraine extending from Kington (SO307574) in a north-westerly direction to Orleton (SO490670) - about 7km north-west of the Amestrey gorge (Dwerryhouse and Miller 1930).

The Kington-Orleton moraine consists mainly of red till of Devonian age mixed with some erratic Silurian deposits from the west such as siltstones, gabbro and dolerite. The moraine varies in content and depth throughout its length but reaches depths of up to 30m in some places such as Shobdon and Titley Mill.

Further east of Mortimers Cross (SO428 637) the moraine becomes less evident and outwash sands and gravels become dominant (Luckman 1966).

The advance of the ice also impounded and diverted the pre-glacial rivers which were mainly flowing in a north-south direction from the Silurian escarpment (Dwerryhouse and Miller 1930). The pre-glacial Lugg left the Presteigne basin and flowed southwest via the Byton gap. With the advance of the ice, this gap was blocked and the river eventually found recourse through a gorge near Kinsham formed from an overflow of an ice-marginal lake. This temporarily joined the Lugg with the Limebrook valley but was also soon blocked and the river once again diverted – around the moraine formed at Covenhope SO (408641) through the gorge at Sned wood, which remains its present course (Luckman 1970).

Another aspect of the diversion created by the glacial advance was the original course of the river Teme, now situated to the west, which originally flowed through the gorge at Amestrey and then southwards along the valley now occupied by the Lugg. This valley is markedly large since this paleochannel was a larger river with many more tributaries than the Lugg, and is now a good example of a river valley 'misfit'.

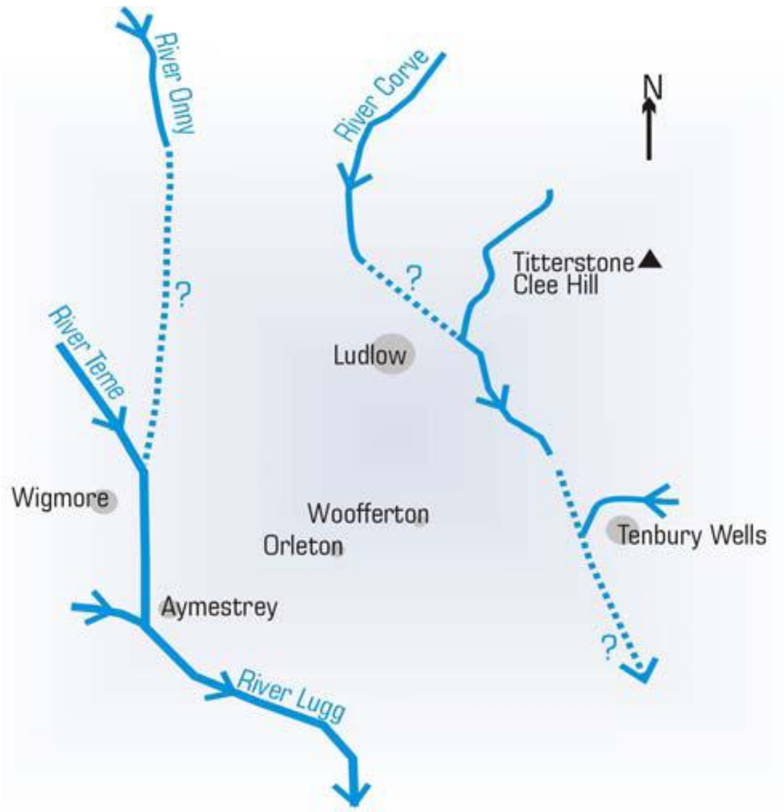


Figure 3.4 Illustration of the Lugg as part of the ancient Onny and Teme river network flowing in a North-South direction. From Rosenbaum (2007)

The Arrow also underwent considerable modification and rather than flowing through the 30m deep valley that cuts south from Lyonshall, cut eastward across a series of drift-infilled valleys and rock interfluves (Luckman 1970).

Artifacts of this glaciation history are in evidence on the drift geology map (figure 3.6) where deposits of glacial till and moraine gravels can be seen throughout the catchment.

3.2.1.2 Catchment characteristics

The following section outlines the main catchment characteristics in terms of relief, geology, soils and land use.

Elevation

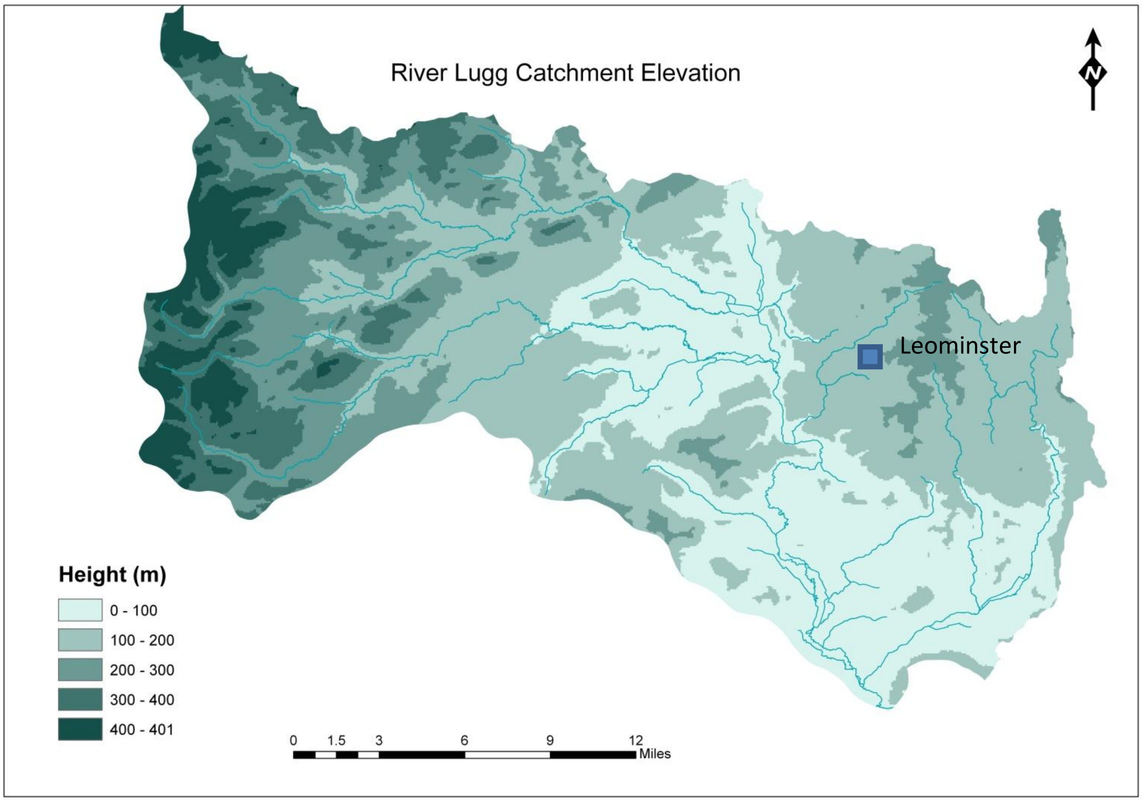


Figure 3.5. Lugg catchment elevation (Source – CEH Wallingford)

Geology

The Lugg catchment could be described generally as impervious in its upper reaches but of sandstone geology further downstream. It also holds extensive valley gravels and sands which provide some base-flow and moderation of flood peaks (Marsh and Lees 2003, Wade et al 2007).

From the source, the river drains an upland area including Radnor forest which is underlain by Silurian mudstones and siltstones, and bedrock geology is the dominant influence on channel form.

Numerous small springs feed the headwaters and combine to cut a steep-sided and rock-bottomed section, descending over 200 m in the first 3 km. The Lugg’s extreme upper catchment is underlain by Silurian rocks and the river has a typically high-energy erosive character. From the border with England, the underlying rock is predominantly non-calcareous and is principally Old Red Sandstone of Devonian age, with some limestone outcropping at Aymestry Gorge. The presence of old Red Sandstone is thought to moderate high flow peaks during wet weather events, and a base flow index value of 0.66 indicates the presence of groundwater in these areas (Marsh and Lees 2003).

Changes in bedrock and river gradient are reflected in the channel substrate. Alluvial deposits are laid along the riparian zone upstream of Amestrey gorge and some glacial moraine deposits are evident in the area around Leominster, with further till dotted about the catchment in a SW-NE direction (evident as grey colouring on map) and may contribute to minor aquifer sources. Along the stretch from the border to Leominster the average flow is fast, with a well-developed pool and riffle system and a river bed predominantly of cobble, pebble and coarse gravel.

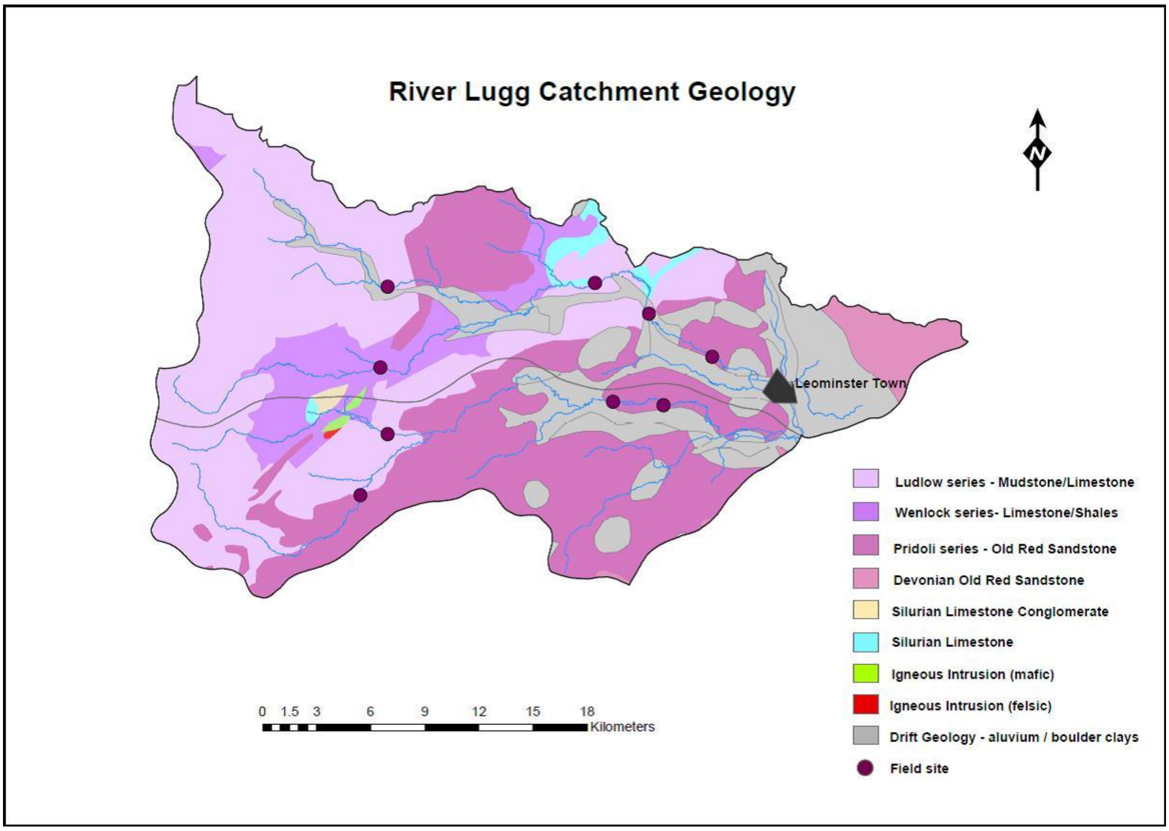


Figure 3.6 Lugg catchment geology with drift geology and field site locations.(Source BGS)

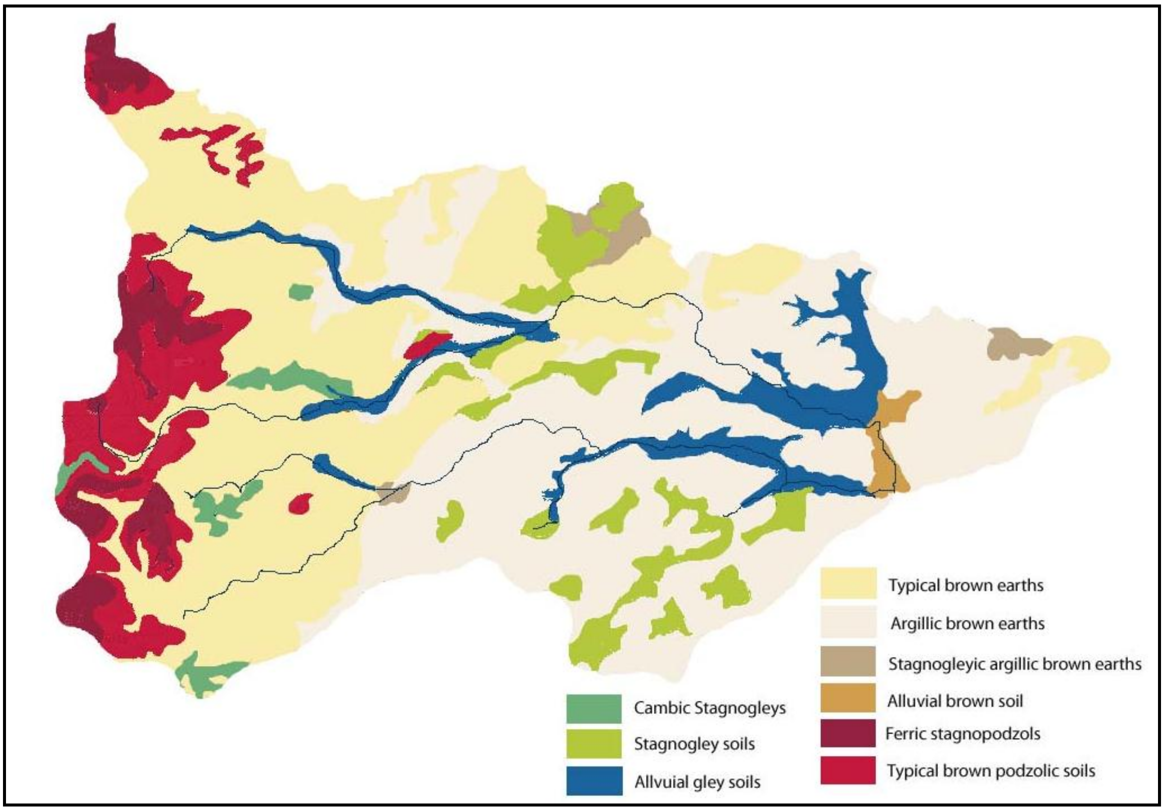


Figure 3.7 Soils map of the upper Lugg catchment (adapted from BGS detailed map)

Soils

The soils in the upper catchment are dense with medium to low permeability. Some alluvium and glacial sands and gravel occur in places along the river channel. There are three main soil types associated with the catchment and these are the Munslow (typical brown earths), Teme (alluvial soils) and Escrick (argillic brown earths) series. The Munslow series is derived from siltstones, has a silty-loamy texture and is particular to this region. The Teme series is a medium-silty river alluvium and carries with it a risk of flooding and erosion. The Escrick series is reddish sandy loam and associated with the underlying old red sandstone. Like the Munslow series, it is particular to the region.

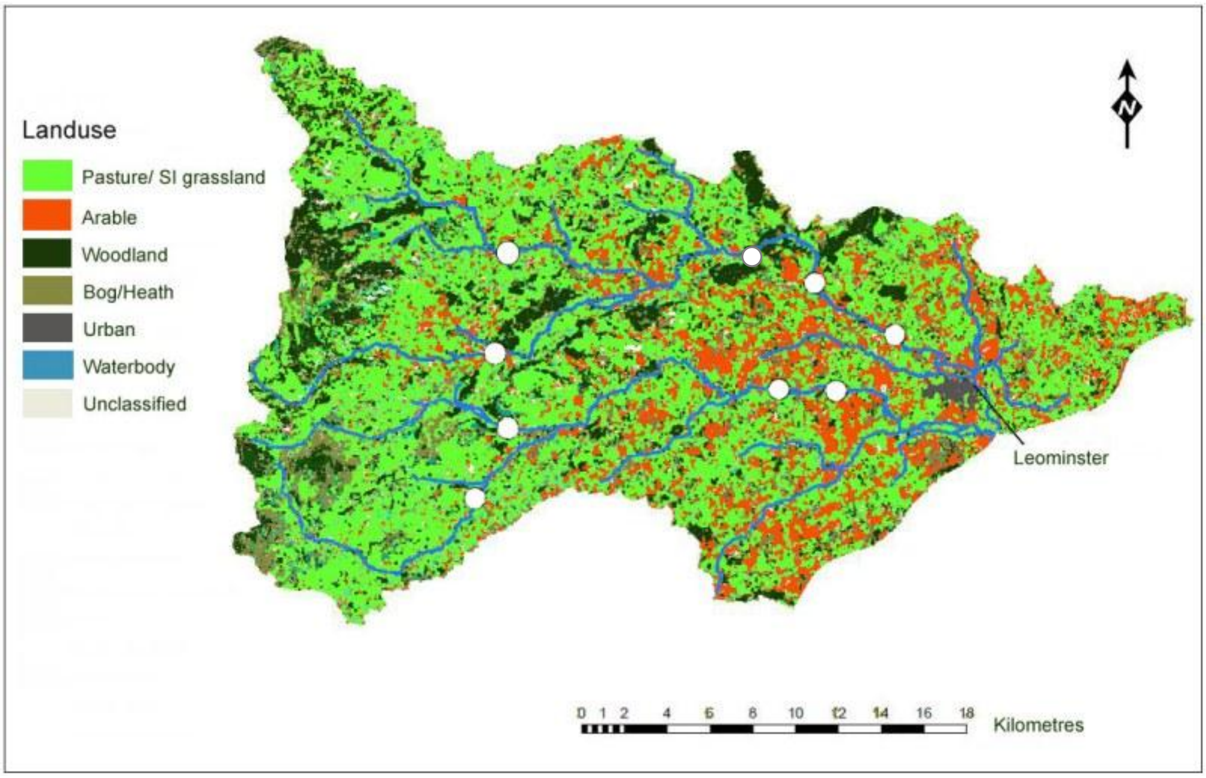


Figure 3.8 Land use distribution in the entire Lugg catchment (Source CEH Wallingford - data derived from CEH Land cover map 2000). Orange areas denote arable land, light green areas, grazed turf and dark green areas denote woodland – which is more prevalent in the upper area of the catchment.

Land use

Land use in the Lugg catchment is mainly dedicated to pasture and arable production. Grassland and woodland dominate in the upper part of the catchment, with some woodland and increasing arable production towards the mid to lower reaches (Lord and Anthony 2000). In terms of livestock, sheep dominate in the upper parts of the catchment with increasing cattle production in the middle and lower reaches. Additionally, some pig and poultry production is seen mainly in the Arrow catchment and the Lugg below Leominster (Wade et al 2007).

Hydrology

The hydrological regime of a river will depend on its underlying geology and the depth and nature of overlying material. Where the geology is entirely impermeable with little or no overlying deposits a freshet regime will usually result. Freshet type regimes exhibit quick responses to precipitation events, rapidly increasing in discharge with levels falling off soon after the event subsides (Dunne and Leopold 1978, Sear et al 1999).

Where the underlying geology is permeable such as in chalk streams, the hydrological response tends to be more gradual as the porous underlying rock accommodates the water thus tempering the storm flow (Sear et al 1999, Howden et al 2004). This generally leads to a delayed peak response as groundwater fed sources contribute to the increased flow. A slower recession limb will also be evident on the corresponding storm hydrograph.

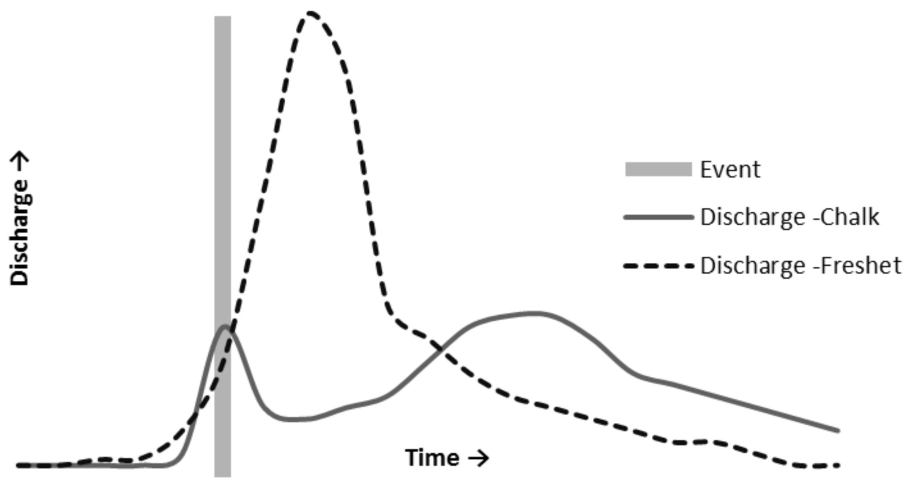


Figure 3.9 Typical storm hydrographs of response types for 1) chalk and 2) freshet streams

Between the two extremes of permeable to impermeable, a range of hydrological responses may occur depending on the degree of porosity or fracturing of the bedrock and on the nature of any overlying material. Drift material such as alluvium, soils, glacial till and gravels may potentially act as shallow aquifers regardless of whether the bedrock is impermeable (Burt 1992). In their study of catchment sediment delivery to the Lugg, Wade et al (2007) reported a base flow index of 0.66 for the whole catchment, reflecting both the impervious Silurian headwater geology and the more permeable sandstone coupled with drift geology lower down, and indicating the possibility of a substantial groundwater component.

Chalk and other permeable catchments tend to have a more stable hydrological regime than freshet rivers and their lower overall suspended sediment yields reflect this. Since bed stability is lower in freshet streams, the residence time of any infiltrated sediment is likely to be shorter than observed in permeable regimes (Burt et al 1996, Sear et al 1999).

In terms of sediment transport resulting from storm flows, freshet regimes will produce sediment yields of an episodic nature, in response to high flow events (Walling and Webb 1992). Sediment yield during these events can be derived from overland flow as well as from channel bank erosion (Walling and Amos 1999). The bulk of the sediment will be washed downstream during the rising limb of a storm flow event, but with infiltration of sediment into the gravel occurring during the slower flow of the recession limb (Carling 1992, Walling and Amos 1999).

The residence time of any infiltrated sediment within the gravel bed matrix is dependent on the mobility of the bed, the frequency of high flow events and the depth of initial penetration of the sediment (Carling 1992).

Table 3.2 below shows data from studies on sediment yields from catchment types of contrasting lithologies.

River	*Lithology*	*Sediment yield* *(T km Yr -1)*	*Reference*
Test	Chalk	11.9	Essaney 1983
Trent	Limestone	10.2	Wass and Leeks 1999
Chitterne	Chalk	2.4	PSYCHIC project
Piddle	Chalk	11	Walling and Amos 1999
Devon rivers	Mixed Clay/Sandstone	24 - 90	Walling 1978
Torridge	Shale/Slate/Sandstone	89	Nicholls 2000
Smisby	Extensive drain system	80	Walling et al 2002
Usk	Mudstone/sandstone	46	Brookes 1974

Table 3.2 Sediment yield data from studies carried out on UK catchments.

As discussed above, the Lugg is a river with a chiefly freshet hydrological regime in the upper catchment. Freshet regimes typically result in sediment transport events during high flows which are of an episodic and seasonally-based nature (Burt 1992). The discharge response to precipitation is usually fast with overland with throughflow being the main sources of water. The quick response generally subsides soon after the precipitation event, with rapidly decreasing discharge once the source has ceased. Summer flows are generally low – interrupted by episodic higher-flow events due to summer storms and showers. Winter base flow is higher with an increased flood risk (Burt1992).

The presence of areas of overlying drift in the upper catchment, including glacial clays, sands and gravels, may serve to slow the hydrological response and temper high-flow events and act as a minor aquifer giving base flow index values that are higher than would be seen in an entirely impervious catchment (Hinton et al 1993, Wade et al 2007).

In figures 3.10a and 3.10b below, the seasonality of flow in both the Arrow and Lugg is highlighted. The flashy discharge regime typical of these upland rivers is evident; with some flood peaks reaching up to $60 m^3 s^{-1}$ on the Lugg and $40 m^3 s^{-1}$ on the Arrow.

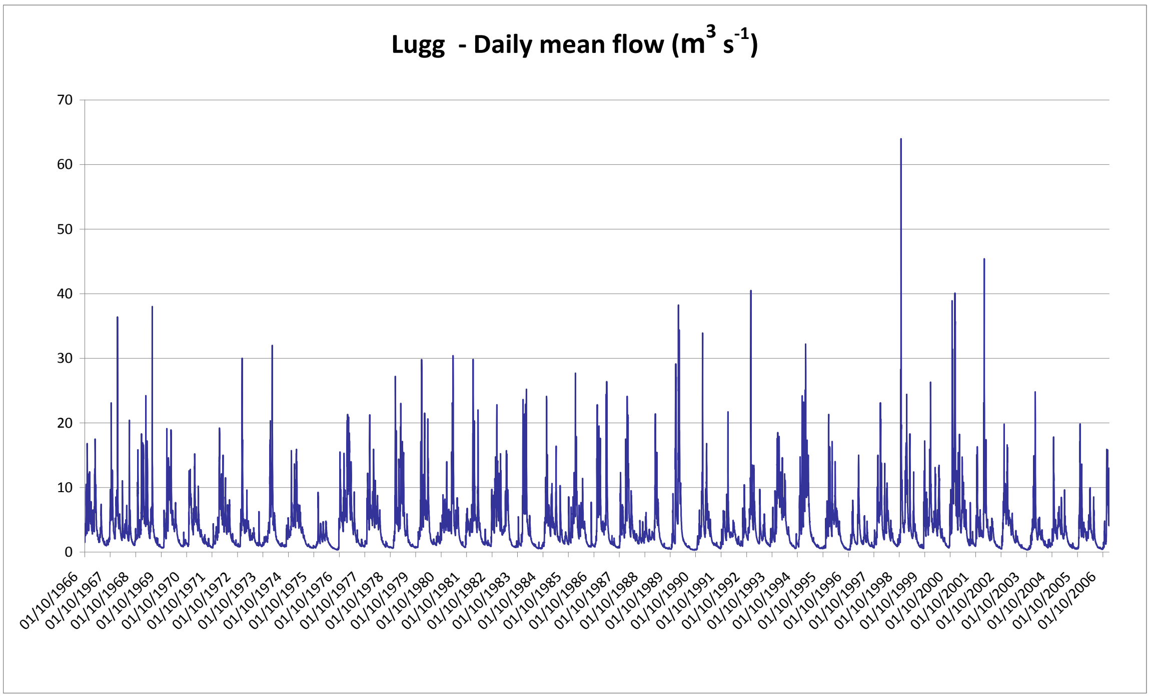


Figure 3.10a Discharge (daily mean flow) for the Lugg at Byton gauging station from 1966 - 2006

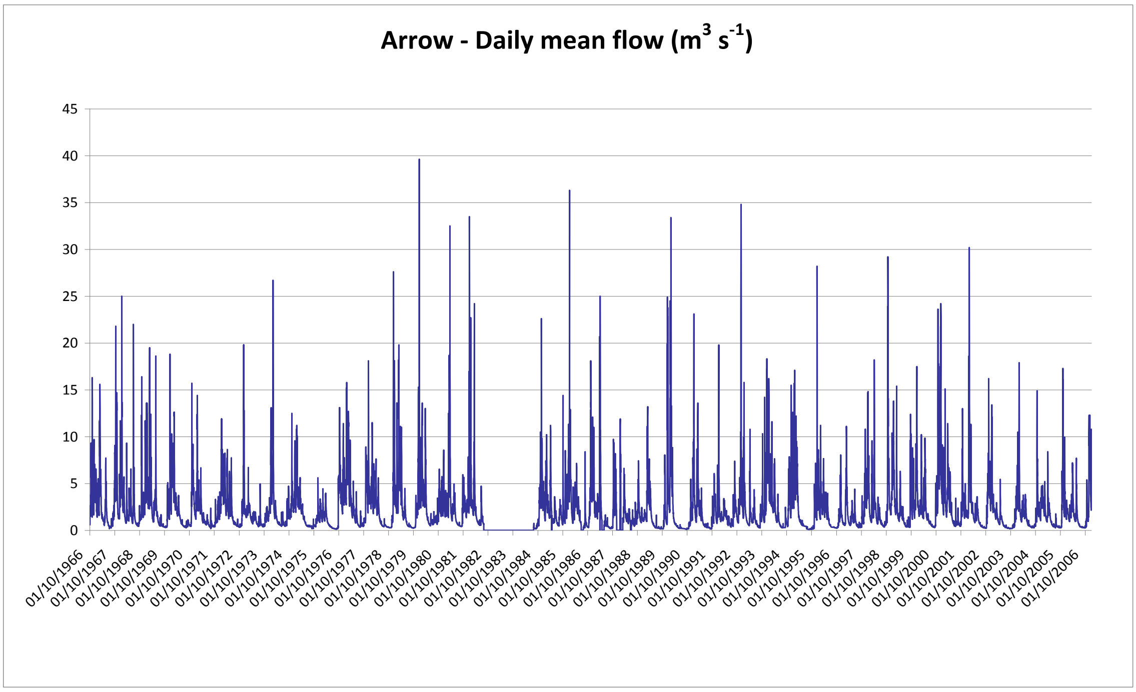


Figure 3.10b Discharge (daily mean flow) for the Arrow at Titley Mill gauging station 1966 -2006

Summary of Lugg catchment characteristics:

National Grid Reference	SO 172 746 (Lugg source) SO 176 553 (Arrow source)
Altitude mean (m)	300
Catchment Area (km²)	1077
Stream Order	3
Discharge (mean) ($m^3 s^{-1}$) 95% Exceedance: 10% Exceedance:	 0.633 8.766
Runoff (mm)	394
Mean Precipitation (1966 – 2006) (mm)	1048 (Lugg above Leominster)
Mean Temperature (1966 – 2006) (°C)	10.15
Baseflow index	0.66

Table 3.3 Summary of Lugg catchment hydrological characteristics

3.2.2 Habitat

3.2.2.1 Ecological community and general status

The Lugg is described as having mainly 'good' ecological status in it upper reaches, excepting the Summergill brook reach which was classed as poor in a recent EA report (2008). The ecological status of most of the Arrow is classed as 'Moderate' (EA 2008). During 2006 water quality sampling campaign, the Arrow at Eardisland and Pembridge is documented as having slightly high BOD (biological oxygen demand), very high solids and high phosphate (EA Lugg sediment mobilization and delivery report 2006).

Flora	**Fish**	**Birds & Mammals**	**Invertebrates**
Liverworts: *Pellia epiphylla* *Solenostoma triste*	Brown trout *Salmo trutta* Grayling *Thymallus thymallus* Atlantic salmon * *Salmo salar*	Dipper *Cinclus cinclus*	Atlantic stream crayfish **Austropotomobius pallipes*
Moss *Rhynchostegium riparioides*	Minnow *Phoxinus phoxinus*	Kingfisher *Alcedo atthis*	Signal crayfish *Pacifastacus leniusculus*
Red algae *Lemanea fluviatilis* *Hildenbrandia rivularis*	Stoneloach *Noemacheilus barbatulus*	Common Sandpiper *Actitis hypoleucos*	Mayflies *Ephemeroptera*
Water-crowfoot *Ranunculus penicillatus*	Bullheads * *Cottus gobio*	Sand martins *Riparia riparia*	Demoiselle Fly *Calopteryx virgo*
Branched Bur-reed *Sparganium erectum*	European eel *Anguilla anguilla*	Common Otter **Lutra lutra*	Pea mussel *Pisidium tenuilineatum*

Table 3.4 Species communities of the upper Lugg catchment (Species protected under Council Directive 92/43/EEC)*

The upper Lugg flora consists of sparse aquatic vegetation due to high flow and unstable riverbed. Encrusting and filamentous algae typically occur here with liverworts moss commonly found. There are a few higher plants present, especially in the peaty pools near to the river's source where intermediate water-starwort *Callitriche hamulata*, water-purslane *Lythrum portula* and round-leaved crowfoot *Ranunculus omiophyllus* can be found.

Species diversity however is poor, with lower plants constituting over one-third of plant species present. The pollution intolerant red algae are found in parts of the river course which act as reliable pollution indicator species (Natural England SSSI report 2007).

In a recent Defra report (SC070043), Whitehead et al (2008) showed predictions of the INCA model which simulates flow, water quality and aquatic plant ecology in these rivers under future climate conditions. The model showed that the ecological dynamics of large water plants (macrophytes) and smaller plants or algae on their surfaces (epiphytes) interact significantly. They suggest that increased drought could create problems by increasing nutrient concentrations. With more sunshine and reduced flows, epiphytic growth will be stimulated at the expense of macrophyte growth.

3.2.2.2 Fisheries

The Lugg upstream of Leominster holds brown trout with plentiful grayling present. Historically it has also been a rich area for salmon, but the counts have fallen drastically over the past 30 years (EA 2007, WUF 2009). Coarse fish are less common above Aymestry which until the installation of a fish pass in 2007, also marked the upper limit of Atlantic salmon migration. Spawning salmon have been sighted in more recent years (2009, 2010) on the Arrow at Eardisland, and on the Lugg above Lyepole bridge (Pers comm. Marsh-Smith 2010). Downstream of Leominster, coarse fish including chub, roach, pike and barbel are more common.

In the Wye Salmon action plan review (DEFRA 2003), the key issues of concern for Atlantic salmon on the Wye and its tributaries were determined by a working group of officers from the Environment Agency, English Nature and representatives from local fisheries groups. The working group established a multi-criteria analysis methodology to identify the main limiting factors to salmon production on the Wye catchment. The main limiting factors identified are described in table 3.5 below:

Wye Salmon limiting factors

Access to spawning/nursery areas
Pesticides
Juvenile survival and recruitment
Compaction/siltation/loss of spawning gravels
Acidification
Eutrophication and other diffuse pollution
Commercial fisheries in the Severn Estuary
Inappropriate management of riparian zone

Table 3.5 Factors deemed limiting to salmon production on the Wye catchment (source: Defra 2003)

3.2.4 Lugg-specific pressures

Figures 3.6a and 3.6b below are based on data received from the Environment Agency Wales in 2007 and highlight the apparent decline of observed salmon fry on the Lugg and Arrow. This decline may in part be due to in observational inconsistencies but may also be indicative of a response to factors mentioned in the review above and other papers which cite the increasing sediment and nutrient inputs to the river channel as potentially causative factors (Russell et al 2001, Wade et al 2007, Deasy et al 2009).

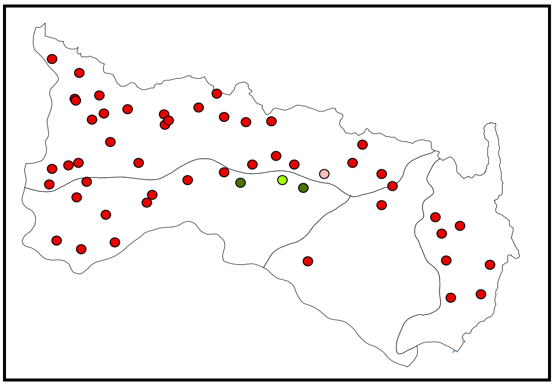


Figure 3.11a .Salmon Fry classifications 2003 (Source Environment Agency -Wales).

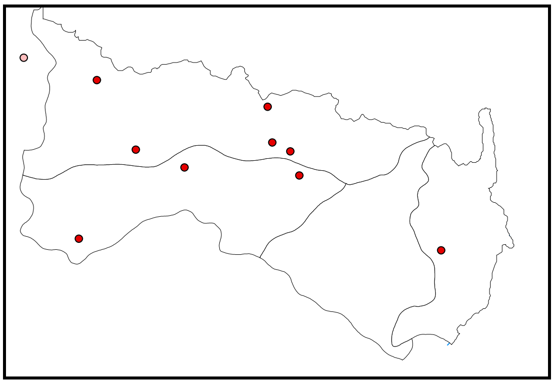


Figure 3.11b. Salmon fry classifications 2007

The PSYCHIC model (Phosphorus and sediment yield characterization project) is a process-based model of phosphorus and sediment transfers within agricultural catchments. It has been applied by Jarvie et al (2003) to the Wye catchment where high and low risk areas for the Lugg and Arrow have been identified. The model output showed overall phosphorus (P) input to the Lugg catchment to be uniformly high, and substantially higher than that predicted for the Wye catchment as a whole. P export rates are highest from Cattle and Sheep across the entire Lugg sub-catchment, with substantial rates of P export from Cereal and Other Arable crop cultivation to the middle to lower reaches of the Lugg.

A recent DEFRA report (Project record FD 2120/PR 2008) states that overland sediment flow has increased due to changes in rainfall and land use, intensive arable farming (potato) and soil degradation caused by decreasing input of organic matter.

In the Lugg catchment, there has been an increase in arable farming, with a gradual land use changeover from grassland to arable. After a period of expansion of forage maize, this has decreased recently with the reduction in dairy farming. Sugar beet production has declined very recently, but the area of potatoes and strawberries under field scale plastic has increased. There has been a reported general increase in the use of contractors for field operations, and an increase in the use of reduced tillage systems (DEFRA 2008).

An Environment Agency report – *Severn District River Basin Management Plan* (2009) highlighted problems of sedimentation within the Lugg catchment. It states that all watercourses in the area around Leominster were shown to be at risk from diffuse inputs following rainfall events. The upper Arrow was also shown to carry high solids and nutrients. Evidence of other factors that may contribute to diffuse inputs such as bank erosion, narrow buffer strips, lack of secondary vegetation and lack of livestock fencing were also reported.

The following sub-catchments were identified as target areas for improved soil management:

Priority/ problem areas	**Problem description**	**Justification**
Pinsley Brook (Lugg)	Nutrients/silt	Failing SSSI/EA Water Quality standards
Curl Brook (Arrow)	Poultry manure/ Nutrients	Failing SSSI/EA Water Quality standards
Arrow below Kington	Nutrients/silt	Failing SSSI/EA Water Quality standards
Stretford Brook (Arrow)	Nutrients/silt	Failing SSSI/EA Water Quality standards

Table 3.6. Target areas within the Lugg catchment for soil management strategies as outlined by the Environment Agency.

The loss of riparian margins has in some places exposed the river course to increased sediment input from land-derived sources (EA report 2003). The increased risk of diffuse pollution is also a concern, mainly due to increased concentrations of nitrogen and phosphorus form surrounding agricultural land (Russell et al 2001, Wade et al 2007, Deasy et al 2009, Lazar et al 2010).

Channelization in some sections of the river has altered the stream flow conditions and correspondingly, the stream habitat; which may reduce the overall species diversity capacity in the altered sections and may interrupt connectivity for the different life stages of the salmon (Jurajda 1995, Pander and Geist 2010).

Barriers to migration pose a problem on both the Lugg and Arrow and are in recent years being addressed jointly by the Environment Agency and local fisheries organizations (EA 2003, DEFRA 2008). Between 2007 and 2010, some 16 separate works on fish passes or weir modifications were carried out, thus allowing spawners access to the Welsh headwaters of the Lugg and Arrow for the first time in 30 years (WUF 2011).

3.3 Study site characterization

3.3.1 Study sites selection

A total of nine sites were chosen on the Arrow and Lugg above Leominster (a sub-catchment area of 371km^2) in stream reaches that reflected typical salmon spawning habitat or where they are historically known to have spawned (EA fisheries officers - Pers comm). The D50 and representative habitat parameters (stream flow, and gravel substrate) of typical spawning gravels as described in the literature were adhered to (Crisp and Carling 1989, Kondolf and Wolman 1993, Crisp 2000, Armstrong 2003, Moir et al 2004, Louhi et al 2008). Sites were also chosen to represent the sub-catchment spatially, with sites representing the major headwater tributaries as well as the main Lugg and Arrow channels.

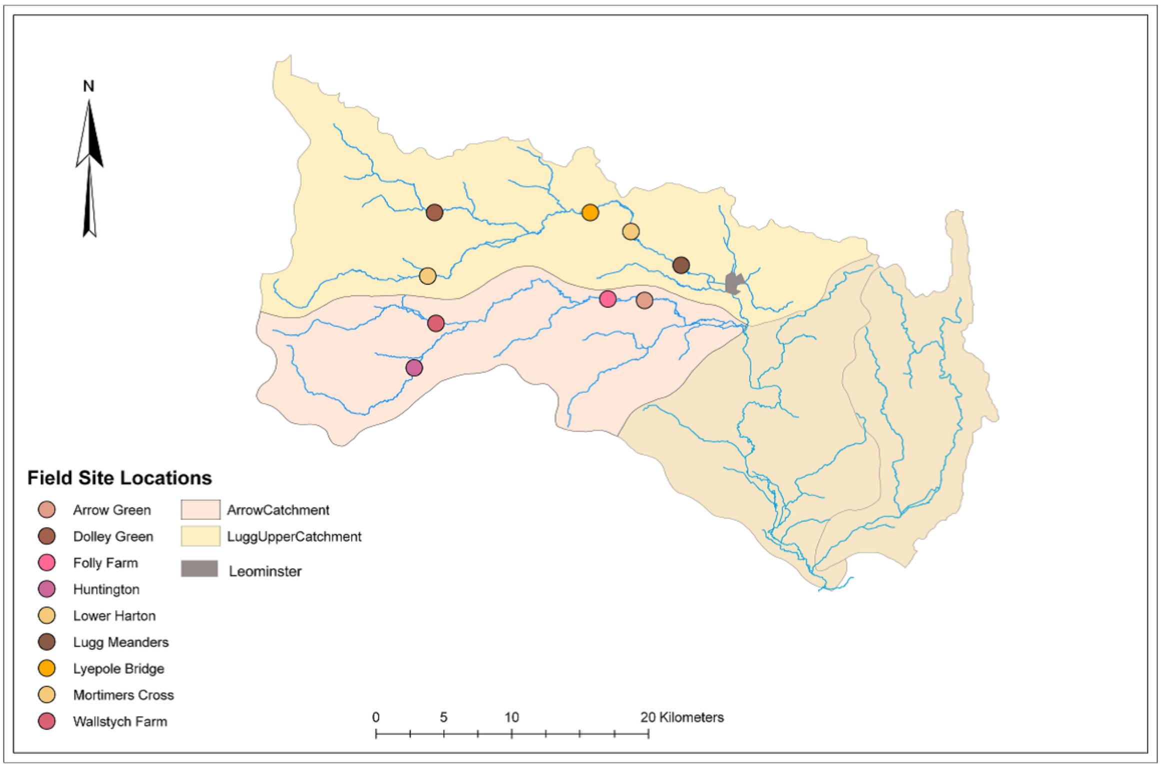


Figure 3.12 The Lugg catchment featuring field site locations.

3.3.2 Field site characteristics

Table 3.7 below highlights the main site characteristics found at each of the field sites.

Site	*Huntington*	*Wallstych*	*Lower Harpton*	*Dolley Green*
Grid Reference	SO 268 537	SO 284 570	SO 278 605	SO 283 652
Sub-catchment area (km^2)	46.77	30.1	56.97	83.64
Channel width	6.1	5.2	6.5	13.1
Spawning flow depth (cm)	15	30	25	16
Bankfull depth (cm)	40.5	125	46	36
Bankfull discharge (Q)	10.15	6.55	12.89	18.9
Reach slope (m/m)	0.006	0.005	0.02	0.0075
Stream power (Wm^{-1})	597	321	2529	1390
D_{50}	32.9	8.02	15.39	20.48
% <2mm	10	17.6	13.8	8.5
%<1mm	3.2	3.3	2.8	2.2
Main land use	Pasture	Pasture/Road	Arable	Pasture
Dominant geology	Sandstone	Mudstone	Limestone	Mudstone
Soil type	Loam, free- draining	Acidic, slow- draining	Wet soils - high groundwater	Wet soils - high groundwater

Site	*Folly farm*	*Arrow Green*	*Lyepole Bridge*	*Mortimers Cross*	*Lugg Meanders*
Grid Reference	SO 410 588	SO 437 587	SO 397 652	SO 427 638	SO 464 613
Sub-catchment area (km²)	184.32	90.25	231.44	252.08	257.77
Channel width	13.5	8.2	12	13.2	17.3
Spawning flow depth (cm)	35	11	15	32	31
Bankfull depth (cm)	96	33	64	56	55
Bankfull discharge (Q)	39.9	19.5	52.3	57.7	59.1
Reach slope (m/m)	0.006	0.008	0.006	0.0085	0.008
Stream power (Wm^{-1})	2522	1532	3078	4815	2895
D_{50}	20.51	14.16	31.37	21.66	18.32
%<2mm	14.2	16.3	11.6	10.5	10.4
%<1mm	3.1	4.2	5.0	3.7	4.0
Main land use	Pasture/ Woodland	Pasture	Woodland/ Pasture	Arable/ Pasture	Pasture/ Arable
Dominant geology	Red Sandstone	Red Sandstone	Limestone, boulder clay	Limestone, boulder clay	Red Sandstone
Soil type	Wet soils - high groundwater	Wet soils - high groundwater	Clay/loam free draining	Clay/loam free draining	Wet soils - high groundwater

Table 3.7. Summary table of field site characteristics

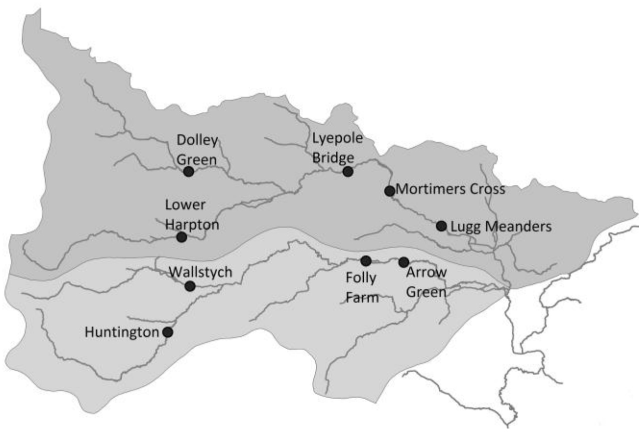


Figure 3.13a Lugg catchment field sites

	Upstream	Downstream
Huntington Location: SO 268 537		
Wallstych Location: SO 284 570		
Lower Harpton Location: SO 278 605		
Dolley Green Location: SO 283 652		
Folly Farm Location: SO 410 588		

Arrow Green

Location: SO 437 587


Lyepole Bridge

Location: SO 397 652


Mortimers Cross

Location: SO 427 638


Lugg Meanders

Location: SO 464 613


Figure 3.13b. Photos of upstream and downstream views of field site locations

3.4 Redd site monitoring program

3.4.1 Methodological approach

The study involved two main field campaigns carried out during the 2008 and 2009 salmon spawning seasons, between the months of January and April. A further study at one site location took place during 2010.

The 2008 field study adopted an integrated approach, looking at survival responses to sediment infiltration and other environmental parameters at 9 field sites. This was done in order to gain an overall assessment of habitat quality of the upper Lugg and Arrow and an insight into the degree of spatial and temporal variability within the spawning gravels, as well as to test new technology such as the continuous monitoring dissolved oxygen probes which were installed at one site (a higher–resolution 'Supersite') for the duration of the spawning season.

The 2009 field campaign looked at both survival and sub-lethal responses to sediment infiltration and other parameters at 3 field sites and was linked to a series of laboratory tests for sublethal effects.

A major part of the 2009 field study was the investigation into the presence of groundwater-surface water interactions as have been advocated by Malcolm et al (2003, 2005). To this end, piezometers and dissolved oxygen probes were installed in the river bed to sense pressure and oxygen gradients, both of which are commonly used to distinguish between different masses of water (ie: groundwater and surface water). During the field season of 2010, an experiment investigating levels of dissolved oxygen concentration at a range of depths was carried out at Lyepole bridge site. This was done to complement information on piezometric readings and dissolved oxygen levels at the site during 2009 and 2010 for groundwater–surface water interactions.

Tying in with the sedimentary effect investigations, a parallel sediment sourcing study was also undertaken, which involved analysis of redd sediment and catchment soil samples taken from each of the 9 field sites and from contrasting land use categories throughout the catchment. The aim of the study was to provide sediment source apportionment for each of the redd sites, and define the main contributing sources.

Figure 3.14 and Table 3.8 below summarize the parameters addressed at each site and during which field season. The following sections provide further detail on the full suite of parameters investigated, and the devices employed during the study.

The catchment map below highlights the sites which were under investigation during each of the field seasons. Blue dots indicate the 2008 season, green indicates the sites which were the focus of the 2009 investigation, and the red dot at the Lyepole bridge site indicates the 2010 study which took place there.

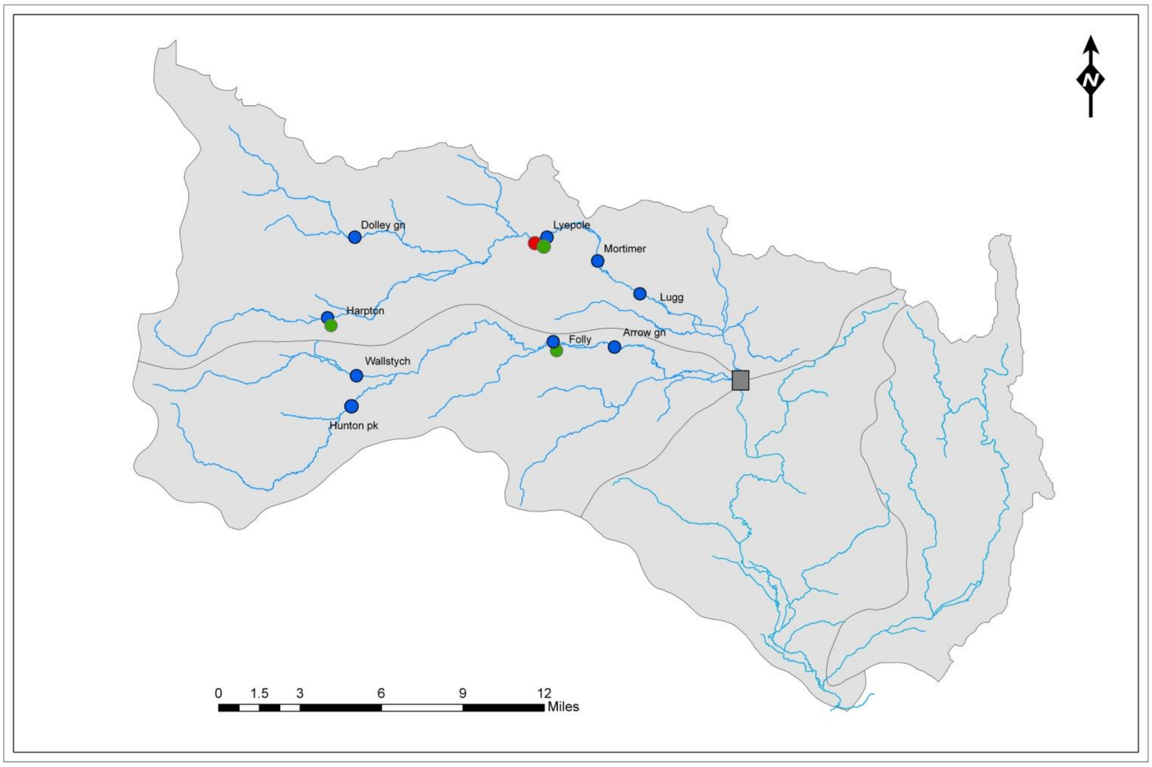


Figure 3.14. Catchment map illustrating field campaigns and site locations during 2008 (blue dots), 2009 (green dots) and 2010 (red dot).

Study focus	*Redd locations*	*Monitoring objectives*	*Equipment*
Survival and sediment studies	All sites ●	•Assess incubation success •Assess temporal trends in dissolved oxygen concentration •Assess intragravel flow velocities over period •Assess sediment accumulation (total) and rates of infiltration over incubation period.	Egg baskets Sediment baskets Standpipes Anoxia stake Scour chain
GW-SW interactions **Sublethal studies** **Water quality** **Bedload impacts**	Sites: ● Lyepole Folly Farm Lower Harpton	In addition to the above parameters – (●), also measured were: • Continuous dissolved oxygen monitoring at all sites • Piezometers installed to measure pressure variations within bed • Dissolved oxygen concentration via silicone tubing to basket • Nitrogenous compounds monitored via Nalgene tubing •Baskets retrieved periodically for sub-lethal testing in laboratory •Bedload movement monitored • Soil and redd sediment samples retrieved for fingerprinting study	Egg baskets Sediment baskets Dissolved oxygen and temperature probes Metal frame holding multiple baskets and silicone tubing Standpipe Piezometers Bedload impact sensors
GW-SW interactions **Dissolved oxygen with Depth** **Piezometer readings** **Bedload impacts**	Lyepole ●	•DO and temperature concentrations measured at 4 different depths to ascertain thermal and DO gradients. •Piezometer installed to measure pressure variations within bed. •Bedload impact sensor installed to monitor bedload movement.	Long outer casing (steel mesh) 4 Anderaa probes Piezometer Impact sensor

Table 3.8 : Summary of redd types and locations of each. Field sites are numbered from 1 – 9 with increasing distance downstream as follows: Huntington (1), Wallstych (2), Dolley green(3), Lower Harpton (4), Folly farm (5), Arrow green (6), Lyepole bridge (7), Mortimers Cross (8) and Lugg Meanders (9).

A summary of the environmental variables measured and corresponding equipment installed over the course of the study is detailed in table 4.7 below.

Variable	Equipment	Sampling frequency
Dissolved Oxygen (stream and redd zone)	Subsites: YSI 250 DO Probe Supersite: Anderaa probe	Weekly and bi-weekly 10 min
Temperature (stream and redd zone)	Subsites: YSI 250 DO Probe Supersite: Anderaa probe	Weekly and bi-weekly 10 min
Conductivity (stream and redd zone)	Conductivity metre	Weekly and bi-weekly
Intragravel flow velocity	Conductiometric standpipe	Weekly and bi-weekly
Pressure differential	Piezometers/Schlumberger mini divers™	Continuous
Suspended Sediment	Isokinetic samplers	Continuous
Suspended Sediment	ISCO™ pump samplers	12 hours
Discharge	Environment agency Gauging station	15 min (where available)
Turbidity	Partech™ IR40C probe	10 min
Bedload movement	Bedload impact sensors- with 'tinytag' logger	10 min
Data Logger (supersite only)	Delta-T Devices DL2	10 min
Stage	Gauge board	Weekly and biweekly
Anoxia	Anoxia stakes	Continuous
Scour	Scour chains	Continuous
Redd-site river cross sections	Dumpy level	Once during incubation period

Table 3.9. Summary of environmental variables measured, equipment installed and the frequency of sampling intervals at the Lugg field sites.

3.4.2 Artificial Redds

In order to assess the effects of sediment and other environmental variables on egg survival in salmonid redds in the field, consideration of the most appropriate monitoring devices for the multi-parameter scope of the field campaign was made. With regard to monitoring of redd sedimentation and oxygen flux within the redd environment, a number of methods have been previously used by researchers in the field.

One of the most frequently used methods is the monitoring of natural redds by means of emergence traps placed upon the stream bed to enable the capture of the emergent alevin and a subsequent separate core or bulk sampler then used to examine the gravel content and size distribution (Chapman 1988, Reiser et al 1998, Meyer 2005). However, emergence traps were not deemed suitable for this river system due to frequent spate and high discharge events which are especially prevalent during the spawning season and incubation period. Events of such magnitude would likely remove emergence traps and influence sedimentation dynamics.

Natural redds, although most representative of actual conditions encountered by salmonid embryos, are both difficult to monitor without emergence traps and require installation of monitoring equipment which may compromise the natural status of the redds. Additionally, it was not feasible in the light of EA restrictions on the disturbance of natural redds. Thus, a field campaign using artificially built redds was thought the most appropriate approach.

Artificial redds enabled the ease of insertion of both eggs and sediment monitoring equipment along with further monitoring apparatus at the time of building. In addition, artificial redds enabled investigation of the spatial variability within and between reaches, and allowed monitoring of conditions in the immediate vicinity of the egg pocket, which may not have been possible under natural redd conditions.

The chief concern in redd building was to seek to emulate natural redd conditions as far as possible. To this end, the location of the redd sites were carefully chosen on or near current or historically active spawning grounds, and the construction and dimensions of the redds were set according to the studied parameters and characteristics of average-sized natural redds (Crisp and Carling 1989, Crisp 2000, Armstrong 2003). This is discussed further in section 7.1.

Supersites

The wide spatial breadth of the 2008 campaign involved monitoring 9 separate sites and as such, there were limitations on the degree of resolution that could be applied to each site in terms of continuous monitoring equipment installed. It was decided therefore to set-up a site location (termed the 'Supersite') where high-resolution monitoring devices were installed and sediment infiltration monitored with higher frequency.

The site at Lugg Meanders (2008) was designated as a Supersite as were the Lyepole and Lower Harpton sites during the 2009 campaign.

At the Lugg Meanders site, continuous oxygen and temperature probes were installed and logged at 10-minute intervals throughout the spawning season.

Additionally, a pressure transducer and turbidity probe were installed upstream of the redd site to enable more precise measurement of the stage and suspended solids respectively, of the river.

During the 2009 season, two of the three sites were considered supersites, with high-resolution gauging of the above environmental parameters.

In order to obtain a temporal representation of the rate of infiltration of sediment, over the field season at the Lugg Meanders supersite, multiple baskets were planted for sequential retrieval at set intervals throughout the incubation period. This enabled plotting of sedimentation trends at these sites, and comparison with discharge and suspended sediment data. Also, a clearer view of which stages of development mortality occurred at became feasible with this approach. The redd site set-up for each of the field seasons is described in further detail in sections 4.2 and 6.2.

3.4.3 Sediment Accumulation

Sediment content is often measured within the artificial redd in the pocket where the eggs reside but is sometimes measured separately in a nearby location using bulk samplers or sediment collectors (Zimmermann and Lapoint 2005). Sediment collectors used in this type of study include perforated boxes filled with gravel (Wesche et al 1989), solid-walled cans with open tops (emphasizes downward infiltration) (Lisle and Eads 1991), and cylindrical mesh baskets (Sear 1993, Acornley and Sear 1999, Greig et al 2005).

The design used to monitor sediment involved placing open baskets of dimensions 12 x 24cm which were surrounded at the base by a compressed bag with attached strings extending to the gravel bed surface. The bag enabled retrieval of the basket and contents with minimal sediment loss. (Acornley and Sear 1999, Greig 2005).

Egg baskets of 7cm height and 5cm diameter were constructed with a mesh size of 2mm in order to prevent escapees post-hatching. The baskets received 100 eggs with a sieved gravel mixture – (truncated at 4mm) and secured with a mesh lid. The egg baskets were placed inside the larger sediment baskets. Both baskets had been cleared of any fine sediment of <4mm diameter by sieving, to emulate conditions found in a natural redd (Chapman 1988).

The multiple accumulation baskets at the Lugg Meanders supersite and at all 2009 sites, were smaller than the standard sediment accumulation basket, with dimensions of 7 x 20cm. The egg basket were the same dimensions as those at standard sites (5 x 7cm).

Fig 3.15 below outlines the structure and equipment installed at each of the field sites during the first field campaign.

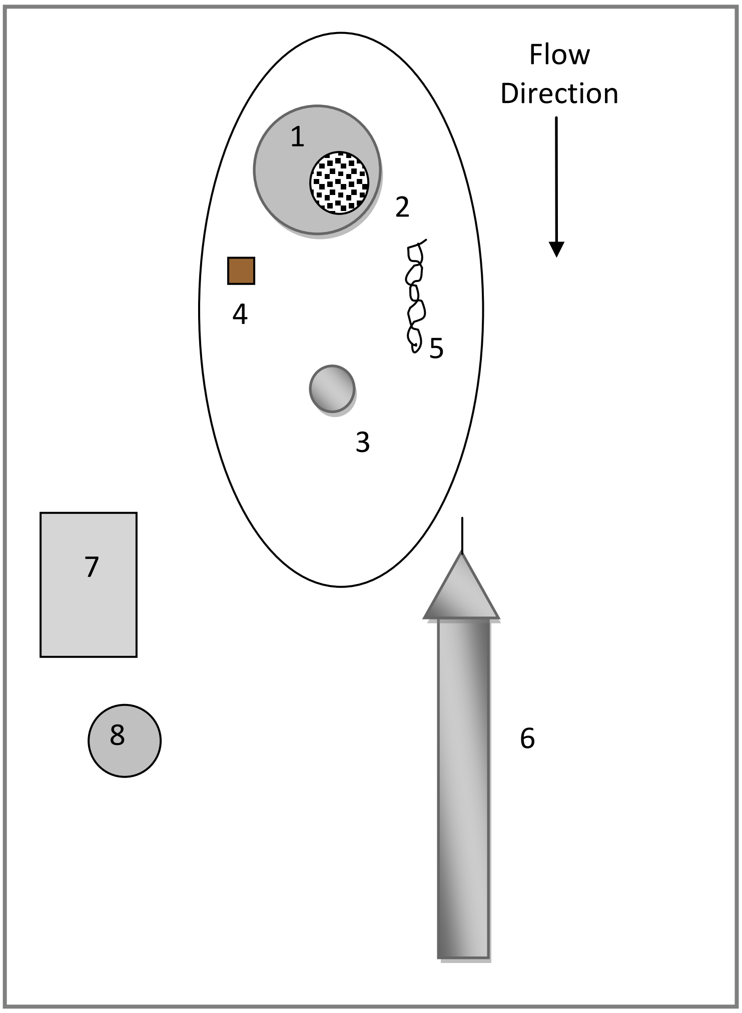


Figure 3.15. Plan view of redd set-up: 1. Sediment basket, 2. Egg basket, 3. Standpipe, 4. Anoxia Stake, 5. Scour chain, 6. Isokinetic sampler, 7. Data Logger, 8. Water Sampler.

3.4.4 Monitoring of redd conditions

The intragravel environment, and in particular the salmonid redd zone, is reported in much of the literature as a challenging habitat to sample and assess. Observations must be carried out by proxy as the environment is by nature occluded from view. Researchers have traditionally chosen either to extract samples (Malcolm 2003, Heywood and Walling 2007) for later analysis or to insert monitoring equipment to record some parameters of the environment (Grieg et al 2005, Meyer 2007).

In the first field season, it was decided to deploy standpipes at each of the field sites, as they were deemed versatile in that they could be used to record information on multiple parameters, and measurements were relatively quick to take. Given the scale of the investigation especially in the first field season, the standpipe technique seemed favourable to our needs.

The standpipes consisted of 100mm long sections of perforated stainless steel, with an aluminium retractable sheath of 260mm. The device was opened by pulling up the aluminium sheath and exposing a maximum area of 60mm of perforated steel – allowing pore water to enter the tube and measurements of water quality and flow to be taken. Closure by pushing down the aluminium sheath, insertion of a cylindrical sponge and a rubber bung ensured that the tube remained free of sediment while buried in the riverbed. Figure 3.16 below outlines the standpipe design and method of use.

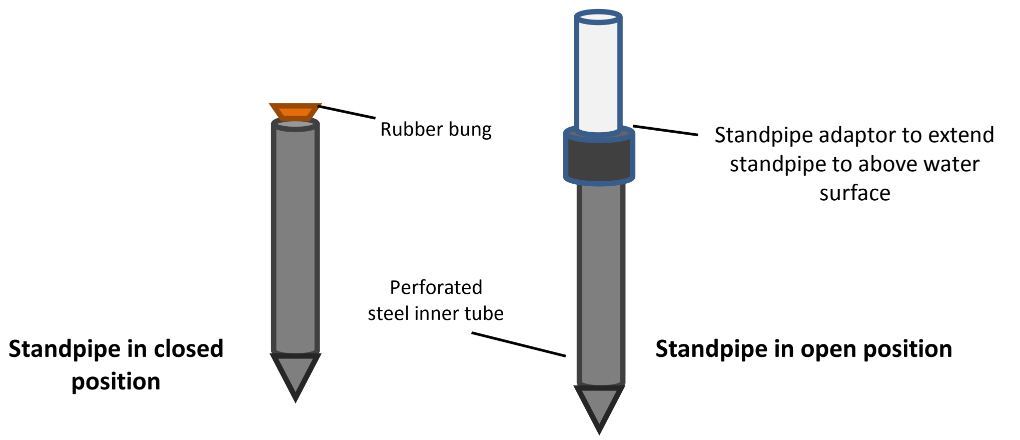


Figure 3.16. Diagram of the standpipe design used for monitoring the intra-gravel environment

Standpipe measurements

Intragravel flow velocity was measured via the conductiometric standpipe technique (Carling and Boole 1986) during periodic visits to the field sites. The intragravel flow was calculated based on the rate of dilution of a saline/alcohol solution. The decline in conductivity during the dilution timeframe (20 minutes) was recorded at 10 second intervals onto a Datahog™ logging device, and post-sampling comparison of the exponent of the decay curve with calibrated dilution curves (Grieg 2004), allowed estimation of intragravel flow velocities (cm/hr). The lower limit of the probe's response is 1 cm h^{-1}, and velocities below the probe's threshold of response are reported as 1 cm h^{-1}. At velocities less than 200 cm h^{-1}, the probe's level of accuracy (standard error) has been defined as 18 cm h^{-1}; and at velocities exceeding 200 cm h^{-1}, the level of accuracy has been defined as 16 cm h^{-1}.

Dissolved oxygen measurements were made via handheld YSI 250™ dissolved oxygen probe, which also recorded water temperature within the redd zone.

Conductivity (in µS/cm) was recorded with a separate Siemens™ metre before the intragravel flow measurements were taken.

In the second field season, standpipes were also deployed, but additional nalgene™ tubing was inserted into the egg zone and extending to the river bed surface thus enabling extraction of egg zone water samples, and allowing both testing for nitrates/nitrites and comparison of dissolved oxygen measurements between the two sampling methods.

Table 3.10 below details the parameters, methods and equipment used in measuring the intragravel environment during the 2009 field season.

Technique	**Parameter**	**Device**	**Units**
Standpipe	Dissolved oxygen concentration	YSI Model 250 Dissolved oxygen probe	Mg/l^{-1}
Standpipe	Conductivity	Siemens™ conductivity metre	µS/cm
Standpipe	Temperature	YSI Model 250 Dissolved oxygen probe	°C
Standpipe	Intragravel flow velocity	Conductiometric standpipe	Cm h^{-1}
Extraction	Dissolved Oxygen Concentration	YSI Model 250 Dissolved oxygen probe	Mg/l^{-1}
Extraction	Temperature	YSI Model 250 Dissolved oxygen probe	°C
Extraction	Nitrogenous compounds (NO_2,NO_3,NH_4)	Nitrite test kit – API Pharmaceuticals	ppm

Table 3.10 Intragravel measurements carried out during the 2009 field season

3.4.5 Egg deployment

Eyed eggs, supplied by the Wye and Usk and Cynrig hatcheries in Wales, were used for this study. Green eggs are extremely sensitive to movement and touch from 36 hours post fertilization up to eyeing time, and thus pose a risk of shock-induced mortality when green eggs are used for experimental field trials (Koski 1966, Bardonnet and Bagliniere 2000).

With this consideration in mind, it was decided to use eyed eggs which were placed directly into newly built redds. Although this signifies a compromise on exact conditions that may be encountered by embryos over a full incubation period, it was considered the surest method of arriving at survival estimates without risking mortality due to handling of sensitive green eggs. Additionally, extension of the field study until predicted emergence time ensured that the embryos and hatched larvae were given adequate time to experience a representative range of infilling and flushing that may occur over the given period. Studies have shown that in the absence of scour and flushing events, most infilling of redds occurs within the first few weeks and that the rate of infill decreases thereafter (Heywood and Walling 2007). Prediction of emergence time was calculated using a temperature–dependent model of development (Gorodilov 1996).

3.4.6 Water quality tests

Tests for water chemistry were carried out to investigate the concentration of nitrogenous compounds within the incubation zone, due either to endogenous waste products which were not being readily evacuated, or to inputs from outside the redd zone.

Nitrites and nitrates are products of ammonia breakdown, both of which are toxic to fish (Kincheloe 1979, Daniels 1987). Testing for nitrogenous compounds throughout the incubation period also allowed consideration of this potential hazard when assessing sublethal effects.

3.5 Monitoring of Groundwater influx

Section 2.9 highlighted the potential impacts of groundwater inputs on the incubation zone of embryonic and larval salmonids (Soulsby et al 2001, Malcolm et al 2003, Malcolm et al 2004). Groundwater-surface water interactions in the hyporheic zone, and hyporheic water qualities, have been shown to vary with stream discharge fluctuations (Malcolm et al 2004).

The chemical, biological and physical properties of surface water and groundwater are known to differ. Depending on the underlying geology and related chemistry, a variety of processes may occur, leading to transformation, precipitation, or sorption of substances that will be distinct from the overlying surface water and thus create a means of detecting groundwater influence within the hyporheic zone water (Boulton et al 1998, Malcolm et al 2003, Soulsby et al 2001, Soulsby et al 2009, Krause 2009).

A number of methods are commonly used to look for groundwater contributions. Hydro-chemical 'tracers', such as stable oxygen and hydrogen isotopes, are sometimes used to distinguish rainfall event flow from pre-event flow, because rain water often has a different isotope composition than water already in the catchment (Kendall and Caldwell 1998). Geochemical tracers, such as major chemical parameters (e.g., sodium, nitrate, silica, conductivity) and trace elements (e.g. strontium), are often used to determine the fractions of water flowing along different subsurface flow-paths (Cook and Herczeg, 2000). Additionally, differences in temperature often occur between the different water bodies, and this can be used to infer interaction if temperatures are measured on a vertical plane within the river gravels (Greig et al 2005).

To ascertain whether groundwater interactions were contributing to conditions in the incubation environment, an assessment of potential groundwater upwelling was made at each of the field sites. This aim was achieved through investigation of both hydro-chemical and hydraulic parameters at the redd sites.

3.5.1 Hydro-chemical assessments

Conductivity was chosen as an indicator of groundwater upwelling during the first field season due to its ease and economy of employment – a simple conductivity metre can give accurate results. The principal behind the method is that groundwater frequently contains a higher concentration of dissolved solids depending on the aquifer and route via which it passes. Thus, any difference between conductivity of redd zone and that of the stream water may indicate some groundwater-surface water interaction (Soulsby et al 2001).

Conductivity measurements were taken at all sites throughout both field seasons 2008 and 2009. Using the standpipes installed within the redds, measurements were taken at approximate 10-day intervals throughout the incubation periods and compared with similar measurements for the overlying stream water.

3.5.2 Hydraulic assessments

To understand the interaction between groundwater and surface water, we can look at the vertical components of groundwater flow and ascertain any discrepancy between expected hydraulic head and observed. The discrepancy can be attributed to groundwater upwelling altering the pressure gradient within the hyporheic zone.

For this study, pressure sensors were used to calculate hydraulic head. Schlumberger™ Mini-divers were installed at depths of 50cm at 2 field sites (supersites) during 2009, and during 2010. The divers measured pressure and temperature at pre-programmed 10-minute intervals and logged the data for retrieval at the end of the field season.

Additionally, pressure transducers were installed at the same location but at stream bed depth to enable calculation of the hydraulic gradient with respect to stream depth.

3.5.3 Vertical trends in dissolved oxygen and temperature

During the 2010 season at the Lyepole site (figures 3.12 and 3.14 above), it was decided to investigate the vertical variability in dissolved oxygen and temperature. This was done to build on evidence of groundwater influences on the redd environment within the catchment. Anderaa probes were deployed in an artificial redd at depths of 30, 45 and 60cm over the field season and logged via a Delta-T device at 10-minute intervals throughout the field season. Further details and corresponding results are presented in section 6.8.

3.6 Additional environmental parameters

3.6.1 Bedload impact sensors

The contribution of spate events to sediment load, infiltration and dynamics within the hyporheic zone, as well as surface gravel movement occurring during the spawning season, may have an impact on the subsequent survival of salmonid embryos. Thus the installation of bedload impact sensors, which recorded any impact above a pre-defined level throughout the period, could be of use in determining any causality between spate events and scour, mechanical shock, sediment infiltration or flushing and the survival/fitness of incubating embryos/larvae.

One of these devices was installed just downstream of the redds during 2009 and 2010 at the supersite locations, to record any bedload movement which might contribute to scour and mechanical shock of the riverbed in the vicinity of the redds.

The impact sensors were originally developed by Richardson et al (2004), and designed to record sediment movement in bedrock channels. They consist of a metal plate with an integral acceleration sensor and logger unit in a watertight housing attached to its underside. Upon being struck by a clast, the sensor counts the impacts detected within a pre-programmed 10 minute interval. The data was stored in the internal memory for retrieval at the end of the field season.

3.6.2 Cross section and topographic surveys

Surveys of each of the stream reaches were undertaken to characterize the channel and to aid calculations in sediment load and discharge.

3.6.3 Freeze cores

In addition to the incubation experiments, freeze core samples were taken at each of the field sites from both artificially-constructed redds and undisturbed river-bed gravels as per the method developed by Carling and Reader (1981). This was done to assess the difference in particle size distribution between ‘cut’ and ‘uncut’ redds and to compare the measured fine sediment from the artificial incubation zones with the uncut freeze cores. The technique is discussed in further detail in section 4.1

3.7 Sublethal Effects study

In additional to studies on survival in the field and their influencing factors, studies into possible sublethal effects of these factors were also considered.

As highlighted in figure 3.14 and table 3.8 above, this was a chief aim of the 2009 field season and the approach involved examining specimens retrieved from the river gravels at the predicted emergence time for that year's cohort.

In order to ascertain whether sublethal effects were being experienced by alevins from a particular site, three separate tests were used as proxy indicators of sublethal stress. The use of 3 proxies was considered a more robust approach to assessing the overall health and fitness of the emergent alevin. A brief outline of each of the sublethal tests is provided below. Further details are found in section 7.2.

3.7.1 Whole body Cortisol

Cortisol is a hormone which is released in teleosts as in higher animals, in response to environmental conditions which it perceives as stressful (Wedemeyer et al 1981, Adams 1990, Schreck 1990). Physiological compensation to stress is a natural response involving the well documented 'fight or flight' mechanism, but chronic stress, even at low levels, may impair performance by diverting energy resources that might otherwise be used for routine activities: growth, immune function, and/or reproduction (Barton and Iwama 1991, Barton et al 2002).

The quantification of blood concentration of this hormone has been used in many studies to indicate the level of stress experienced by an organism. A delay in metabolism of cortisol between perception of a stress and release of the hormone has singled it out as a practical tool in fisheries research as it allows measurement of pre-existent stress levels rather than a potential stress response due to experimental intervention (Schreck 1990, 2000, Barton 2002, Sink 2007).

Extraction of cortisol was achieved via a whole-body extraction procedure developed by Sink et al 2007, which enabled the analysis of hormone levels of individual fish, rather than expressing the mean value of a number of individuals.

An enzyme immunoassay test for cortisol was carried out on individual samples from each of the cohorts against a hatchery control to test for differences in cortisol concentration.

Further details of the tests and results are presented in chapter 7.

3.7.2 Behaviour

Behaviour is often used as an endpoint in environmental and toxicological studies because an animal's behaviour represents an integrated expression of its physiological response to its environment (Fuiman 2006, Murphy et al 2007).

The behaviour of an individual within a cohort and an ecosystem as a whole can have repercussive effects on its long term viability (Cada 2003). In particular, an individual's ability to escape a predatory attack is the most immediate example of how differences in fitness can impact on likelihood of survival to later life stages (Fuiman 1986, Hale 1996).

Studies on fish responses to both artificial stimuli and actual predators have both been used to assess an individual's escape potential and have been shown to agree (Fuiman et al 2006).

For this study, the escape response to an artificial stimulus was measured via slow motion video technology, and resulting swimming velocities and distances travelled were recorded. Comparisons of each cohort's performance were made with each other and against a hatchery control.

3.7.3 Ontogenic state

Suboptimal oxygen concentrations can also slow growth and result in fry with a smaller mean weight (Koski 1966, Hamor and Garside 1977, Tappel and Bjornn 1981). Thus, in order to discern whether the alevin cohorts had been affected by suboptimal conditions, the developmental state of each sample individual was assessed according to a system of predicted ontogenic states developed by Gorodilov (1996), which defines a series of described 'states' characterized by the appearance of certain key physiological features.

The system is based on defined 'states' of development which may be reliably predicted according to stream temperature in an optimal environment. The unit of measurement; the 'Tau unit', is the time taken to form a somite pair at a particular temperature. By tracing the temperature history of the stream temperature during incubation, the expected developmental state may established. By then comparing this state with the observed state of the specimen, deductions on the degree of developmental retardation can be established.

Further details on the components and characteristics of key states are given in section 7.2.1. Implementation of this third proxy again involved comparisons between each of the cohorts and against a hatchery control.

3.8 Model Applications

3.8.1 Fingerprinting Study

As mentioned in section 2.12, the fingerprinting of sediment found in river beds is a relatively new practice that may help to elucidate the sources of the material found in salmonid redds, ascertain whether they are allochthonous or autochthonous in origin, and discover what kind of spatial and temporal variation in sediment content exists between redds in the same river catchment. Additionally, determination of whether certain land use types are more prominent at certain redd sites and whether they may be related to survival indices was considered.

For this study, sediment samples from all redd sites and 50 soil samples from four land-use types throughout the catchment were analyzed for geochemical properties. Suites of elements were then derived in order to establish a set of defining characteristic 'fingerprints' for each of the land-use types. A mixing model was applied (as per Collins and Walling 1997, 2006, 2007) to ascertain the best match between the redd samples and each of the soil types, thus indicating the probable provenance of the redd sediment. This topic is further addressed in chapter 5.

3.9 Operational limitations of field strategy

Artificial redds: While building artificial redds was the only practicable option for studies of incubation in the field and efforts were made to emulate the structure and characteristics of natural redds, the possibility that conditions in natural redds differ from artificial constructs should be recognized, and so any estimates of survival must be more accurately described as % survival as pertaining to artificial redds.

Oxygen and flow measurements: These measurements were made in redd locations that were proximal or adjacent to the egg zone but not actually within. Therefore, small-scale spatial variations within the egg zone may be unaccounted for in these readings.

In addition, measurements of any kind were impossible during spate events which occurred around the 15th of March 2008 during the incubation period and so oxygen measurements remain unaccounted for at some sites during these periods (excepting for Lugg Meanders where continuous DO measurements were made by means of a buried probe and a logging device).

Baskets: There were considerations that the sediment and egg baskets that were used may have had an influence on the infiltration mechanism and flow paths through the redd but porosity for the baskets was 90% and 85% respectively so it was concluded that any influence on depositional and flow interactions would be minimal.

The action of retrieval sometimes caused difficulty where the bag became snagged on part of the basket and retrieval of sediment was compromised due to some loss at the top of the basket. This occurrence was rare but did constitute a rethink as to the future design and retrieval action of the bags.

Standpipe (in situ): The design of the in-situ standpipes was such that the action of opening the standpipe after a period of dormancy caused some difficulty at some sites. Some fusing of the outer casing seemed to have taken place at some redd-sites, with the resultant uncertainty whether an 'opening' action was causing the entire standpipe to emerge from the redd or simply the outer casing. A modified design was deployed for the next field season. Also, during spate events and high water levels that followed, measurements of DO, temperature, conductivity and intragravel flow were impossible even with the standpipe adaptor applied, so some measurements were impossible to make.

Conductiometric standpipe: The probe's diminished level of accuracy at low velocities has been recognized (Grieg 2004). It was also found that during spate conditions at some sites, the readings recorded were erratic - with numerous 'spikes', and did not reflect the expected dilution decay curve.

Isokinetic samplers: Spate events again interfered with the smooth functioning of this equipment. The nozzle through which collection of suspended solids occurred sometimes became bent so as to project at an angle into or sometimes out of the stream. This resulted in some short periods of data loss before the situation was rectified on discovery of the fault. At one site, the entire sampler was washed downstream during an extreme spate event. Considerations for subsequent field seasons included a sturdier design for the Isokinetic samplers.

Scour chains: some of the scour chains could not be found at the end of the field season– perhaps an indication of deposition at that location, but the possibility of human error in spotting chains that did become discoloured over the months submerged must also be considered. Evidence of scour was however found at some of the sites. Improvements to the scour chains might include increased visibility throughout the incubation period and ease of implantation.

Groundwater: The potential impacts of low-oxygen (high residence time) groundwater has been another issue highlighted (Malcolm et al 2003). We did not check for this phenomenon during the first field season, but considered it a variable for measurement in subsequent field season(s) at the Lyepole Bridge and Lower Harpton sites.

Seasonal conditions: As mentioned above, some readings were omitted due to flooding which made access to some of the sites on the visit of 18^{th} March 2008 impossible.

Freeze Cores: The corer device used did not always retrieve a representative portion from each depth. Some of the cores attempted did not freeze sufficiently to the corer and emerged without sediment attached. A second or third attempt usually produced more successful results.

Chapter 4

Sediment dynamics and accumulation in the Lugg catchment

4.1 Introduction

Sediment infiltration and accumulation into salmonid spawning gravels has been recognized as exerting a negative effect on incubation success (Harrison 1923, Hobbs 1937, Krough 1941, Hayes 1951, Wicket 1954, Cooper 1965, Koski 1966, Philips et al 1975, Tappel and Bjornn 1983, Lisle 1989, Koski 1966, Tappel and Bjornn 1983, Lisle 1989, Chapman 1988, Bjorn and Reiser 1991, Acornley and Sear 1999, Theurer et al 1998) and many studies have focused on single granular characteristics alone as determinants of larval survival (Lotspeich and Everest 1981, Shirazi and Seim 1981, 1982; Beschta 1982). Typically, parameters such as % fine sediment below an arbitrary threshold, D50, D16/D10, Fredle index and Geometric mean have been used as prognostic indices of survival (Koski 1966, Phillips 1975, Petersen and Metcalfe 1981, Tappel and Bjorn 1983, Platts et al 1983, Young et al 1991). However, other studies have shown that while sedimentary character and fine sediment may be instrumental in defining the incubation success, it is the secondary effects produced due to the presence of the sediment, which may impact survival more directly (Chapman 1988, Chevalier and Murphy 1985, Greig et al 2005).

Infiltrated sediment is thought to act via two main mechanisms; very fine silt/clay-sized sediment has been seen to have a disproportionate effect on survival (Chapman 1988, Acornley & Sear 1999, Armstrong et al 2003, Greig et al 2007), and is thought to reduce the flow of oxygenated water through the redd, thus decreasing the availability of oxygen for respiration within the incubation zone (Chapman 1988,). Secondly, where larger sand-sized particles infiltrate the gravel framework and have been reported to form a seal at the redd surface which impede the emergence of fry (Bjornn 1969 , Phillips et al. 1975 Beschta and Jackson 1979, Harshbarger and Porter 1982, Crisp 1993, Alonso et al 1996, Kondolf, 2000).

In terms of the infiltration of very fine sediment, oxygen availability may additionally be influenced by the type of sediment which is infiltrated. Organic sediment and some inorganic substances cleaving to sediment particles may exert their own oxygen demand and further deplete oxygen supplies in the redd. Recent studies have also shown that clay particles may physically cover the egg surface and physically block respiration due to grainsize particle of a similar size to the micropore canals through which the embryos respire (Greig et al 2005).

The wide degree of variation in survival studies between and within catchments relative to granular metrics alone indicates that a more complex interaction of factors may be operating than has previously been considered. As such, the transferability of constructed relationships between sediment and survival may not be valid. So, while granular metrics are fundamental to investigations into the larval /embryonic environment, emerging evidence indicates that the interaction of a suite of factors with which sediment may be linked but not principally causative, must also be addressed.

In terms of main physical effects of sediment on the redd environment, studies have shown that different size-classes of sediment will have differing effects on permeability and so affect permeability and oxygen flux into the redd system to varying degrees. (Lapointe et al 2005, Greig et al 2005).

External hydraulic forces will also control the rate of flux of water into the redd zone such as the topography of the redd which itself creates areas of high and low pressure which influence subsurface flowpaths (Sear et al 2008 , Harvey and Bencala 1993, Tonina and Buffington 2005). Reach slope and hyporheic connectivity with catchment aquifers - which can vary seasonally and depend on catchment wetness, can also influence the flow of water through redd gravels (Fraser and Williams 1998, Soulsby et al 2001, Malcolm et al 2003).

The infiltration of fine material into the redd zone is thought to be influenced by these flowpaths which can infiltrate sediment into the gravel matrix according to the differential pressure gradients produced by the form of the redd (Allan and Frostick 1999, Packman et al 2000). These studies hypothesized that sediment is infiltrated into the redd structure due to a drop in pore water pressure during times of increased flow. The mobility of riverbed gravels is thought to play a part in sediment infiltration, since the dilation of framework gravels during higher flow velocities is thought to be associated with the infiltration of fine sediment (Allan and Frostick 1999).

The action of scour and fill has also been implicated in fine sediment intrusion into the redd in mobile river beds, but which may also activate the flushing of fines during spate events. (De Vries 2008, Sear et al 2008).

Therefore, the spatial and temporal patterns of fine sediment infiltration will be controlled by a complex of factors including the topography of the bed form which influences flow paths and sediment entrainment in the redd, the porosity and permeability of the redd, the mobility of the gravel bed, the flow regime of river and the supply of sediment to the river.

Further explanation of both the mechanisms of sediment infiltration and the effects on permeability and the influence of hydraulic gradients and bedform topography have been discussed in sections 2.4 and 2.6 respectively.

This chapter presents the results of a study on sediment infiltration and dynamics within the redd sites during two field seasons relative to intragravel flow velocity and dissolved oxygen concentration.

The objectives of this section are to:

Define the sedimentary character of the field sites and incubation period by:

- Establish the suspended sediment loads for each of the field sites and seasons.
- Quantify the composition of the infiltrated sediment within the incubation zone
- Define the temporal and spatial variability in sediment dynamics at the field sites
- Examine granular determinants for their ability to predict survival
- Provide an overview of Lugg catchment sedimentary pressures in the context of wider UK studies
- Discuss the effects of sediment intrusion on intragravel flow velocities and dissolved oxygen content.
- Consider other factors which may have an effect on incubation and survival

In results and discussion of fine sediment size categories, three separate grainsizes are used. The most important fine sediment category for this study was defined at the start of the field campaign as the clay and silt sized portion (<63µm). This category is thus also reported in this chapter as the main threshold for 'fines'. However, due to comparisons necessary with suspended sediment and some significant results involving the larger sand-sized category (<2mm), it has been included in some graphs and tables. Additionally, although direct measurement of a <1mm category was not carried out in the lab, comparison of this category with other similar studies necessitated its usage in places. The derived Lugg values for this category were achieve by interpolation of the <63 µm and <2mm data.

4.2 Methods

4.2.1 Field monitoring strategy

Artificial redds were constructed during the field seasons 2008 (9 field sites) and 2009 (3 field sites) in known spawning locations or locations historically used by spawning salmon. Sediment pots were placed for the duration of the incubation period. Within the sediment pots, smaller baskets containing the fertilized eggs were positioned. This set-up was similar to that used by Grieg et al (2005) during their investigations on salmon spawning redds.

Care was taken to emulate the shape and granular structure of a natural redd. River gravels were sieved to 4mm thus clearing them of fines - effectively similar to the cleansing action of a hen salmon during redd -building. Centrum particles which are typically derived from the upper armor layer of gravel, were placed into the redd base - as are frequently found in natural redds (Burner 1951, Peterson and Quinn 1996).

In order to determine the sedimentary pressures at each of the field sites and the potential impact on larval survival, analyses of the sedimentary characteristics of the sites were carried out. The study involved three main areas of investigation;

1. An investigation into the sedimentary pressures present at each of the field sites. This involved an analysis of the pre-spawning granular characteristics of each site, the suspended sediment load and the hydrological conditions present during each field season.

2. Calculation of accumulated sediment over the field seasons 2008 and 2009 and the relative survival recorded within the redds.

3. An assessment of the effect of sediment intrusion on intra-gravel flow velocities and dissolved oxygen concentrations during the incubation period.

Additionally, in order to ascertain the mobility of the river bed gravels, two separate devices were deployed – one during each field season. Scour chains were installed during the first field season (2008), providing a broad indication of the presence of scour action at each of the nine field sites. Bedload impact sensors as developed by Richardson & Carling (2004) were deployed to gauge the number of impacts during discrete 10 minute time intervals throughout the 2009 and 2010 field periods.

'Supersites' – which recorded dissolved oxygen and temperature data at a higher resolution were installed with multiple baskets which were retrieved throughout the incubation period, were used to measure the rate of sediment accumulation over that time frame. One supersite was installed during the 2008 season and two during the 2009 season. The seasons were defined according to the natural estimated spawning time for the catchment.

4.2.2 Field methods

4.2.2.1 Freeze cores of cut and uncut gravels

Freeze-core samples from undisturbed gravels from each of the sites were taken for grainsize analysis. Four cores were taken from each of the redd sites and an average value used as representative sample. The uncut redd samples represented the undisturbed gravel composition at each of the field sites. Additionally, freeze core were also extracted from specially constructed artificial redds. These 'cut' gravel cores represented the granular characteristics of a newly constructed natural redd after winnowing of fine material from the bed. The cores were extracted via hollow steel standpipe which was inserted into the riverbed to a depth approximating the average depth of a salmonid redd. Liquid nitrogen was used to freeze exterior sediment to the standpipe after the method developed by Carling and Reader (1981). A winch system was then used to retrieve the frozen cores.

4.2.2.2 Suspended sediment measurements

Suspended sediment samples were retrieved via two methods;

1. Time-integrated isokinetic samplers

2. ISCO pump samplers (daily suspended solids)

1. Isokinetic samplers similar to those used by Phillips et al (2000) were deployed at each of the field sites during both the 2008 and 2009 seasons. The sediment samplers utilize ambient stream flow to induce sedimentation by settling within the cylindrical chamber. This enabled collection of time-integrated bulk samples for the incubation period and enabled spatial and temporal (inter-annual) comparison of suspending sediment loadings. They also enabled the collection of sufficient suspended sediment to permit particle size analysis which would otherwise have been impossible using pump sampler data alone (Phillips et al., 2000).

2. ISCO™ suspended solid samplers are automatic pumping systems which were programmed to extract single daily samples over the field period of 2009. Samples were extracted from 0.6 depth at each supersite into 1000ml bottles (pre-programmed) . This enabled determination of the daily suspended sediment load for both field seasons through creation of a turbidity – suspended solid calibration curve. The calibration curve was constructed based on measured turbidity readings (averaged for the hour around the time of the pump samplings).

3. Continuous recording turbidity probes were installed at the three 2009 supersites and the Lugg meanders 2008 supersite to monitor changes relative to discharge and to enable sediment delivery calculations at these locations.

Further details on the processing and calculation of suspended sediment loads are provided in section 4.2.3 on lab methods below.

4.2.2.3 Bedload movement

Scour Chains

Scour chains were employed during the field season 2008 in order to determine the presence and magnitude of scour experienced at each of the field sites. The chains were installed during redd creation leaving 10cm of chain exposed above river bed. The length of the exposed chains was measured during periodic visits to the field sites and any change - either lengthening or shortening of the chains was noted. Lengthening resulted from scour of the bed surface, whilst shortening resulted from deposition over the redd.

Bedload Impact Sensors

One of these devices was installed just downstream of the redds at each 2009 supersite, to record any bedload movement above a pre-defined threshold which might contribute to scour and mechanical shock of the riverbed in the vicinity of the redds. The impact sensors were originally developed by Richardson et al., (2004), and designed to record sediment movement in bedrock channels. The device works by detecting the resultant acceleration on a steel plate fixed to a rock or riverbed and counts the impacts detected within a pre-programmed 10 minute interval. The data was stored in the internal memory for retrieval at the end of the field season.

4.2.2.4 Assessment of sediment accumulation

As outlined in section 3.4.3., artificial redds were constructed into which sediment pots were placed. The cylindrical sediment pots (240mm x 120mm diameter) were constructed of 10mm mesh and were filled with freshly sieved gravel truncated at 4mm diameter to imitate the state of newly deposited natural spawning gravels.

Small baskets of dimensions 70mm x 50mm diameter was positioned inside the sediment pots and contained 100 eggs per basket. A 2mm mesh ensured that the alevin would remain within the baskets for the duration of the incubation period and until predicted emergence time. A retractable rip-stop bag surrounding the base of each sediment pot was connected via nylon strings to the gravel bed surface. This device enabled fast retrieval of the pots at the end of the incubation period with minimal loss of infiltrated material.

Single sediment baskets were planted for each of the 9 field sites during the 2008 season, and multiple baskets in grid formation were planted for the 3 sites during the 2009 season.

Diagram 4.1 below illustrates the redd setup for each field season and the basket types used.

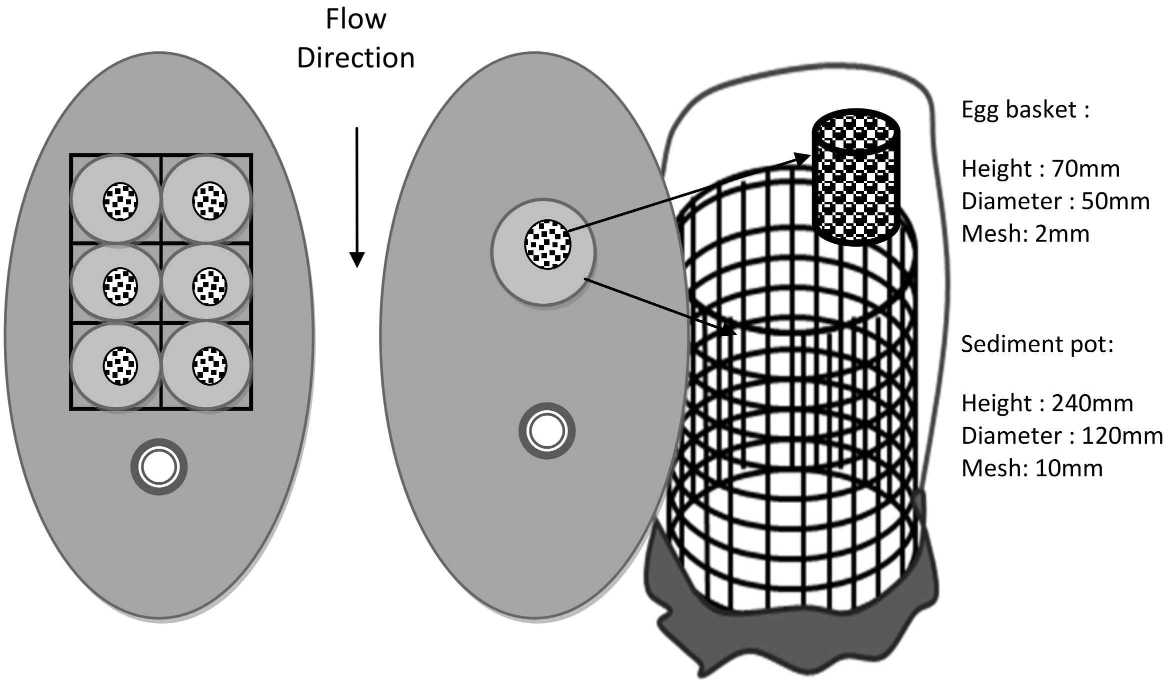


Figure 4.1 Diagrams of baskets setup used during field season 2009 (left) and 2008 (right), with standpipe location for intragravel flow measurements. The 2008 supersite at Lugg meanders had the same format as the 2009 sites.

Despite best efforts to imitate natural redd conditions as closely as possible, there remain some discrepancies; for example, the natural cleansing of redds results in a partial rather than full cleansing of fines, depending on the amount of fine sediment initially present in the gravels (Kondolf 1993). Additionally, the use of eyed eggs meant that a certain period of sediment infiltration was omitted and the embryos were not exposed to interstitial conditions for as long as they might be in the wild. Thus, our estimates of infiltration of fine sediment are representative of the conditions experienced over the period of incubation post-eyeing.

At the end of each field season, total accumulation of sediment could be calculated and grainsize distributions for each site and year determined. For the 2009 field sites and the 2008 supersite, accumulation rates were possible due to sequential retrieval of baskets from the multiple redds.

4.2.2.5 Periodic measurements

Standpipes which had been placed slightly upstream of the sediment pots within each of the redds (see figure 4.1 above) were opened and used to measure intragravel flow velocities and dissolved oxygen concentrations at approximately 10-day intervals throughout the field seasons (see Greig et al 2005, 2007). Intragravel flow velocity was estimated using the conductiometric standpipe technique (Carling and Boole, 1987) and the recalibrated equations described by Greig (2005) to obtain an estimate of velocities within the egg zone. The conductiometric standpipe technique involves recording the dilution curve of an injected saline solution in terms of conductivity. Later analysis of the conductivity decay curve allows calculation of intragravel velocity via comparison with calibrated dilution curves (See Grieg et al 2005b).

4.2.3 Lab Methods and Calculations used

4.2.3.1 Laboratory analysis methods

Particle size analysis: A two-stage particle size analysis was carried out in order to characterize each of the nine field sites' gravels. Material from both uncut and cut gravels was processed using a standard wet sieving method (Briggs 1977) to give a particle size distribution down to a grainsize of 63µms. Samples of sediment that passed through the 63µm sieve were retained as a sediment slurry to avoid aggregation during desiccation and then analyzed by Coulter counter laser particle sizer. The resulting grainsize distribution was then added to the larger grainsize data to give a full suite of grainsize distribution categories.

Infiltrated sediment retrieved from the redds were similarly sieved but since the grainsize of infiltrated sediment was mainly of interest, only smaller size sieves were used – (<4mm). Again, the coulter counter laser particle sizer was used to analyze the portion of sediment finer than 63µms.

For each sample grainsize distribution, a series of descriptive parameters were reported to enable comparison to the wider literature. These incuded the geometric mean (Lotspeich and Everest 1981), skewness, kurtosis (Trask 1931), and sorting coefficient (Trask 1932) of each sample. Other sediment size criteria - D_{10}, D_{25}, D_{50}, D_{75} and D_{90} are also given. The program Gradistat (Blott 2000) was used to enable rapid statistical analysis of the grainsize distribution of the all samples.

Organics processing: Loss on Ignition (at 550 °C for 24 hours) analysis was carried out on sub-samples of fine sediment (<63µm) from the infiltrated sediment from each redd site and from the suspended sediment from the isokinetic samplers to determine the labile organic content of each sample.

4.2.3.2 Suspended Sediment analysis

Sediment retrieved from the Isokinetic samplers was processed in a similar way as the redd sediment. Since the suspended sediment was of a very small particle size, only the

63µm sieve was employed before the samples underwent coulter counter grainsize analysis. The calculation of sediment load data involved a multiplication factor applied to the area of the inlet pipe of the isokinetic sampler. Since the velocity of the water flowing into the pipe is comparable to stream velocity, the sediment load passing an arbitrary cross-sectional width of riverbed could be calculated by applying a multiplication factor of the sampler's inlet nozzle (Phillips et al 2000) to the area of interest – with respect to average stream depth for that site. It was decided to calculate the amount of sediment (kg/s) passing a transect of width approximating that of a sediment pot, to enable comparison between accumulated sediment and suspended sediment estimates for the same time period.

4.2.3.3 ISCO Samplers

In order to create higher-resolution suspended sediment load estimates, daily sediment samples from the ISCO™ automatic pump samplers were matched with turbidity data from the same period and SS-turbidity regression models built for each 2009 supersite.

Sediment from the pump sampler was processed using laboratory vacuum pumps onto Whatman ashless grade 40 (8µm) filters and oven dried and weighed. All filters had been individually weighed prior to filtration and this weight subtracted from the complete paper and dried sample weight to obtain a sample weight to the nearest 0.1mg.

Suspended sediment load calculations were made through creation of a turbidity (NTU) – suspended solid (mg/l) calibration curve. This was constructed based on measured turbidity readings (averaged for the hour around the time of the pump samplings). At the Folly farm site, only spot samples which had been retrieved during periodic site visits were available, so a calibration curve for this was made against turbidity data.

Turbidity data was supplied by calibrated YSI 950 Sondes which had been deployed at each of the 2009 sites by the Environment Agency Wales. Discharge data was obtained from nearby Environment Agency Gauging stations and adjustments made according to the catchment area of the field sites.

Daily suspended sediment load was calculated by applying the SS-turbidity data to discharge data for each of the field sites. Additionally, by applying the Lyepole 2009 SS-Turbidity regression model to the 2008 supersite Lugg meanders turbidity data, an estimate of daily suspended sediment load was constructed. Suspended sediment load (tons) estimates for the entire field season were also made.

4.2.3.4 Limitations

Since field equipment and resources were limited, there is a need to highlight the main constraints on the river bed and suspended sediment sampling strategies and potential limitations of the resultant data.

Isokinetic samplers used during the field season have been documented to have reduced efficiency during high flows such as those experienced during the 2008 field season which was a spate year (Philips et al 2000). This may result in underestimates of suspended sediment at field sites during this season. The main spate event during 2008 resulted in some of the samplers being damaged and their nozzles misaligned from the main current. This was rectified during the subsequent field visit, but some data loss occurred due to this event. The Isokinetic sampler at Mortimer Cross site was washed downstream in the spate, so no data is available from that time onwards, for that site. Philips et al (2000) also reported a maximum efficiency of 71% when the samplers were tested in laboratory conditions. Thus there is a tendency for underestimates of suspended sediment inherent even before any reduction in functionality due to high flows or misaligned/blocked sampler inlet nozzles.

ISCO samplers provided daily samples at 9am throughout the 2009 field season. Despite relatively high frequency of sampling, the limitations here are the lack of sampling over an entire range of flows and the potential loss of the full range of sediments due to stratification of sediment in the water column. However, the samplers were placed within the riffling part of the reach at each field site, so reducing the potential stratification effect. Lastly, ISCO samplers can be susceptible to underestimates of sand-sized fractions due to isokinetic bias however, since this is more likely to occur during higher flow conditions, the low flows during 2009 year are unlikely to result in significant error.

The suspended sediment ratings curves were based on suspended sediment-turbidity relationships which had between 16% and 23% unexplained variability within the site-specific models for Lower Harpton and Lyepole bridge respectively.

The coring strategy only allowed for 4 cores from each field site to represent uncut and cut gravels. There are therefore intrinsic limitations on the resultant representativeness of samples (Church Mclean & Wolcott 1987, Bunte et al 2001).

4.3 Results

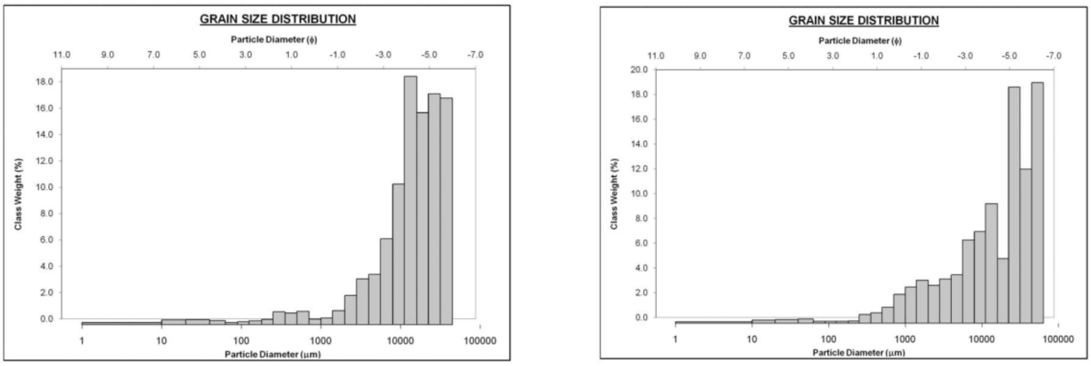
4.3.1 Composition of uncut and cut gravels in the Lugg catchment (grainsize analysis)

As described in section 4.2.2, freeze core samples were taken from newly built artificial redds and adjacent uncut riverbed. The uncut gravels represent the undisturbed state of the riverbed gravel, and the cut gravels represent the gravel characteristics at the beginning of the egg incubation period.

4.3.1.1.Composition of uncut gravels in the Lugg catchment

Generally the catchment gravels can be described as coarse to very coarse, poorly sorted, unimodal, finely skewed and highly leptokurtic (highly peaked). River gravels are generally separated into two populations; framework and matrix, where framework gravels comprise of the larger self-supporting, interlocking clasts. Matrix material consists of the smaller grainsize portion - generally of less than 1mm- 2mm diameter which settles in the interstices between the framework gravels (Carling and Reader 1982).

Bimodality can be seen in gravel bed rivers with modes occurring within the primary gravel-sized range and secondarily in the sand-size range - with a paucity of sediment in the pea-sized (small pebble) sizes (Pettijohn 1975, Kuhnle 1993, Greig 2004). The Lugg gravels however, exhibit a unimodal distribution in this respect, with only small plateau evident above the sand sized portion at 2 sites. (Lower Harpton and Dolley Green). This distribution pattern agrees with other findings where a large-scale study of Calabrian river gravels were found to be unimodal in distribution and bimodality was not a characteristic of those rivers. Another study on salmonid spawning gravels (Kondolf 1988) reported only 10% of 76 gravels inspected as bimodal.



Lower Harpton *Dolley Green*

Figure 4.2. Grainsize distribution of uncut gravels from two sites: Lower Harpton and Dolley Green. Further particle distribution plots for individual field sites are presented in the appendices.

Box and whisker plots for each of the field site uncut data is presented in figure 4.3 below. The 'box' enclosed the middle 50% of the grainsize distribution with the horizontal mid line marking the median grainsize or D_{50}. The two exterior edges of the box mark the D_{25} and D_{75} and the 'whisker's represent the D_{10} and D_{90} of the distribution. The data is plotted on a logarithmic axis for particle size to better encompass the relatively wide range of data. The box and whisker presentation was chosen for clarity of the range and central tendency of the gravels and thought a clearer alternative to a series of conventional overlapping cumulative distribution curves (See Kondolf et al 2008).

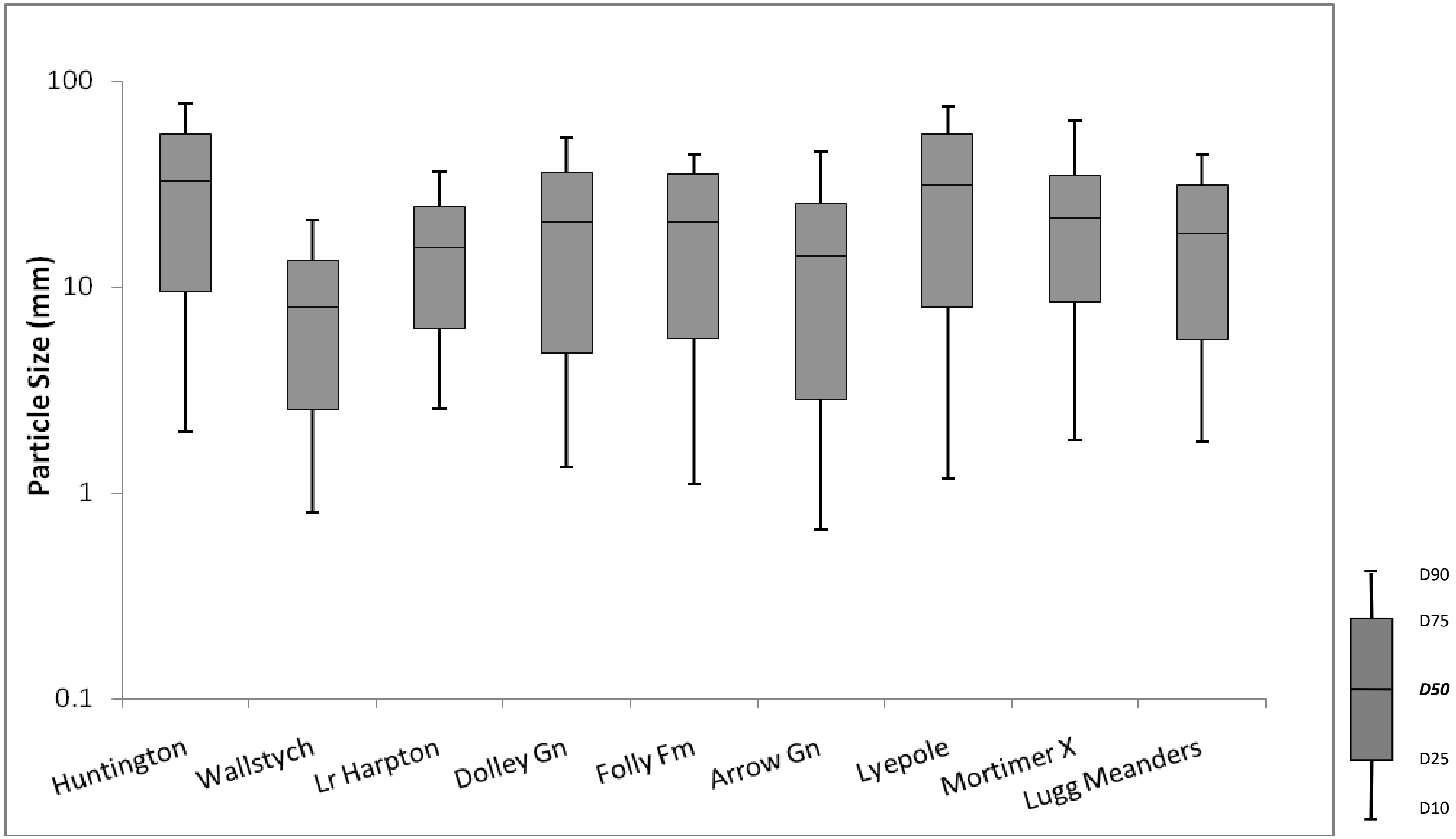


Figure 4.3. Box and Whisker plot (Tukey 1977) of freezecore grainsize distributions for each of the field sites.

There is wide variation in gravels size within the the catchment with median grainsize ranging from 8mm to 32mm. With the exception of the upper Huntington site, there is a trend towards larger median grainsize in the downstream sites.

Kondolf et al (2008) reports that in a study of 135 salmonid spawning gravels, Median grainsize diameter ranged from 5.4mm to 78mm with 50% falling between 14.5mm and 35mm.
Data from all Lugg field sites fall within this range, which is consistent with historical records of active salmon spawning throughout the river catchment, despite declines in spawning numbers in recent years.

Louhi et al (2009) reviewed findings from studies on Atlantic salmon spawning gravels and created a series of generalized suitability curves based on this data. Figure 4.4 displays spawning gravel suitability curves relevant to Atlantic salmon. Again, the Lugg gravels fit within the interquartile range of this curve.

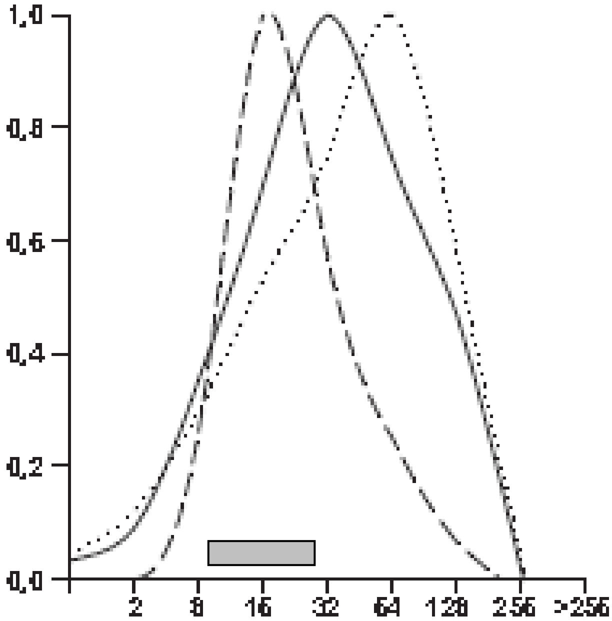


Figure 4.4 : Substratum composition (mm) in Atlantic salmon redds from other studies (From Louhi et al 2008). Dashed line represents river with discharge of <10m^{3}s^{-1}, dotted line represents river with discharge of <10m^{3}s^{-1} and solid line represents high and low discharges combined. The grey box represents the interquartile range of the combined Lugg sediments.

Salmonid spawning gravels characteristically contain less than 20% fines (<1mm) (Crisp and Carling 1989, Moir 1998). The Lugg gravels are consistent with these findings with all sites containing <12.1% fines, which are less than the predicted threshold for typical spawning habitat.

Site	D50	D10	Sorting	Skewness	Kurtosis	%<4mm	%<2mm	% <1mm	%<63µm	%<2µm
Huntington	32.1	2.0	4.52	-0.52	1.64	14.3	8	4.33	3.4	0.4
Wallstych	8.0	0.8	3.58	-0.41	1.25	29.6	11.5	5.6	3.3	0.3
Lr Harpton	15.4	2.6	3.22	-0.40	1.64	14	7.1	3.8	2.8	0.3
Dolley Gn	20.5	1.3	4.11	-0.48	1.02	20	7.6	3.7	2.1	0.2
Folly Farm	20.5	1.1	4.32	-0.57	1.19	19.7	9.1	4.6	2.9	0.3
Arrow Green	14.2	0.7	5.28	-0.52	1.25	25	12.1	6.0	3.4	0.5
Lyepole Br	31.4	1.2	5.97	-0.59	1.72	15.9	9.6	5.6	5	0.6
Mortimers X	21.7	1.8	4.15	-0.50	1.64	15.7	7.6	4.3	3.7	0.4
Lugg M	18.3	1.8	3.95	-0.46	1.54	15.3	8.3	5.0	4	0.5

Table 4.1: Granulometric characteristics of uncut River Lugg spawning gravels

4.3.1.2. Comparison of cut with uncut gravels

Comparative grain size distribution curves were created for the uncut and cut freeze-core data. This enabled characterization of the granular properties before and immediately after redd construction at each site. Additionally, it provided reference data for the sediment accumulation at the end of each field season. The grainsize data from the freeze cores was also used to compare with redd grainsize characteristics periodically during the field season (at the high resolution supersites) and at the end of the field seasons (all sites).

By comparing the average grainsize distributions for the uncut and cut gravel at each of the field sites, an idea of where the main differences in sediment distribution occurred. Figure 4.5 shows a comparison between the data from uncut and cut cores by means of a paired t-test. The significant differences between the two sample sets for each particle size category were noted. The most marked contrast between the two was in the <63µm category, where the cut gravels were found to be almost free of fines and the uncut contained an average of 4% silt and clay.

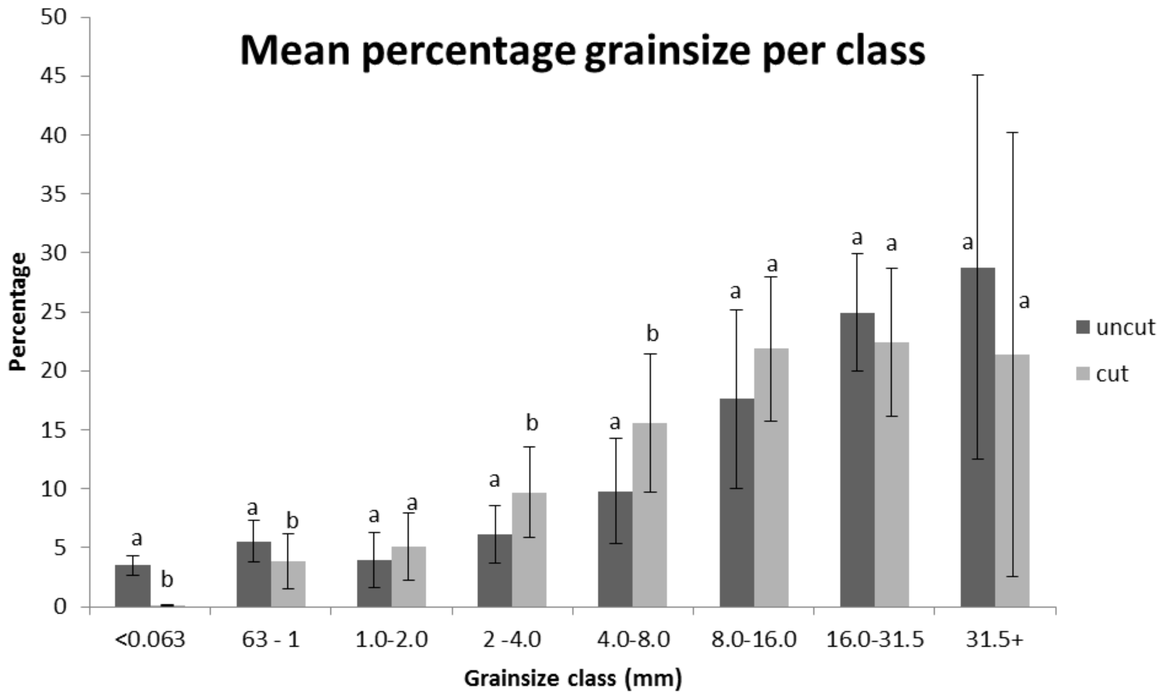


Figure 4.5. Mean proportion of particle size classes in Cut and Uncut redds. Bars are means ± Standard Deviation (after Bourgault and Magnan 2002). For each particle size class, percentages with different letters are significantly different as determined by a paired t-test (P=0.05). Bars represent the range within each of the sample sets.

Figure 4.6 represents the recorded difference in the above generalized graph in a comparison of <63µm sediment of uncut against cut samples for each individual site. An assessment of whether the final amount of fines at emergence is similar to uncut gravel percentages was also carried out. It should also be noted that the initial 'cut' state may not accurately represent the natural winnowing effect produced by the hen salmon – which is reported to only partially remove fine material (Kondolf and Wolman 1993, Kondolf 2000).

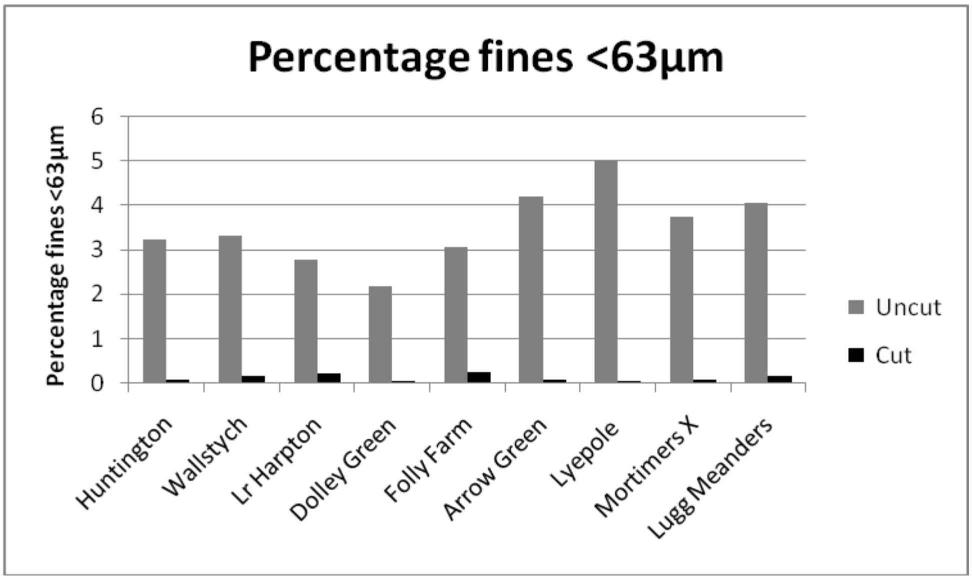


Figure 4.6. Percentage fines (<63 µm) data from cut and uncut freeze cores.

4.3.2 Suspended sediment

Prior to calculating the mass, composition of accumulated sediment within the experimental redds, an analysis of the suspended sediment load and rate was carried out. This was calculated relative to seasonal hydrological influences and based on the data retrieved from the ISCO suspended solid samplers and the time-integrated isokinetic samplers.

Suspended sediment load regimes were calculated for each of the 2009 site based on daily suspended /turbidity data and discharge. Suspended sediment load at each site was based on the following equation (Webb et al 1997):

$$\text{Suspended sediment load: } = \sigma \sum_{i=0}^{n} QC \qquad (4.1)$$

Where σ is the interval (in seconds) between sampling, Q is the discharge ($m3s^{-1}$), and C is the suspended sediment concentration (kgm^{-3}).

Suspended sediment load calculations were derived from the regression models for Lyepole Bridge, and Lower Harpton sites for Turbidity–SS relationships (Table 4.2).

Site	*Regression model*	r^2
Lyepole	SS = 3.4633x + 33.014	0.6375
Lower Harpton	SS = 2.6897x + 21.28	0.7316

Table 4.2. Turbidity – Suspended sediment relationships for the 2009 sites at Lyepole bridge (downstream) and Lower Harpton (upstream) on the Lugg.

A suspended sediment yield estimate for the Arrow site at Folly farm, was attempted but proved impossible due to the poor quality of the turbidity data at this site.

Since the ISCO data was collected only during the 2009 field season, an extrapolation of the suspended sediment-turbidity model was required to create an estimate of sediment delivery during the 2008 field season. The Lyepole bridge 2009 site is some 8 kilometres upstream of the Lugg meanders 2008 supersite, and is similar in discharge capacity, with no major tributaries between the sites. By applying the Lyepole model to Lugg Meanders 2008 turbidity data an estimate was created for suspended sediment flux during that field season and is displayed in figure 4.9 below. Since variations within the SS-turbidity relationship can depend largely on the optical qualities of the suspended sediment, it was thought that the proximity of the Lyepole site would lead to minimal variation in suspended sediment particle composition and optical qualities and thus in SS-turbidity relationship.

The sediment flux for the 2009 sites is variable and peaky, which may be expected from a freshet upland stream of this kind. However, the overall rates of sediment being delivered are relatively low during this field season. The Lyepole bridge site which is the furthest downstream exhibits the highest flux values, whereas the Lower Harpton site has consistently low suspended sediment fluxes with only two peaks evident during the incubation period - on 8th March and 15th April. The Lyepole bridge 2009 site exhibited a range in suspended sediment concentrations of 0 mg/l – 278 mg/l and a mean value of 68 mg/l and Lower Harpton ranged between 0 mg/l -222mg/l with a mean concentration of 48 mg/l for the same period. In the context of EU targets of 25mg/l (as an annual average), this is remains above recommended values.

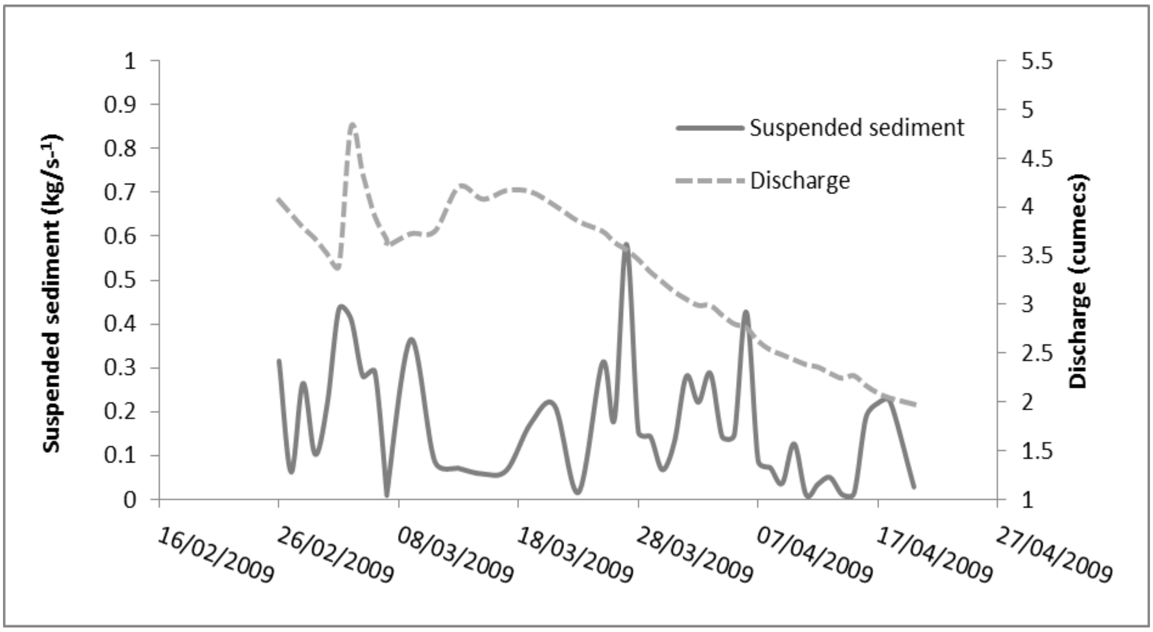


Figure 4.7. Temporal variation in suspended sediment load at the Lyepole bridge field site

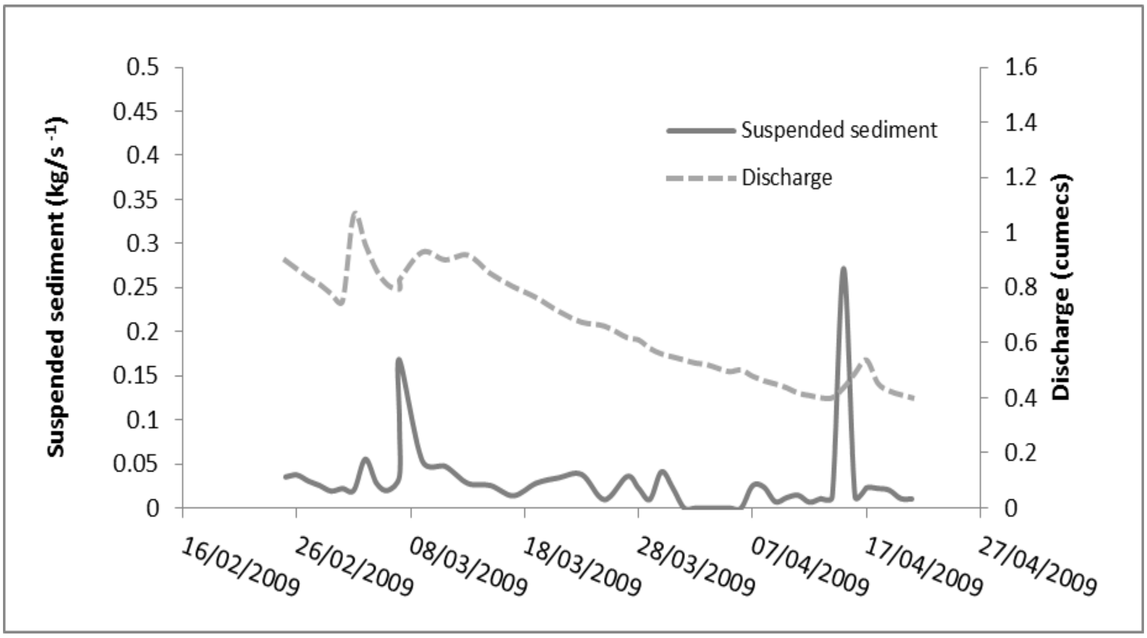


Figure 4.8. Temporal variation in suspended sediment load at the Lower Harpton field site 2009.

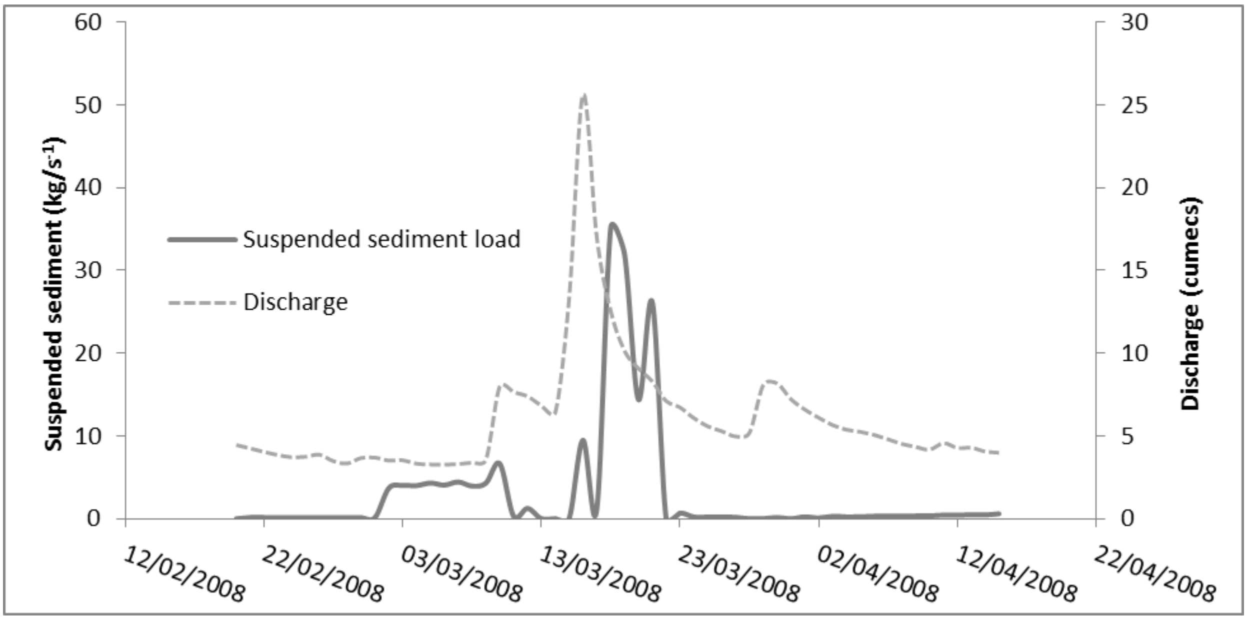


Figure 4.9. Temporal variation in in suspended sediment load at the Lugg Meanders field site 2008.

Again, the suspended sediment flux for the season 2008 is peaky in nature, but with maximum estimates that exceed the maximum 2009 levels by 2 orders of magnitude. The 2008 season experienced high discharge , spate conditions with maximum flow conditions occuring at around predicted hatching time for the eggs.

In terms of rainfall estimates for the catchment for the January to April period, the 2008 precipitation was 22% higher than the 30 year average for this time of year, so sediment delivery estimates may be higher than normally experienced on this catchment. Conversely, precipitation for 2009 field season was 16 % lower than the 30-year average for this time of year. Consequently, sediment delivery estimated here may reflect the lower range of sediment delivery for this part of the catchment.

Total suspended sediment load estimates for the each of 2009 field sites and the Lugg Meanders 2008 supersite were calculated from discharge, suspended sediment and field site transect data. The estimated total loads delivered past the field sites were 774 tons and 1487 tons at Lower Harpton and Lyepole bridge (2009) respectively. The suspended sediment delivery estimate for Lugg Meanders (2008) was 14,417 tons. The maximum load recorded for Lugg Meanders is similar to that reported for the Ithon at Llandewi, which drains a neighbouring catchment to the Lugg. Comparison of the catchment specific loads shows the Ithon to have the highest sediment load per unit area, but the Lugg sites in general are higher than those recorded for the other lowland catchments studied by Grieg et al., (2005).

Site	***Dates***	***Suspended sediment concentrations (mg/l)***	***Discharge (m^3s^{-1})***	***Total Yield (Tons) and specific sediment yield (T/km^2)***
Upstream site Lower Harpdon	Feb-April 2009	Min 0 Max 622	Qmax 1.06 Qmin 0.41	774 13.5
Middle Site (Lypole Bridge)	Feb-April 2009	Min 3 Max 278	Qmax 6.1 Qmin 1.6	1487 6.4
Downstream site (Lugg Meanders)	Feb-April 2008	Min 33 Max 2798	Qmax 25.6 Qmin 3.25	14,417 55.9
Ithon (Grieg et al 2005)	Dec-Mar 2002	Min 0.68 Max 1414.8	Qmax 129.2 Qmin 1.35	9995 89.72
Aran (Grieg et al 2005)	Dec-Mar 2003	Min 2.13 Max 740.2	Qmax 3.50 Qmin 0.60	24 2.00
Blackwater (Grieg et al 2005)	Dec-Mar 2003	Min 1.7 Max 86.1	Qmax 7.32 Qmin 0.22	273 2.73
Test (Grieg et al 2005)	Dec-Mar 2002	Min 16.9 Max 30.8	Qmax 5.13 Qmin 3.82	350 3.37

Table 4.3: Summary sediment and load data for the study sites and for comparison the sites studied by Greig et al (2005).

To provide comparative values and to give an estimate of the load potentially passing the approximate width of a natural redd during each field season the load passing a 1-metre wide transect of each of the field sites was calculated. The estimates were based on the sediment load divided by the channel width at each of the field sites in question.

As highlighted in table 4.4 below, the Lower Harpton 2009 site recorded the lowest suspended sediment delivery across a one-metre transect. The Lugg meanders 2008 site recorded the highest suspended sediment across a transect of the same width. This is in agreement with the expected estimate considering the location of the sites; lower Harpton being the further upstream and Lugg Meanders the furthest site downstream and considering the contrasting discharge levels of the two years in question.

Site	**Lugg Meanders (2008)**	**Lyepole Bridge (2009)**	**Lower Harpton (2009)**
Suspended sediment load (tons m^{-1})	833	51	23

Table 4.4 Suspended sediment for entire field season passing a one-metre transect at each of the field sites. Calculations are based on the suspended-sediment –turbidity relationships as detailed above.

4.3.2.1 Isokinetic samplers and suspended sediment calculations

Calculations based on the amount of sediment retrieved from the isokinetic samplers for each field site and each field season, were made in order to assess both the load and the nature of the sediment within the samplers, in terms of particle size distribution and organic content.

For the 2008 field season, it was decided to calculate sediment load passing each site for the period up to 28/03/08 (67% of total period of study) as 4 of the isokinetic nozzles were distorted during the spate event mid- season and one sampler was lost (Mortimers cross site) thus rendering the data retrieved after that period unreliable in terms of accuracy of samples recorded. The flow past a width of a basket was calculated to enable comparison of suspended sediment flux and accumulated redd sediment over the given timeframe. This was achieved by multiplying the nozzle area of the sampler to the required area of interest, with respect to depth at each site. Suspended sediment amounts for each period were calculated for a cross-section of width equivalent to a sediment accumulation basket.

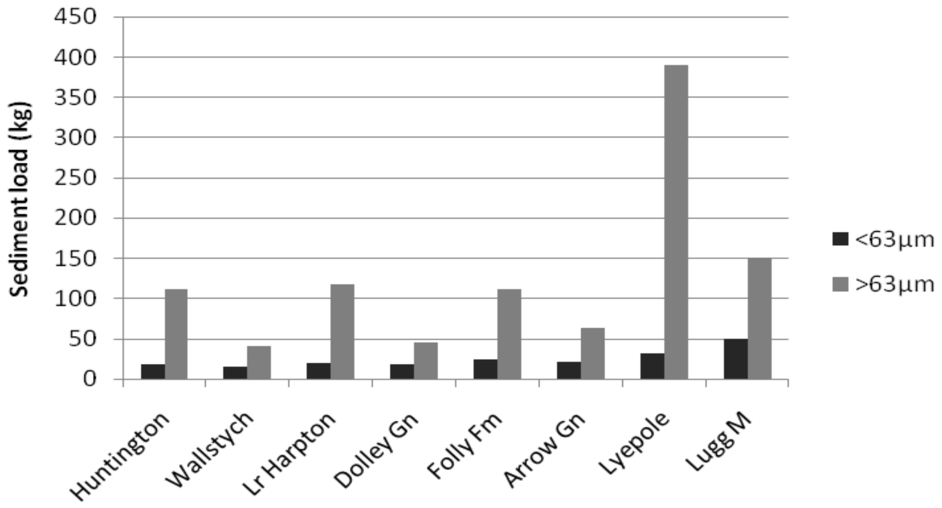


Figure 4.10. Suspended sediment load calculations for period 18/02/08 - 28/03/08 as calculated for a section of width equivalent to a sediment accumulation basket.

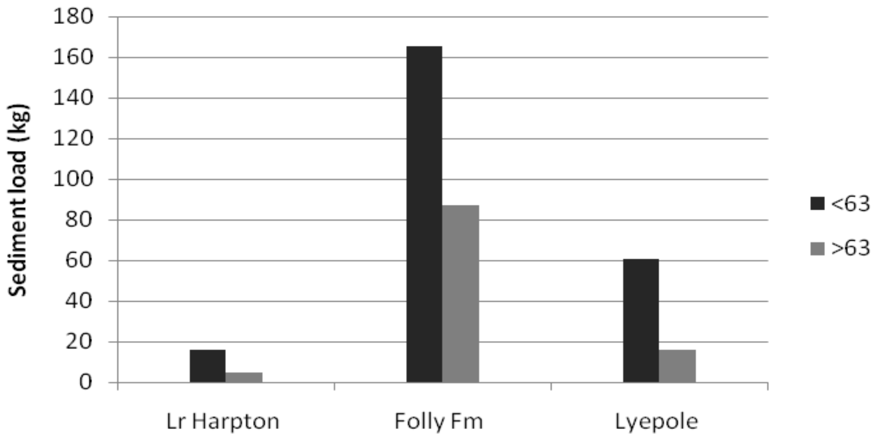


Figure 4.11. 2009 Suspended sediment amounts for period 25/02/09 – 21/04/09 as calculated for a section of width equivalent to a sediment accumulation basket.

Despite sampling limitations causing the periods under consideration for the field seasons to be of different length, the estimates give an indication of the larger sediment delivery for 2008 field sites as compared with 2009 sites. Another limitation which should be highlighted is the documented fall in performance of the samplers under very high flow conditions (Philips et al 2000).This may additionally have affected the 2008 data resulting in the underestimated suspended loads for the each of the field sites.

In spite of limitations, it is interesting to note the contrasting relative distributions of the sediment for each of the field seasons. As displayed in figures 4.10 and 4.11 above, and in the tables below, there is a clear inversion of particle ratios of <63 to >63 µm sizes. This is a phenomenon which has been documented by other researchers (Walling et al

2000) and is thought to be related to the increased transport capacity of coarser sediment during higher flow events.

It should also be noted that there is a considerable difference between suspended sediment load estimates made through the isokinetic samplers and those made via the daily suspended sediment -turbidity relationships. Potential causes for this discrepancy can be partly attributed to the known loss of functionality of the isokinetic samplers during high flows which would have impacted on the 2008 estimates coupled with a maximum sampling efficiency of around 70% (Philips et al 2000), so again, a tendency to underestimate. Estimates based on the suspended sediment-turbidity relationship calculations relied on R^2 correlation values of 0.64 and 0.73 at Lyepole bridge and Lower Harpton respectively.

A comparison was made against suspended sediment load estimates for the Lugg and other UK catchments – as seen in table 4.4 above and figure 4.12 below. Figure 4.12 displays annual specific yield estimates calculated by Webb and Walling for 6 UK catchments, of which the Lugg is one – with a specific yield ranging between 20 and 80 Tonnes/km^{-2}. In this context, the estimate of the Lugg Meanders 2008 yield of 55 T/km^{-2} made via the regression model, seems feasible.

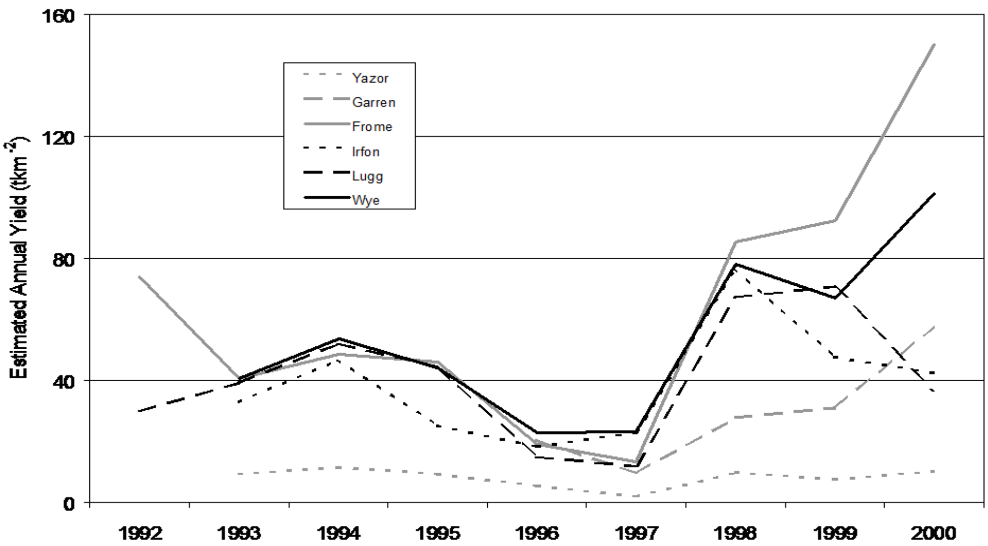


Figure 4.12. Annual sediment yield estimates(from Webb et al 2002) for a number of UK rivers including the Lugg

4.3.2.2 Grainsize distributions of suspended sediment

Table of grainsize distributions (in mass and percentage) of suspended sediment from isokinetic samplers for the <63 µm and >63 µm categories.

2008	**Mass <63µm (g)**	**Mass >63µm (g)**	**% <63µm**	**% >63µm**
Huntington	13.93	37.67	26.91	73.19
Wallstych	4.31	10.45	29.2	70.8
Lr Harpton	5.92	32.58	15.4	84.6
Dolley Green	7.3	15.87	31.5	68.5
Folly Farm	11.01	21.35	34.1	65.9
Arrow Green	9.12	29.34	23.8	76.2
Lyepole	16.34	94.53	14.7	85.3
Lugg Meanders	19.91	32.89	37.7	62.3
2009	**Mass <63µm (g)**	**Mass >63µm (g)**	**% <63µm**	**% >63µm**
Lower Harpton	10.6	3.2	76.81	23.19
Folly Farm	59.72	31.52	65.45	34.55
Lyepole	38.77	10.1	79.33	20.67

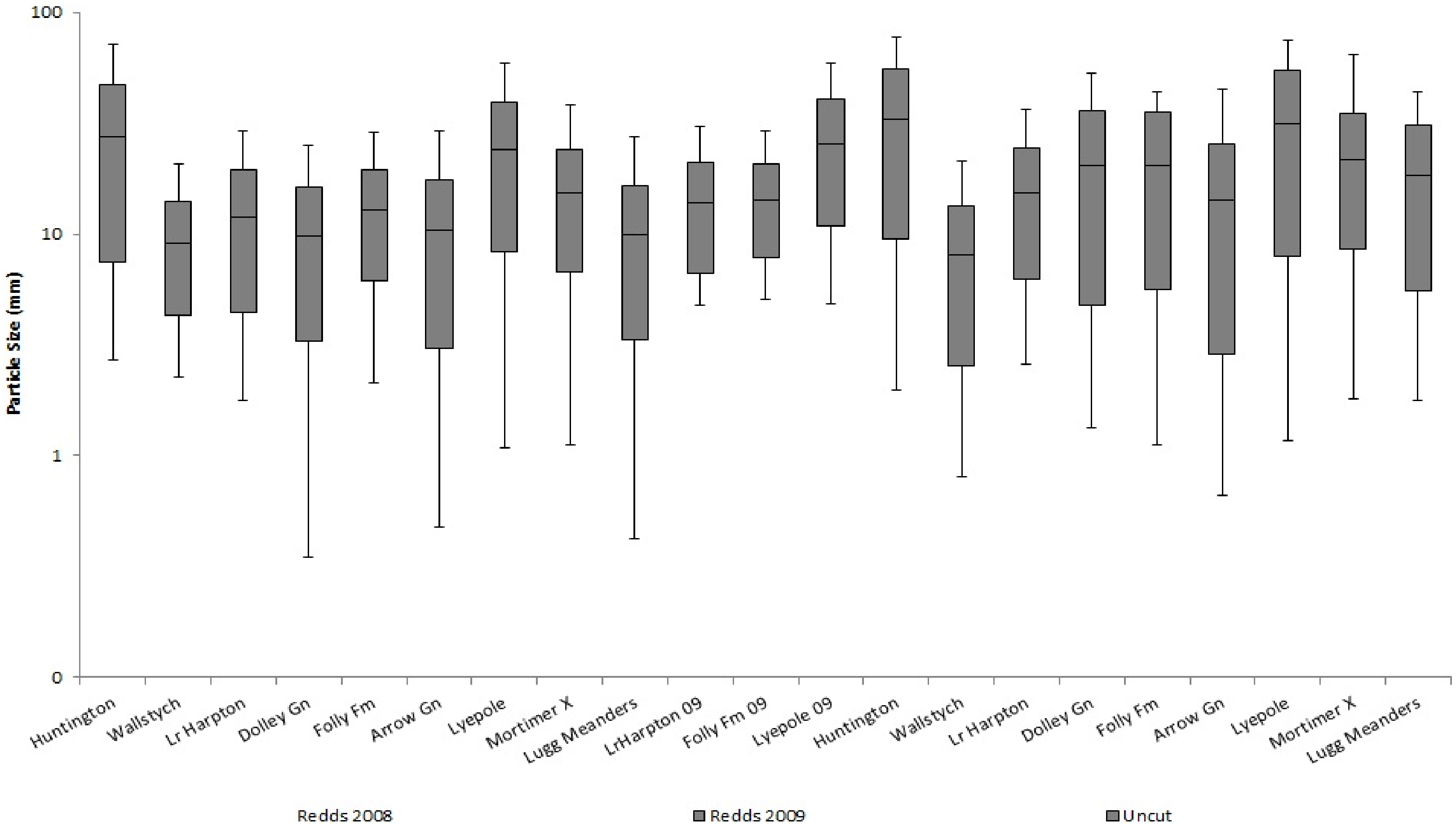
Table 4.5 grainsize distributions (in mass and percentage) of suspended sediment from Isokinetic samplers

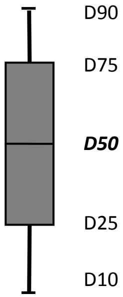
Grainsize distributions of the silt/ clay fine sediment portion (<63µm) from isokinetic samplers for each field site are detailed in the appendices. In terms of total mass, the Arrow site during 2009 is higher than either of the Lugg sites, but during the 2008 season is the mean value of arrow site is 34.2g (grams) against a mean value of 56.3g for the Lugg sites. A general trend towards increasing suspended sediment with increasing catchment area with the lower Lugg sites featuring the highest suspended sediment values overall. A comparison of this data with infiltrated fine sediment and uncut data is presented later in section 4.3.4.

4.3.3 Composition and quantity of infiltrated sediment

The grainsize characteristics of the bulk grainsize of the Redd sediments after the field seasons redd sediment are displayed in box & whisker format in figure 4.13. There is a fairly wide range of gravel sizes but all fit into the expected range for spawning habitat (Kondolf 2000), with only the upstream Wallstych site – with a D_{50} of 9.1mm outside the median 50% range of spawning gravels reported in the literature.

Figure 4.13. Grainsize characteristics for each site (2 redds at each site) at end of incubation period against uncut redd grainsize distributions for all sites.





By comparison with uncut data, it is evident that the 2008 sites there is no statistically significant difference between the median grainsize of 2008 Redds and uncut spawning gravels at the end of the incubation period (U-test, $p<0.001$). Similarly, 2009 data is similar to uncut data, with higher D_{50} values on the downstream sites (once again excepting the upper Huntington site).The 2009 redd sediment grainsize distributions are broadly similar in nature to the 2008 data for the same sites. The D_{50} values are similar, but D_{10} values differ in that the 2008 values encompass a wider range of fine sediment values and is reflected in elongated 'whiskers' as compared to the 2009 sites.

Table 4.6 below outlines the granular characteristics at each of the field sites, with the percentage of four categories of fine sediment (<4mm, <2mm, <1mm, <63µm) alongside the survival indices for each site.

Site	*D_{50}*	*D_{10}*	*Dg*	*Sorting*	*%<4mm*	*%<2mm*	*<%1mm*	*%<63µm*	*Survival (%)*
Huntington	27.5	2.7	21.3	4.3	12.3	7.3	3.8	2.9	32
Wallstych	9.1	2.3	8.8	2.8	13.8	7.7	3.5	1.7	35
Lr Harpton	11.9	1.7	10.8	3.2	14.6	8.4	3.4	0.8	55
Dolley Green	9.8	0.5	6.3	4.6	24.9	15.1	6.3	1.6	65
Folly Farm	12.9	2.1	11.2	3.4	13.9	8.3	4.3	3.1	31
Arrow Green	10.3	0.5	8.4	4.5	23.5	12.3	6.2	4.0	29
Lyepole Br	23.8	1.7	18.2	5.1	12.9	9.7	5.5	4.9	35
Mortimers X	15.4	1.1	13.4	4.3	12.8	9.7	5.5	4.8	39
Lugg M	10.1	0.4	7.9	4.3	20.3	12.7	6.3	3.9	28
Lr Harpton 09	13.8	4.7	12.9	2.2	5.5	4.7	2.9	3.1	78
Folly Farm 09	14.3	5.1	13.3	2.1	5.2	4.4	2.8	3.1	79
Lyepole 09	25.6	4.8	21.2	3.7	7.5	5.7	3.6	4.1	75

Table 4.6 Granular properties of redd sediment for all sites against survival.

From table 4.6 it is evident that the larger percentage of fines present during the 2008 season is reflected in the higher D_{50}, D_{10} and geometric means for the comparable sites Lyepole, Lower Harpton and Folly farm. The sorting coefficient is correspondingly lower during 2009, reflecting the absence of grainsizes toward the smaller end of the spectrum.

4.3.4 Fine sediment accumulation within the incubation zone

Calculation of the amount of fine sediment within each of the pots was made to enable comparisons of spatial and temporal variations in deposition throughout the catchment. Figure 4.14 below shows the total fine sediment (silt and clay fraction) amounts (kg/m^3) retrieved from the redds at the end of the spawning season.

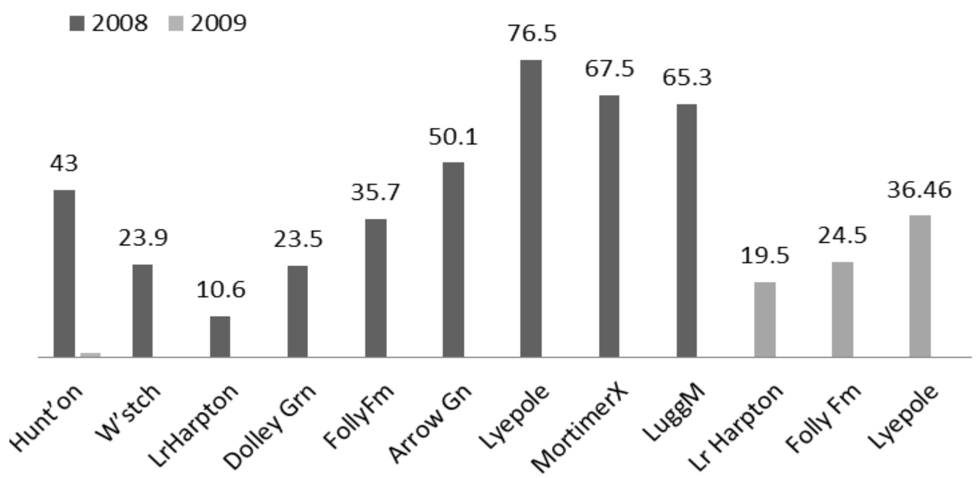


Figure 4.14. Mass (kg/m^3) of fine (<63µm) sediment accumulated in redds over 2008 and 2009 seasons

The high intra-site variability in very fine sediment deposition at the 2008 sites is demonstrated in figure 4.15, with a trend towards higher accumulation at the downstream sites as compared to upstream. This reflects the increasing availability of sediment for deposition with progression downstream.

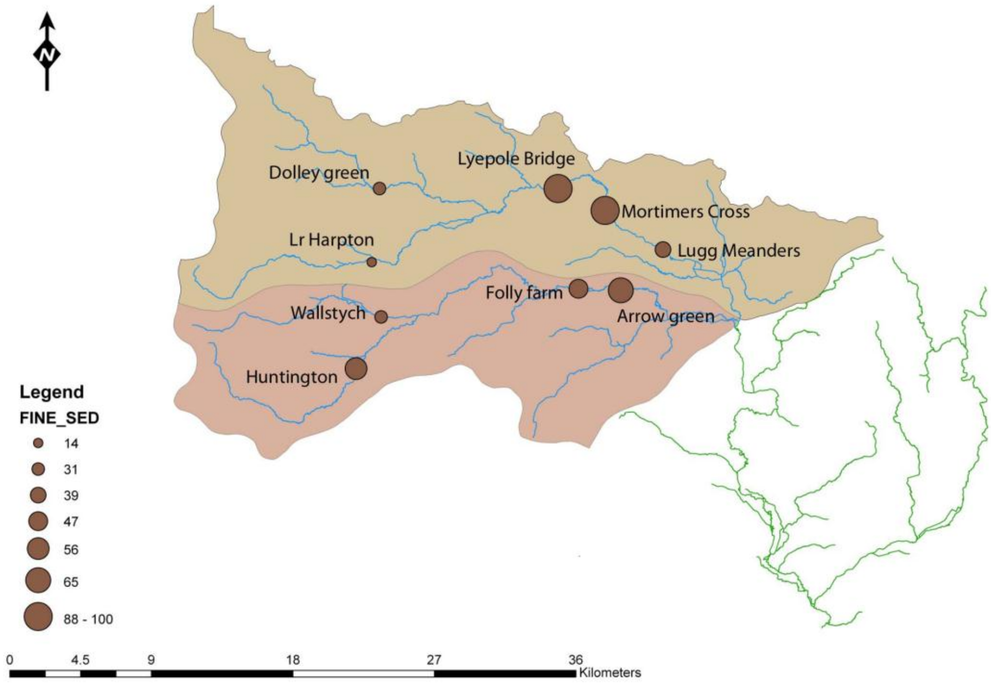


Figure 4.15. Spatial variability in deposited fine sediment (<0.63mm) during the 2008 field season

Based on the mass present in each of the sediment pots, the rate of accumulation of fine sediment (<2mm) for each site was calculated to enable spatial and temporal comparisons within and between UK catchments. Table 4.7 highlights the Lugg 2008 and 2009 infiltration rates in comparison with other similar studies.

Study site	*Infiltration rate (kg/m²/day)*	*Source*
Lugg 2008	0.40 – 1.09	*This study*
Lugg 2009	0.10 – 0.36	*This study*
Arrow 2008	0.48 – 1.63	*This study*
Arrow 2009	0.12 – 0.42	*This study*
Turkey Brook	1.68 -31	Frostick et al., (1984)
Great Eggleshope Beck	0.008 (baseflow) 0.29 - 2.5 (flood)	Carling and McCahon (1987)
North Tyne	0.005 - 0.086 (baseflow) 0.013 - 1.574 (flood)	Sear (1993)
Test	0.1 – 7.0	Acornley and Sear (1999)
Wallop Brook	0.3 – 2.85	Acornley and Sear (1999)
Ithon	0.48 -1.23	Greig and Sear (unpublished)
Cascapedia river	0.041 – 0.119	Zimmerman and Lapointe

Table 4.7. Fine sediment (<2mm) Infiltration rates of spawning gravels on the Lugg catchment against documented rates from other field studies (after Sear et al 2008)

Although based on data from fewer sites, there is a lower intra-site variability during the 2009 season as compared to the range for the same sites during 2008.Fine sediment accumulation is higher overall during the 2008 season than during 2009 and broadly follows trends in flow magnitude and coincident suspended sediment loads for the two years; where higher loads and flows were reported for the 2008 season as compared to 2009.

The apparent inversion of this inter-annual trend at the Lower Harpton site is the exception to this, and may be attributed to bedload instability due to spate conditions. However in the absence of information on more detailed evidence of bedload movement and transport for the 2008 season this cannot be confirmed.

In comparison to other studies the infiltration rates were most similar to those reported for the river Ithon, which is an adjacent catchment with similar geology. Lugg infiltration rates were within the range of all other studies but less than most other maxima, the exception being the Cascapedia river study which reported very low infiltration rates.

4.3.4.1 Accumulation rate of sediment within the redds

In sites where multiple baskets had been placed, sequential retrieval of baskets was possible, and thus calculation of the rate of accumulation at each of these sites. In 2008, only the Lugg Meanders supersite was set up with multiple basket for this purpose, and the amounts of fine sediment (<63μm) calculated from the sequential retrieval of baskets are displayed in figure 4.16 below. Accumulation data for the 2009 sites is displayed alongside the 2008 data.

From the data allow there seems to be a steady rate of increase throughout the season; however, spate conditions during this season, limited how many retrievals could be achieved. Some studies report a higher rate of sediment infiltration at the beginning of the incubation period (Grieg et al 2005) when the gravel are initially clear of fines, followed by a gradual slowing of infiltration as the gravels become in-filled progressively from bottom to top.

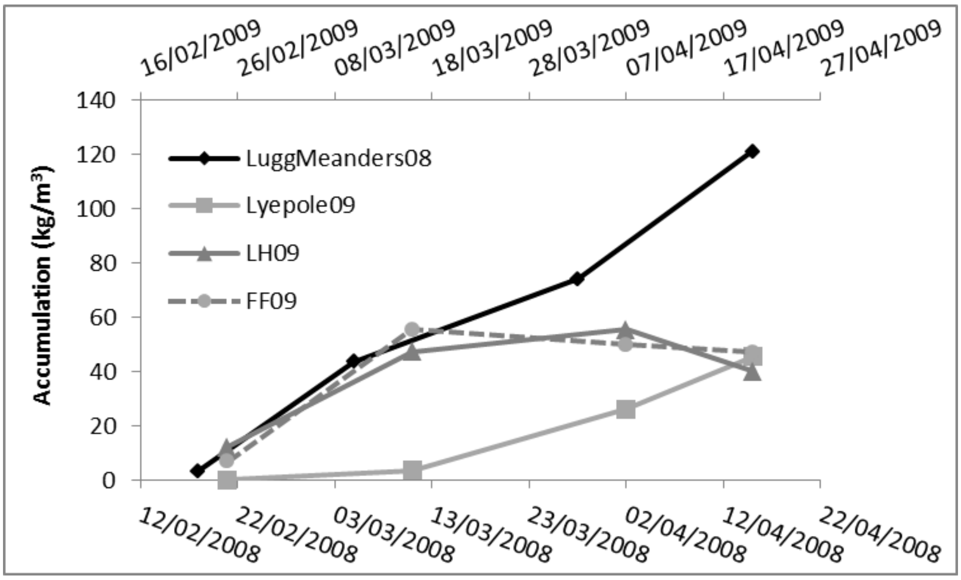


Figure 4.16. Accumulation of fine sediment (<2mm) at the Lugg meanders redd site during the field season 2008 and for the 2009 sites, showing progressive accumulation at Lugg Meanders and Lyepole bridge, and an initially high rate of accumulation followed by a period of stable accumulation rate and in the LH09 and LH 09 are decrease in the last period.

Final fine sediment (<2mm) concentrations for the other 2008 field sites (where periodic basket retreival was not possible) are displayed in table 4.8 below for comparison.

Huntington	Wallstych	Dolley Green	Lower Harpton	Folly farm	Arrow green	Lyepole bridge	Mortimers X	Lugg Meanders
120.6	118.3	140.5	109.1	110.2	178.7	171.2	151.1	121.2

Table 4.8. Final sediment accumulation (kg/m3) for the 2008 redd sites

For the 2009 season, variable rates of accumulation of fine sediment are reported. Initially, accumulation rate is highest for the Folly Farm site on the Arrow. The other sites exhibit slower growth during the initial stages with a subsequent acceleration in accumlation between 28th March and 7th April. Finally, the sites at Lower Harpton and Folly Farm show a slight decrease in total sediment recorded within the final basket. This recorded decrease in fine sediment mass may be due to heterogeneity within redd itself and minor differences in sediment deposition between adjacent baskets (Sear 1993, Acornley and Sear 1999).

4.3.5 Comparison of uncut and accumulated sediment

Uncut gravels were compared to the redd gravels at the end of the incubation period to ascertain whether the redds gravel had returned to their original granulometric state in terms of fine sediment content. The mean values from all uncut freeze cores and accumulation baskets for three grain-size classes of fine sediment (<4mm, <2mm <63µm) are displayed in table 4.9 below.

Particle size fraction	*Redd sediment*	*Uncut freeze cores*
% <4mm	*13.9 (6.37)*	*18.83 (5.37)*
%<2mm	*9.69 (4.56)*	*8.98 (1.77)*
%<63µm	*2.88 (1.27)*	*3.4 (0.82)*

Table 4.9. Mean grainsize comparison of uncut and redd sediment on the Lugg catchment for three grainsize classes. Standard deviations in brackets. Sample size based on 2 cores at each field site (18 total) and sediment data from 24 baskets.

For the 2008 season, the proportion of fine sediment in the <4mm category is 0.83 times the amount found in the uncut cores, so substantial infilling seems to have taken place over the incubation period. For the <2mm and the <63µm categories, there was 1.1 and 0.93 times the equivalent amount found in the freeze cores, respectively.

During the 2009 season, less sediment infiltrated over the incubation period than were found in the uncut cores. Best fit lines showed on average 0.4, 0.5 and 0.77 times the mass of sediment in uncut cores for the 4mm, 2mm and 63µm categories, respectively.

4.3.6 Suspended sediment and accumulated sediment

Other studies have found that the siltation rate of any one redd site tended to be related to the suspended sediment rate of the overlying stream water (Acornley and Sear 1999, Grieg et al 2005, Zimmerman and Lapointe 2005). This was investigated with respect to the Lugg data for each of the 2 field seasons.

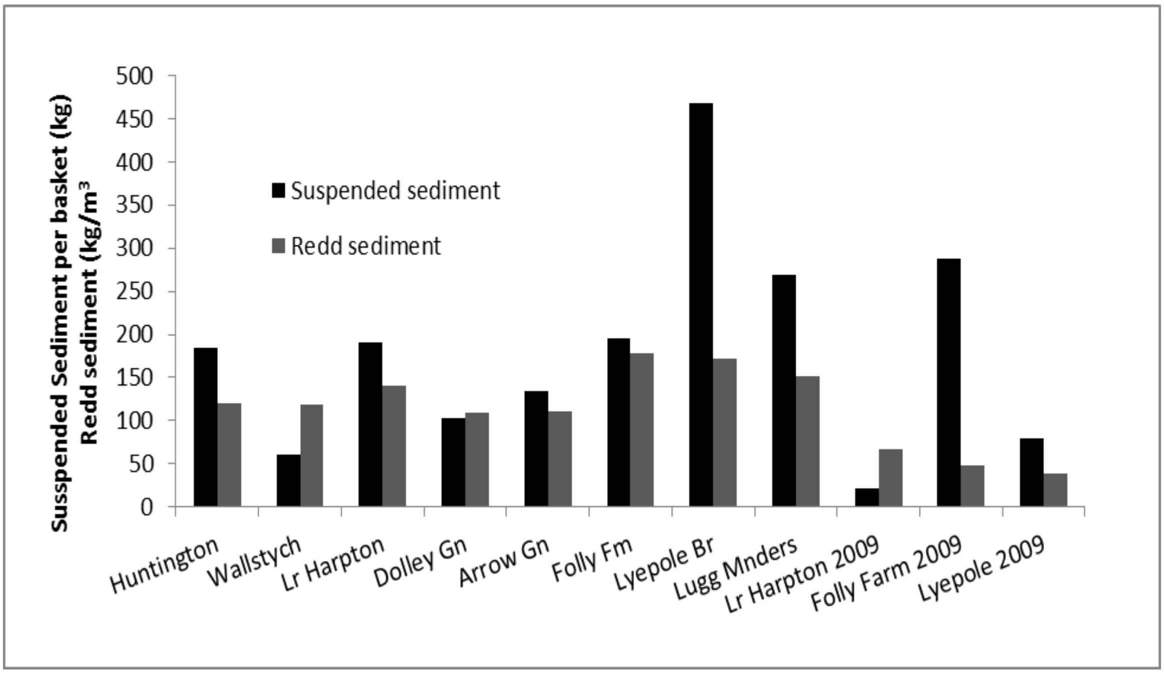


Figure 4.17. Total suspended sediment load against total sediment intruded for each of the sites. Suspended sediment is the total mass passing the width of a basket over the incubation period, and accumulated sediment is the total fine sediment (<2mm) intruded over the same period(kg/m^3). The Pearson correlation between the two variables is 0.49.

For each of the field sites, a comparison of the accumulated fine sediment proportions (<2mm and <63mm) against suspended sediment was made, in order to highlight any similarities or differences in loadings between the two. Two grainsize categories each of suspended sediment and accumulated sediment were investigated, and tests for correlation between grainsize categories at each site carried out.

Figure 4.18 Below highlights the proportional contribution as percentages, of each grain size fraction for each of the sites. The inversion of grain size proportions for Suspended sediment (dark grey) is evident here; with the 2008 site dominated by >63 sizes sediment portion, and the 2009 sites dominated by the silt/clay <63 sized fractions. There is no suspended sediment data for the Mortimer's Cross site, due to destruction of the sampler during the mid-season spate event.

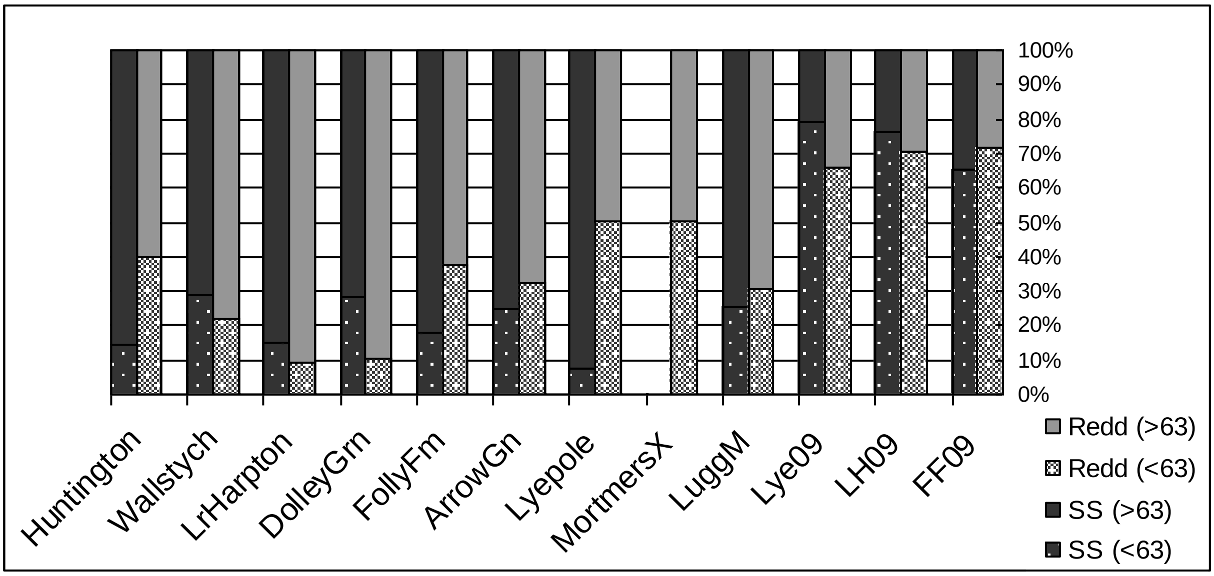


Figure 4.18 Proportional contribution of the <63 µm and >63µm size fractions of suspended sediment and deposited redd sediment.

Actual amounts of sediment found at the sites showed a moderate correlation in terms of suspended sediment versus sand and silt-sized redd sediment (r^2 = 0.49; $p < 0.001$), and there was a strong correlation between the total amount of suspended sediment passing a site and the amount of fine sediment of <63 size category in that site. A Pearson test for correlation between these two variables gave a coefficient of 0.72 at the 95% level. Thus the accumulation in the redds is a function of sediment load passing over the redd, with relatively little intragravel sediment sources.

The trend for higher proportions of larger coarser suspended sediment during 2008 and smaller grainsize dominance during 2009 is reflected in the accumulated sediment proportions. As mentioned in section 4.3.2 above, other researchers (Walling et al 2000) investigating the link between discharge and sediment grainsize distribution found that the lack of significant relationships with discharge reflects the fact that sediment particle size is largely supply-controlled, rather than a function of flow and hydraulics but that there was evidence of a pulse of coarse sediment on the rising limb of the hydrograph during high flow events. This phenomenon may be reflected in the Lugg data, where and prevailing flow conditions during a particular field season effected a higher rate of entrainment and transport of larger particles during the higher flow period i.e.: the 2008 field season.

As with the redd sites, there is an even more distinct spatial trend in sediment amount oberved with distance downstream, with a general trend toward higher suspended sediment yields at the lower sites in the the catchment. This has been found in other studies (Verstraeten and Poesen 2001) and is thought to be related to the catchment area and discharge applicable to that site, but may also be linked to land use type and soil erodability (Collins and Walling 2004, Walling 2006) in the adjacent riparian zone. This aspect is addressed further in Chapter 5 where sediment sources and contributions to the redd sediment in each of the sites are investigated.

4.3.7 Organic content

Since infiltrated sediment can be described as having two separate components – inorganic, the minerogenic portion and the organic portion, it was deemed necessary to calculate the amount of organic fine sediment that was contributing to the <63mm fraction of both suspended and redd sediment. Organic sediment can influence the redd environment in two main ways; firstly organic matter can cloy to inorganic surfaces and impede flow mechanically – this can additionally be exacerbated by the presence of organic biofilms creating a conjoined network of strands which progressively block any interstitial space which may initially have been present (Chen and Li 1999). Secondly, organic sediment has its own biological oxygen demand thereby reducing the amount of dissolved oxygen available for respiration by salmonid larvae.

Studies of river sediment organics from the literature report that most organics are within in the silt-clay fraction (Gjessing 1976).

Site	*Redd <63*	*Isokinetics <63*
Huntington	8.32	13.65
Wallstych	7.22	10.58
Lr Harpton	9.97	8.83
Dolley Green	6.6	9.62
Folly Farm	7.56	8.38
Arrow Green	6.53	8.22
Lyepole	7.26	5.23
Mortimers X	5.62	-
Lugg Meanders	6.45	6.69

Table 4.10 Percentage of organics in redd (<63μm) and suspended sediment (<63μm) from 9 field sites.

Organic content of both redds and suspended sediment were measured by loss on ignition, and on average, the suspended sediment was found to have 19% higher organic content.

Study stream	*Mean (range) Organic matter content (%)*	*Source*
Tadnoll Brook	18.2 (0.5 – 31.5)	Welton (1980)
Lambourne	13.5 (12.0 – 15.0)	Welton (1980)
Thames	15.0	Welton (1980)
Great Eggleshope Beck	16.4 (3.8 – 31.5)	Carling & McMahon (1987)
North Tyne	13.5 (3.5 – 29.1) Baseflow	Sear (1993)
	15.0 (5.2 – 29.0) Hydropower	
River Test	19.78 (2.3)	Greig (2004)
River Blackwater	3.43 (0.84)	Greig (2004)
River Aran	7.52 (0.69)	Greig (2004)
River Ithon	5.3 (1.1)	Greig (2004)
River Langvad	12.8 (7.0 – 17.5)	Conallin (2004)
River Ledreborg	24.5 (14.0 – 39.0)	Conallin (2004)
River Lahn	13.0	Seydell (2000)

Table 4.11 Percentages of redd organic matter reported in the wider literature (after Sear et al 2008)

The percentage of organic matter found within the river gravels is within the lower quartile of the range found in other studies on organic content in freshet streams (Carling and Mc Cahon, Sear 1993, Greig 2004). One reason for this may be that due to its low specific gravity, organic matter is more susceptible to flushing during spate conditions than the inorganic sediment fraction, and this may be reflected in these values from the 2008 spate season. The higher percentage values within the suspended sediment samples may also point to this phenomenon.

Overall, we can say that in comparison to other streams the percentages of organics are comparatively low, and so may not be of major consideration in terms of its potential biological oxygen demand on the incubation environment, since the rate of SOD is known to be a function of the mass of organic matter (Alonso et al., 1996).

4.4 Lugg fine sediment in context

In order to put the Lugg accumulation data in the context of other UK-based studies on sedimentation effects on salmonids, the cumulative percentage of fines (of <1mm) from each of 68 salmonid redd studies at the end of the incubation period were plotted together. From figure 4.19 it is evident that in a metadata context, the Lugg gravels are relatively clear of fines, with all sites featuring in the lower 30th percentile of the national data. This implies that the Lugg gravels represent high quality spawning habitat where fine sediment is the main control on incubation success.

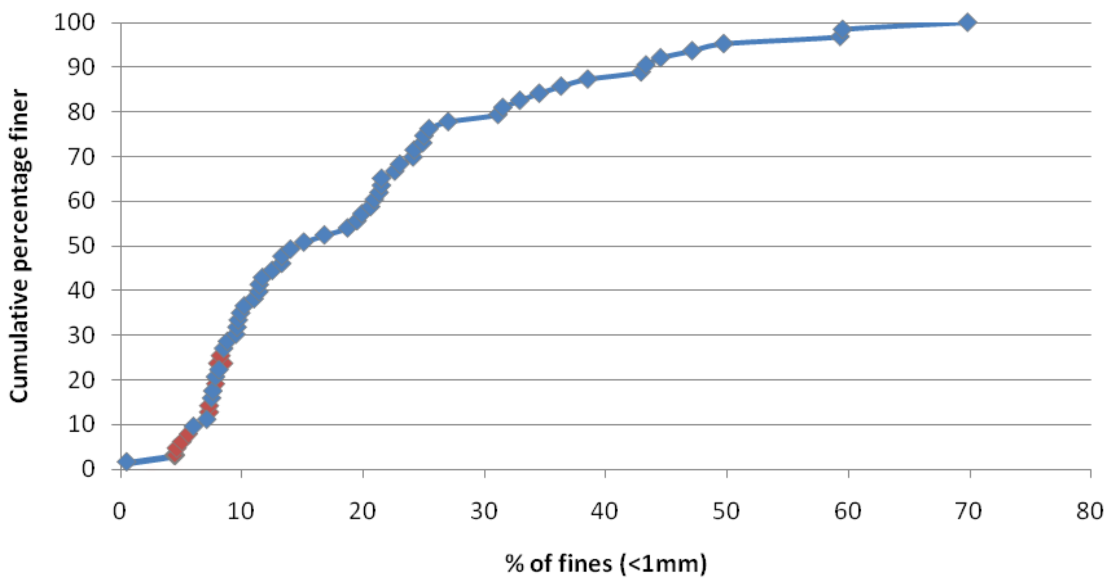


Figure 4.19. Cumulative grainsize distribution of fines (<1mm) Lugg and UK metadata. Lugg data points are highlighted in red.

4.4.1. Fine Sediment and Survival – 2008 and 2009

The Lugg data on egg survival in relation to red sedimentary environment are presented below in the context of 7 similar UK-based studies from the wider literature to demonstrate subtle differences between the two field seasons, plotted within the range of data available.

Figure 4.20 below graphically combines a range of data sourced from similar studies on Atlantic salmon spawning gravels. Hollow circles represent data points from runoff-dominated catchments, and black circles represent those from chalk river catchments (groundwater fed systems). The Lugg field seasons, which differ significantly in flow conditions, are represented by red and blue circles (2008 and 2009 seasons respectively). From this, the contrast in response between the two field seasons is evident; with the 2008 sites plotting in the mid-range of the wider metadata with relatively large intra-site variation and the 2009 site plotting in the highest percentiles of survival from the UK data and with much reduced variability between sites. The results indicate that the Lugg redd siltation problem closely resembles that of other Salmon river spawning sites in the UK; however, it adds dimensions of inter-annual and inter-site variability introduced by flood reime and suspended sediment loads. In years with relatively few flood events and / or low suspended sediment loads, productivity of the Lugg spawning gravels is high.

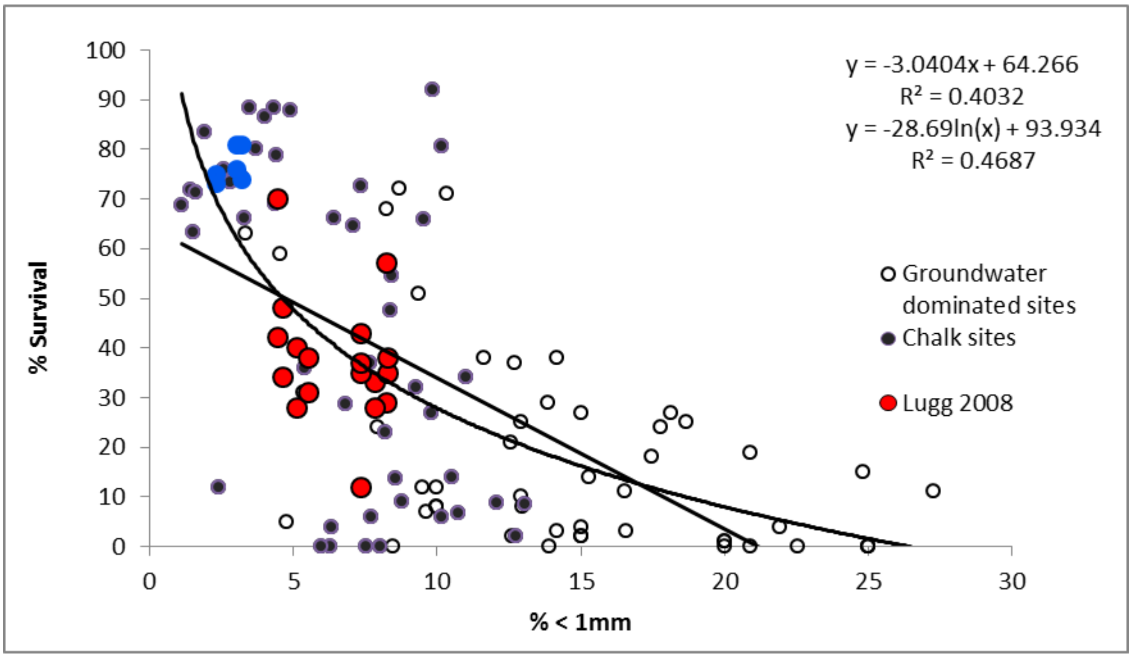


Figure 4.20 Linear and logarithmic relationships between fine sediment and survival from the Lugg catchment in the context of UK-wide studies. The linear relationship shows an R^2 value of 0.4032 for all combined sites.

Using the data recovered from each of the redd sites over the two field seasons, the significance of the relationship between fine sediment amount and survival was tested by simple correlation between the two variables.

A moderate negative link between fine sediment (<1mm) and survival was observed for the combined (Lugg) datasets, with an R^2 value of 0.279. When the annual datasets are separated however, it is clear that there is a difference in survival for the 2009 dataset as compared with the more variable 2008 dataset. Individual R^2 values for each field season are 0.29 and 0.089 for 2009 and 2008 respectively. So, while the 2009 r^2 value is higher, which may point to the lack of fine sediment promoting good survival (based on a very small dataset), the lower 2008 R^2 may point to an interplay of other factors in addition to fine sediment loading, in turn dependent on flood regime.

From the data recovered from each of the redd sites over the two field seasons, a plot for fine sediment amount against survival was created and tests for correlation between the two variables carried out.

A moderate negative link between fine sediment (<1mm) and survival was observed for the combined datasets, with a corresponding R^2 value of 0.279. When the annual datasets are separated however, it is clear that there is a difference in survival for the 2009 dataset as compared with the more variable 2008 dataset. Individual R^2 values for each field season are 0.29 and 0.089 for 2009 and 2008 respectively. So, while the 2009 r^2 value is higher, and which may point to the lack of fine sediment being instrumental to good survival albeit based on a very small dataset, the 2008 lower R^2 may point to fine sediment loading playing a role in survival but subject to an interplay of other factors.

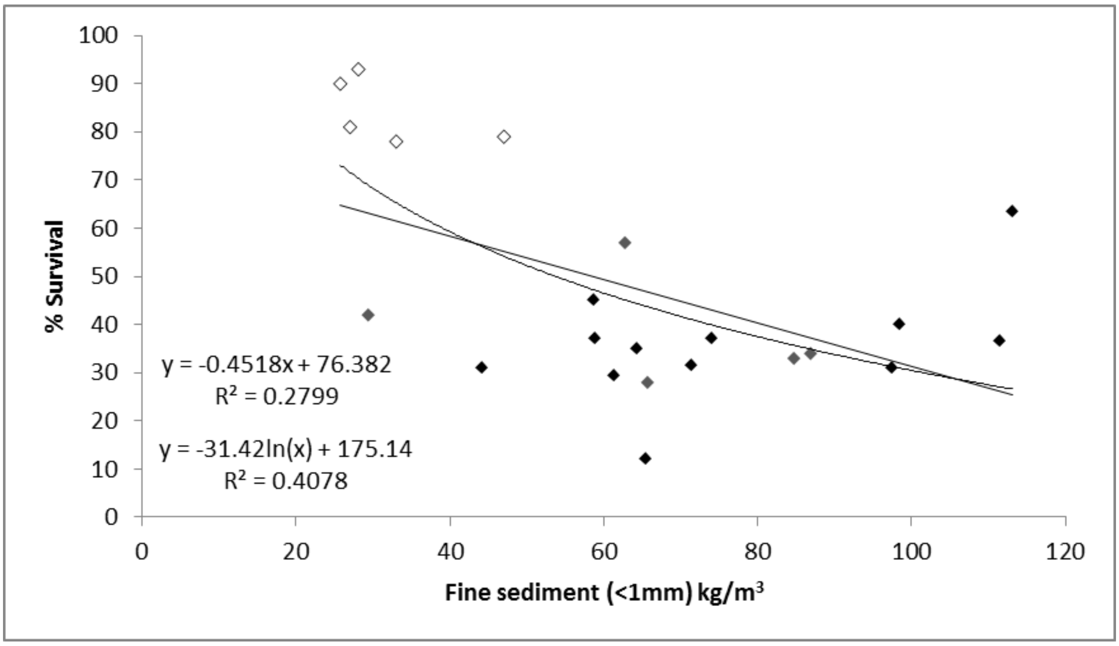


Figure 4.21 A linear relationship between fine sediment and survival in the form y=ax+b, with an R^2 of 0.279. A logarithmic relationship produces an R^2 value of 0.4078. Black points signify the 2008 sites and white points, the 2009 sites.

Tests on the performance of other granular determinants were carried out through Pearson correlation analysis. In general, physical granular parameters were poorly correlated with survival. In addition to fine sediment coefficient values related to survival, tests were carried out on the D50 and the Dg of the gravel present in the field pots, and their Pearson coefficients recorded.

D_{50}	Dg	<2mm	<1mm	<63µm
0.152162	0.066548	-0.495	-0.529	-0.22

Table 4.12 Pearson coefficient values of granular parameters with survival

D50 and Dg do not predict survival for the Lugg sites. Both < 2mm and <1mm sediment grainsize portions showed a weak to moderate correlation with survival, while the <63 µm portion was less strongly correlated with survival. This indicates that while the silt-sized portions may be have some effects on survival success, the cumulative effects of all fine sediment albeit mainly that within the <1mm category, should be considered when looking for sediment – survival associations. This contrasts with studies undertaken by

Zimmerman and Lapointe (2005) who found that in particular the <63 sized fraction had most deleterious effect on survival. Other workers have commented on the possibility of sand-sized particulates playing a part in interstitial pore structure in redd, and aiding retention of smaller silt and clay fractions thus influencing other parameters such as water flow through the redd and oxygen supply in that way (Sear et al 2008). The data here supports the observations by Greig et al (2005) who demonstrate that grainsize based determinants are poorly correlated with survival. Instead, Greig et al highlight the stronger correlations between dissolved oxygen and in particular DO supply rate.

4.4.2. Physical disturbance of river gravels

4.4.2.1 Scour

Despite the focus on fine sediment effects on spawning gravels, consideration should also be given to the potential harm caused by physical movement of the gravels within the redd zone. Scour and fill action can also alter stream composition to an extent as important as through the action of sediment infiltration, and can result in the fatal entrainment of embryos (Lisle and Lewis 1992).

In a review on scour depths which would cause disturbance of egg pockets, de Vries (1997) proposed scour depths of 15cm to the top of the eggs pockets, while scour depths of 30cm would reach the base of the egg pocket and result in complete mortality of the eggs or larvae.

Scour chains were placed at each of the field sites during the 2008 field season and although simple in design, gave an indication of whether scour was occurring at any particular site. Chains were checked for any change in length (through scour or infill) during each field visit through the incubation period, thus giving an indication of the rate of change at each site.

Table 4.13 outlines the degree of scour chain exposure (in cm) found at the field sites during season 2008. The length of the exposed chains was measured during periodic visits to the field sites between 4th March and 15th April 2008.

	4th March	*18th March*	*27th March*	***15th April***
Huntington	+ 1	+ 2	n/v	n/v
Wallstych	0	0	+ 3	+1
Lr Harpton	- 1	n/v	0	+ 1
Dolley Gn	0	- 1	+ 2	0
Folly Farm	- 1	n/a	n/v	+ 3
Arrow Green	+ 2	n/v	- 8	- 2
Lyepole Br	+ 6	n/a	+ 10	+ 12
Mortimer's X	+ 3	n/a	n/v	n/v
Lugg Meanders	+ 14	n/a	+ 20	+ 25

Table 4.13. Scour chain exposure (cm) as measured during the 2008 field season. Positive values indicate scour, negative values indicate infilling. n/a and n/v indicate site visits during which the chains were not accessible, or visible.

Access to sites was impeded during high flows, and the chain ends could not be located – due to infill or lack of visibility. Nonetheless, there were indications of bedload scour occurring at during the incubation period at all sites, but in particular the lower Lugg Meanders site and to a lesser extent at Lyepole bridge. Fill events are evident during the incubation period at four sites. The Lower Harpton and Dolly Green sites show limited scour and fill.

While there is evidence that bed scour depths are correlated with flood discharges (Carling et al 1987, Ziemer et al 1991) there remain reach and time-dependant variables such as substrate composition and slope of redd zone which need to be factored into predictions of potential bedload movement of a redd during a given time period

(Lapointe et al 2000). Nonetheless, given evidence from 2008 Lugg sites which demonstrate scour, we should consider whether future years experiencing flood event intensities higher than those experienced during 2008, could be capable of egg entrainment and redd destruction. The action of scour and fill and the activation of the flushing of fines during spate events has been looked at by others (De Vries 2008, Sear et al 2008) and it is thought possible that this action may produce an accompanying rise in dissolved oxygen concentrations as oxygenated water penetrated into the egg zone. The following section investigates the available evidence for this phenomenon at the Lugg field sites.

4.4.2.2. Bed mobility and Dissolved Oxygen Concentration.

Indications of scour and thus bedload movement during the 2008 field season prompted the installation of Bedload Impact sensors (Richardson et al., 2004) during the 2009 season. The sensors were installed at the Lyepole Bridge and Lower Harpton field sites to measure the rate and magnitude of impacts due to moving clasts as an index of bed mobility. The impact sensors were located immediately downstream of the Redd tail.

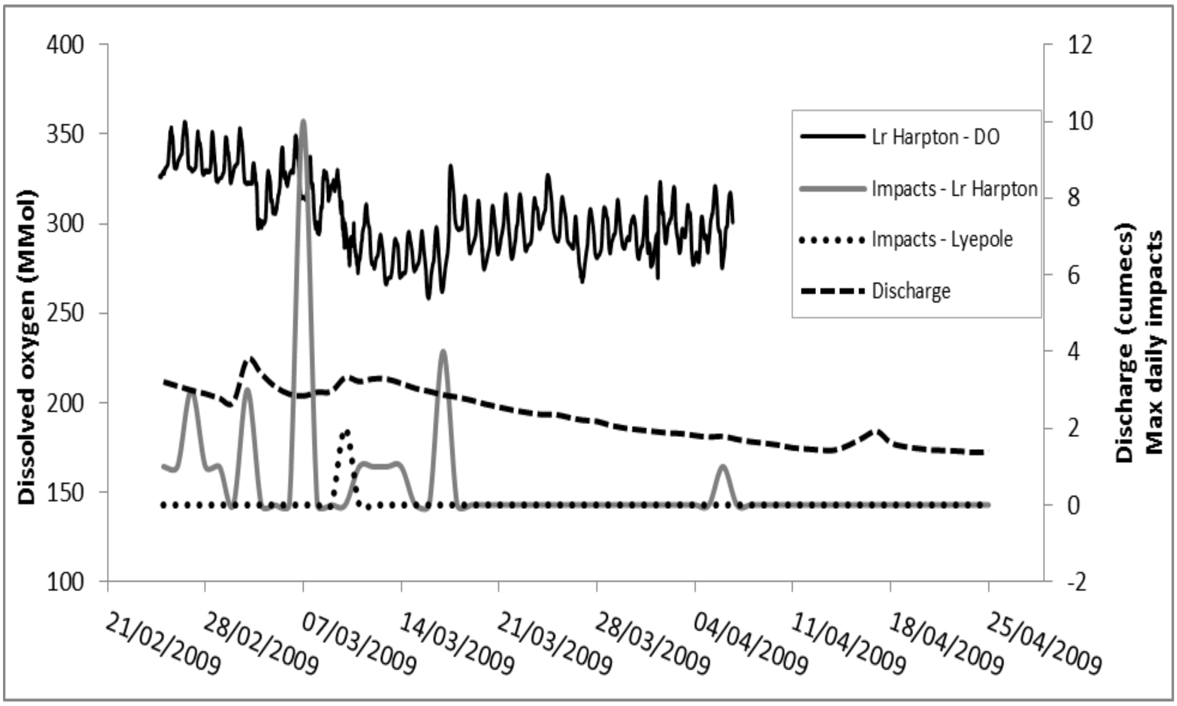


Figure 4.22. 2009 field season bedload impacts relative to discharge data and dissolved oxygen within the redd zone at Lower Harpton (high resolution dissolved oxygen data was not available for the Lyepole 2009 site). Bedload impact data shown is the maximum count recorded within a 10-minute interval per day.

Despite the low discharges experienced during the 2009 field season, where all values fell below the average Q value for daily mean (3.88 cumecs), there is evidence for bedload movement at the Lyepole bridge site and the upstream site at Lower Harpton. Dissolved oxygen in the redd zone at Lower Harpton fluctuates during periods of bed mobility with peaks evident at times of recorded impact. Impact rates are very low compared to those recorded for a bedrock channel in flood (Richardson et al., 2004). As a result, it is difficult to determine if there is a causal link between DO and bedload impacts at such low discharges.

At the 2010 Lyepole site, higher discharges mid-season are coincident with bedload impacts and highly fluctuating oxygen concentrations in the redd zone. This evidence does not support the findings of Sear and de Vries 2008 who observed slight increases in oxygen concentration in the redd zone with incidences of bedload transport. Again, impacts are low compared to Richardson et al (2004) which suggests that the mobility is limited to surface particles rather than scour or mobility of the active layer. Thus, another controlling mechanism for DO fluctuations is sought and is explored further in chapter 6.

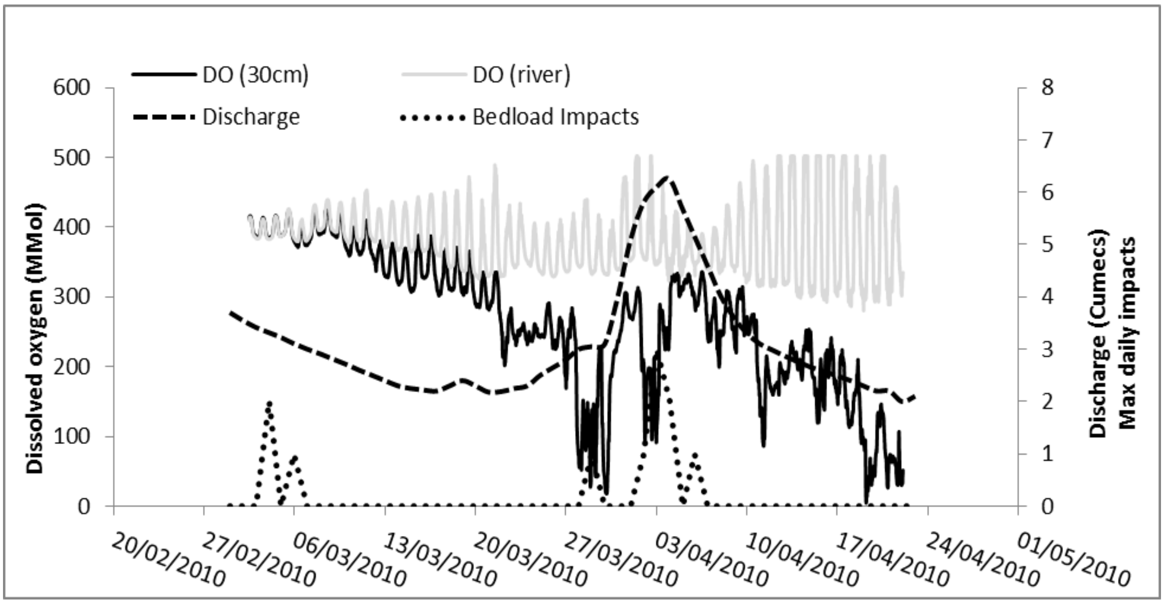


Figure 4.23. 2010 field season bedload impacts relative to discharge data and dissolved oxygen within the redd zone and in the water coloumn at Lyepole bridge. Bedload impact data shown is the maximum count recorded within a 10-minute interval per day.

Montgomery et al (1996) showed that where egg burial depths are known, expressing scour depth in terms of bed-load transport rates provides a means for predicting embryo mortality resulting from changes in watershed processes that alter shear stress or sediment supply. While it has not been within the scope of this study to calculate rates of bedload transport, future investigations could address this in terms of likelihood of certain discharges to create scour which and exceeds egg zone limits.

While the 2009 discharge values are very low, consideration should be given to the possibility of egg scour occurrence during flows of increased intensity during spate events and conditions that may result from the effects of climate change and associated increased flood risk (Arnell 1998, Macklin 2009). Evidence from 2008 scour chain data confirmed the occurrence of scour on the Lugg during high flow events, with scour depths of 25cm recorded at the Lugg Meanders site. Considering that the 2008 flood saw relatively low flood discharges (max. 25 cumecs) as compared to a 5-year flood of 30 cumecs, it can be assumed that event-related egg excavation is probable at this site.

4.4.3 The effect of sediment intrusion on Intra-gravel flow velocities and DO

The intragravel flow at the Lugg Meanders supersite was plotted against the mass of accumulated fine sediment during the incubation period. Despite the small number of datapoints, a clear negative linear relationship was observed, with an R^2 value of 0.9137.

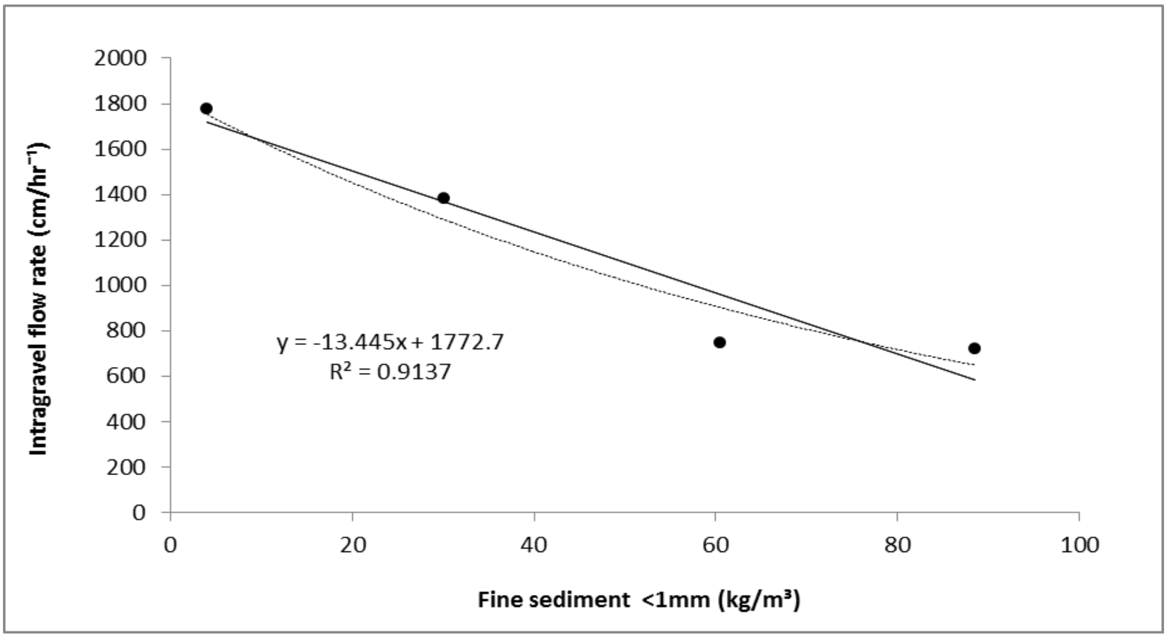


Figure 4.24. Lugg Meanders 2008 total fine fine sediment accumulation against intragravel flow rate. A strong negative relationship exists as found by Greig (2004).

Equivalent data for all sites was plotted for each of the redd sites (two redds at each field site) and the data plotted in figure 4.23. Here, the data is more widely distributed in terms of a linear relationship, although a negative trend is still apparent – this time with an R^2 value of 0.35.

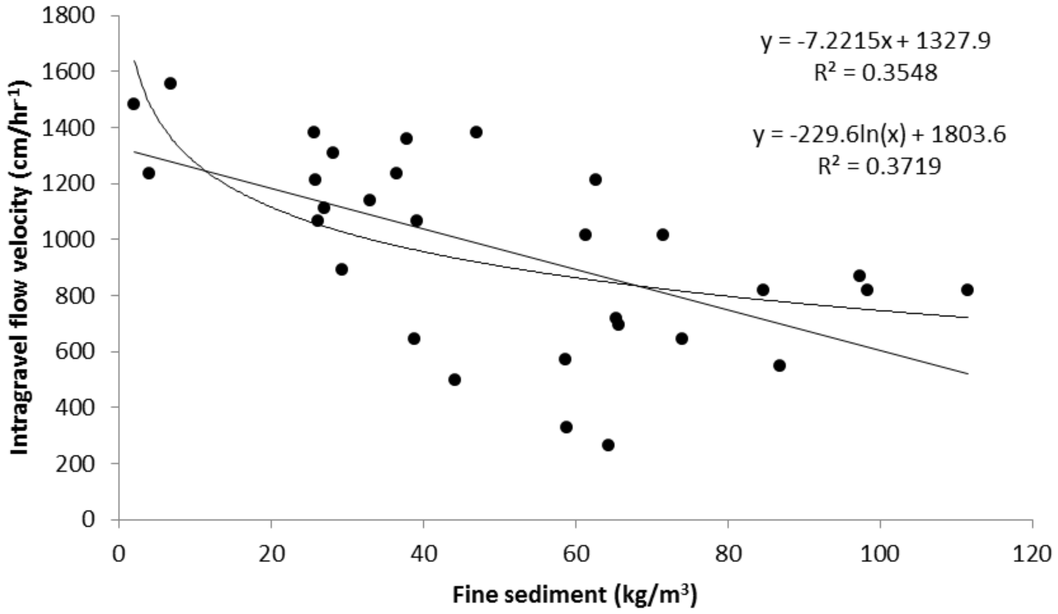


Figure 4.25. The fine sediment – Intra-gravel flow velocity relationship for all sites.

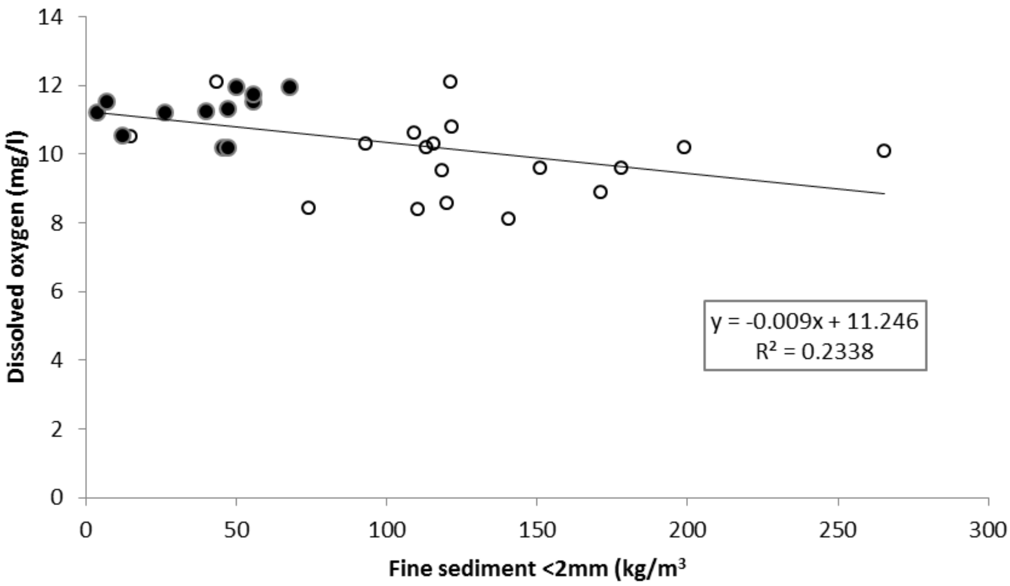


Figure 4.26 Fine sediment – dissolved oxygen relationship for all sites. (Black points signify 2009 sites, and hollow points the 2008 sites).

Dissolved oxygen was plotted against fine sediment infiltrated for all sites, and a weak to moderate linear trend was observed.

Since intragravel velocity flow is influenced by permeability, hydraulic gradient and surface flow within a reach, and sediment accumulation acts as a key control on these parameters within the gravel bed, the above evidence indicates the involvement of discharge in terms of magnitude of response of these variables. By plotting the timeline of sediment accumulation in relation to Discharge (2008 vs 2009 years, we can see the relationship between the high discharge values during 2008 and the correspondingly high accumulations of sediment just following a peak flow event. Similarly, low 2009 values for discharge coincide with low sediment infiltration values for that season.

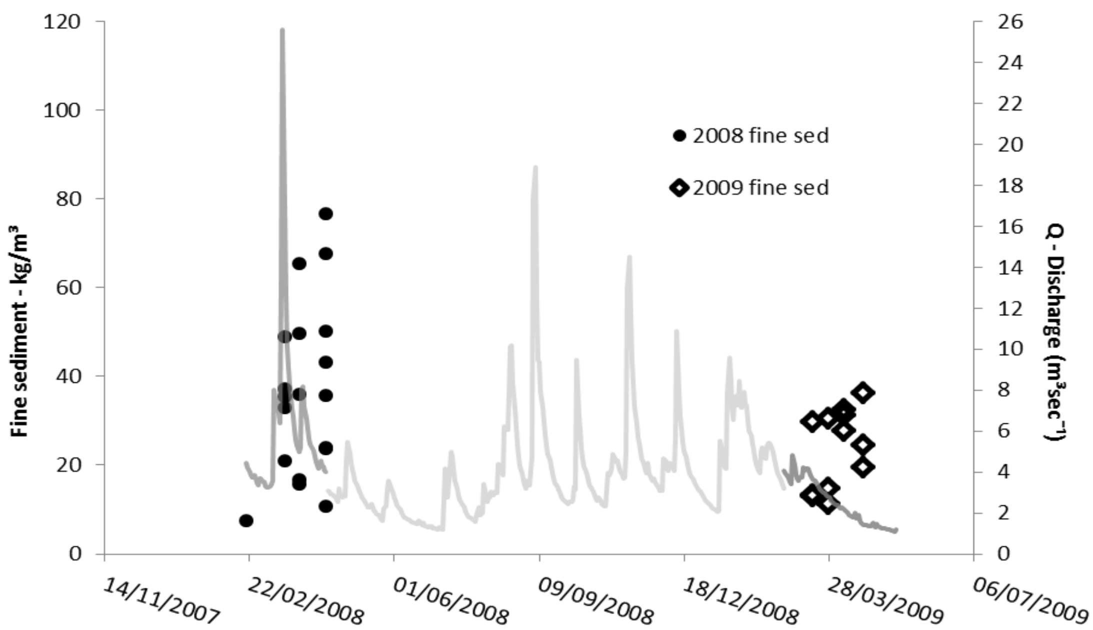


Figure 4.27. Discharge in relation to fine sediment retrieved from redds over the two field seasons.

4.5 Discussion and Summary

The total amount of sediment (<4mm) infiltrated on the Lugg catchment was 16.5% by mass for the 2008 field season, and 6.1% for 2009 season. As shown in table 4.14 below, the 16.5% value fits within the range typical of accumulated sediments recorded during previous UK-based studies. The 6.1% value is lower than previous recorded average values, and results from the low discharges in this incubation period.

Study site	***% fine sediment (<4mm)***	***Source***
Great Eggleshope Burn	10	*Carling & Mc Cahon (1987)*
North Tyne	11	*Sear (1993)*
River Piddle	22.6	*Walling and Amos (1994)*
Wallop Burn	17	*Acornley & Sear (1999)*
Newmills Burn	23.1	*Soulsby et al (2001)*
River Ithon	28.9	*Greig (2004)*
River Aran	15.7	*Greig (2004)*
River Blackwater	12.2	*Greig (2004)*
River Lugg (2008)	16.5	*This study*
River Lugg (2009)	6.1	*This study*

Table 4.14 Total fine sediment recorded from UK-based studies on spawning gravels

Spatial variability in sediment deposition between the study reaches was higher during the 2008 season with a range of between 12.3% and 24.9% in fine sediment deposition during the incubation period. For 2009 the inter-site variability ranged between 5.2% and 7.5%. Thus, both temporal and spatial variation is a feature of sediment dynamics on this catchment, and highlights the need for full coverage of a catchment when undertaking studies of this kind in order to obtain representative data. Additionally, although only 3 field sites were studied during 2009, spatial variability between those three sites was higher during the 2008 season, which may point to a higher spatial variability during wet years with higher discharges. Additionally, as seen in section 4.3.3, grainsize distributions of the finer portions had a wider range during 2008 than in 2009.

While the Lugg data indicates the contributory role of sediment interactions in spawning habitat quality, the moderate nature of the correlations suggests that other factors may play a part in the fate and viability of incubating embryos.

A weak to moderate fine sediment-dissolved oxygen relationship was observed (R^2 = 0.23) but a stronger fine-sediment – intragravel flow velocity (R^2 =0.37) relationship.

Dissolved oxygen levels were correlated with Intra-gravel flow at Lugg Meanders. But the periodic nature of the data taken during site visits requires further validation of the relationship. However, continuous data was retrieved from probes installed within the redd zone which point to possible additional causes. Interestingly, one possible contributory factor to low survival rates at this site comes from data retrieved from continuous dissolved oxygen probes at the site.

The high discharge spate event of the 16th March was coincident with plummeting dissolved oxygen readings within the egg zone. Dissolved oxygen readings via the handheld device (or any other readings) were not possible at this time due to limitations on access during the spate conditions.

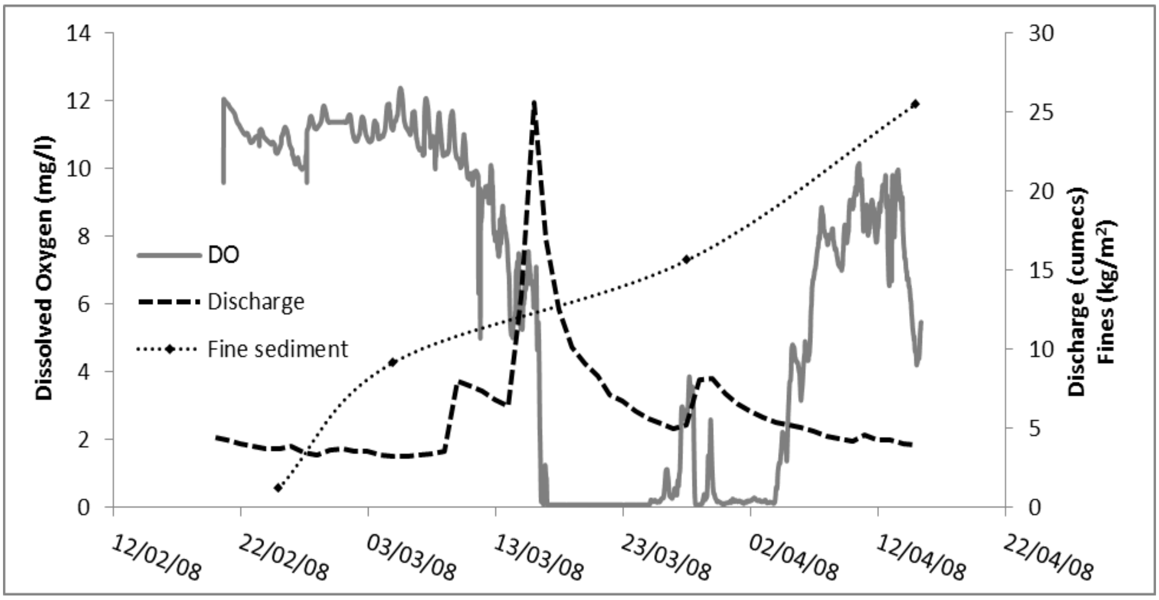


Figure 4.28. Discharge, dissolved oxygen and fine sediment accumulation at Lugg Meanders 2008

The dissolved oxygen data report periods of very low oxygen lasting for over a week each time, which correspond to the occurrence and falling limb of the spate event. This may point to the presence of low oxygen upwelling groundwater interactions within the hyporheic zone (Malcolm et al 2003, 2005, 2006 and Soulsby et al 2009).

This example highlights the need for further investigation into other concomitant causes of lowered survival within the incubation zone, and the major controls that act on the spawning habitat. With this in mind, factors that can broadly be seen as measures of spawning habitat quality may be classed as: Geomorphic, Hydrologic, and catchment (land-use) based, and interacting combinations of these controls should be considered when assessing catchment scale pressures on spawning environment.

In terms of geomorphic indices, we recognize that fine sediment is deleterious and remains a significant contributing factor to incubation success primarily via its impact no intragravel flow velocity as a result of occlusion of the pores within the redd gravels. While there is a weak to moderate correlation of the <2mm and <1mm sized fractions with survival, D_{50} and Dg do not predict survival for the Lugg sites. Additionally, the potential for scour and bedload movement should be addressed and considered in more depth. While there is some evidence from the Lugg data for increased oxygenation during times of bedload impact, more intense fluctuations and even decreased oxygen concentrations seen at some sites during these times may point to other potential contributing factors such as groundwater upwelling.

Hydrology is an important contributing factor and aside from the traditionally observed indices of flow throughout the hyporheic zone, the source of this water – whether from low-oxygen groundwater or overland flow needs to be addressed. Additionally, hydrological controls in reactions to increased spate occurrence and intensity or other climate-related effects (drought) should be factored into appraisals of habitat quality.

Land-use practices are intrinsically tied into the supply and nature of sediment delivered to a river system. Indeed the type of sediment and degree of organics supplied (Fertilizers, agricultural waste, animal faeces) can greatly alter the BOD of the sediment intruded into the redd system; an important consideration when looking at intensively managed agricultural catchments.

It is with this in mind that consideration of these additional controls on habitat will be further addressed in later chapters. Chapter 5 reports a study querying the provenance of the sediment from varying land-use types within the catchment, and Chapter 6 will address other potential incubation environmental factors that may play a part in defining incubation habitat quality.

Chapter 5 Sediment Fingerprinting Study

5.1 Introduction

Fine grained sediment influx and transportation in streams is part of the natural functioning of a river system and is essential to the hydrological, geological and ecological systems of which the river system is a part. In recent times however, particularly in areas of increasing population density and intensive land-use, the range of anthropological practices have altered the way in which sediment interacts within these systems (Walters 1995, Owens and Walling 2002, Krishnappan et al. 2009). This has resulted in changed and sometimes permanent damage to riverine ecosystems.

Sediment transported in streams is derived from a variety of sources, but can be broadly attributed to three main sources: (1) erosion of upland surfaces due to overland flow (2) erosion of channel banks and (3) erosion of the stream bed. The main controls on stream channel bank and bed sediment are hydraulics and stream morphology, whereas land use practices act as one of the main controls on overland derived sediment (Owens 2005).

The concept of 'connectivity' is used in geomorphology to highlight the linkages between sources, stores and sinks of sediment within river systems (Hooke 2003) and is defined broadly as the 'physical linkage of sediment through the river channel system'. Further analysis of landscape compartments can lead to discrimination between *types* of connectivity – Lateral; driving the supply of materials to a channel network, Longitudinal; driving the transfers of sediment flow through a system and Vertical; referring to surface-subsurface interactions (Ward 1989, Brierley et al. 2006). Within this context, the degree of slope-channel and channel-floodplain connectivity - both lateral processes, addresses the relative ease with which land-derived sediment is delivered to the stream channel and is based on catchment-specific characteristics such as slope, land-use, runoff potential; drainage density and soil type.

In a river–management context, one of the chief controlling factors on sediment delivery from the land surface to watercourses is riparian land-use, and studies have shown that human-induced changes in these areas – often due to the intensification of agricultural practices, have resulted in altered sediment yields to river systems (Allan et al. 1997, Walling 1999, Owens 2005).

The study by Allan et al. (1997) in a catchment of 2776 km², found that measured sediment concentrations during low flows were much higher in areas of more intensive agriculture. In a comparison of two neighbouring sub-catchments, sediment yields were up to ten times greater in the more intensely farmed sub-catchment, in response to similar storm events. As part of the same study, a distributed parameter model linked to a geographical information system predicted that an increase in forested land cover would result in dramatic declines in runoff and sediment and nutrient yields (Allan et al. 1997).

Research into land-channel connectivity has resulted in the recent development of sediment mobilization and delivery models such as Psychic (Davison et al. 2006, Collins et al. 2007, Stromqvist et al. 2008) and INCA-Sed (Lazar et al. 2010) which predict the efficiency of sediment delivery from the land surface to the watercourse in pre-defined catchment areas based on input factors such as runoff potential, slope steepness, slope shape, drainage pattern, land use and sediment characteristics. Psychic output for the Lugg catchment is presented later in section 6.3.

Increased sediment production from the land surface area has been shown in row crop cultivation in or near floodplain areas - particularly where topsoil is exposed during fallow periods or preparation for autumn-sown crops during the period before peak rainfall in the UK (Chambers et al. 2000). In arable production, economies of scale have led to the creation of larger fields and 'block cropping' practices widespread throughout Europe, thus, increased areas of cultivation, coupled with larger average field sizes and continuous arable cropping, increase the exposure of soil to erosion due to wind and water (Chambers et al. 1992, Evans 1996, Stott et al. 2001, Bilotta and Brazier 2008).

In agricultural area devoted to pasture, increased sediment yields can result from overgrazing and poaching (Armour et al. 1991). Also, field drainage systems acting as conduits to river channels and increased runoff due to soil compaction may play a part in sediment mobilization and transport (Owens 2005, Deasy et al. 2009).

Sediment yield may also be produced from other land use practices such as forestry (Walters 1995, Sheridan et al. 2006) mining (Nelson et al. 1991) and urban development (Walters 1995). Roads have also been pinpointed in some studies as a potential source of sediment and a conduit for secondary sediment from other sources (Collins and Walling 2004, Grusowski et al. 2006, Collins et al. 2010, Tetzlaff et al. 2007, Bilotta and Brazier 2008).

Also, where the sediment load has a high organic content, its decomposition will result in an increased oxygen demand, depleting in-stream oxygen levels which may be critical to fish and other aquatic species (Ryan 1991).

Sediment input into streams resulting from upland erosion plays a significant role in determining the health of ecosystems by impacting on in channel biotic communities as well as stream water quality. A variety of studies have looked at these effects and documented the relative effects on fish communities, invertebrates and primary producers (Scullion 1983, Sigler et al. 1984, Clarke and Wharton 2001, Bilotta and Brazier 2008).

In terms of the sediment deposition with the river gravels, studies have documented the detrimental effects on hyporheic exchange (Packman and Mackay 2003) and with this, the decline in permeability of fish spawning gravels (Carling and Mc Cahon 1987). Further studies have shown the detrimental effects of accumulated sediment load on the hatching and survival success of salmon larvae (Koski 1966, Turnpenny and Williams 1983, Crisp 1993, Reiser and White 1988, Acornley and Sear 1999, Greig et al. 2005, Julian and Bergeron 2006, Heywood and Walling 2007).

In addition, the above papers describing the effects of increased suspended sediment load on invertebrate populations (Scullion 1983, Bilotta and Brazier 2008) has shown a decreased population size which in turn would have knock-on effects for emergent salmon fry and parr which feed on these populations. This highlights the compound effects of increased sediment load on salmon recruitment in UK rivers.

On the Lugg, there have been concerns regarding sedimentary contributions to suspended sediment load from eroding land areas such as pasture and arable land (Russell et al 2001, Wade et al 2007, Deasy et al 2009, Lazar et al 2010). Disregard for riparian buffer zones has also been addressed as an increasing concern as the intensity of agricultural practices have increased in recent years (Environment Agency report 2003). Also, in a study by Grusowski et al (2006), roads have been shown a significant contributing factor in a nearby Hereford catchment. An Environment Agency wet weather survey (2006) reported that 66% of point samples made over 6 month period were above EU recommended standards, and a DEFRA report on the application of the PSYCHIC model (Davison et al., 2008) to the Lugg catchment states that significant reduction in sediment (and Phosphorus) transfer to the river course from both pasture and arable areas could be prevented by mitigation efforts such as reducing connectivity to the water course and the timing of crop harvest and planting and fertilizer applications.

Thus, it has been recognised that there is a need for sediment control strategies in affected systems such as the Lugg. However, the lack of information on the exact source of the sediment deposited in salmonid gravels has impeded the development of land management strategies and efforts to manage sediment influx from riparian zones would benefit from catchment-specific knowledge of land-surface contributions to the sediment budget.

Images of potential sediment sources within the Lugg catchment are shown below and outline the typical riparian land use in the area and from the categories used to define fingerprinting source categories within this study.

Arable 1 (fallow)

Arable 2

Pasture

Woodland

Roads

Channel bank

Sediment fingerprinting techniques have been developed over recent years from broadly qualitative roots as outlined in section 6.2 below, and now provide a means to identify the source components of fluvial sediment - including the interstitial fines of salmonid gravels.

There is still however a dearth of knowledge on the source type contributions of fines in salmonid redds and to date; only one other study has addressed this subject. Walling et al. (2003) carried out a broad reconnaissance survey looking at the proportion of either land-surface or channel bank derived sediment in some UK river catchments based on the composite fingerprinting approach. Preliminary results showed a marked variability in the proportions of sediment sources, with results ranging from 97% surface sources (Itchen river) to only 3% surface sources (Camel river).

This study builds on the approach taken by Walling et al by investigating sediment provenance at a finer scale within the Lugg and Arrow catchment, and which incorporates both spatial and temporal trends.
We investigate the source of salmonid redd sediment relative to 5 potential source categories: Woodland, Pasture, Arable, Road verges and Channel-banks. The respective importance of the potential source categories relative to the redd sediment samples is also identified.
In addition, the study investigates contributions to redds on both a spatial (catchment – wide) and temporal (seasonal and annual) scale and presents the variability of influx relative to storm events. The relative source type contributions between redd sediment and suspended sediment were also investigated.

Other fingerprinting studies – most of which have addressed suspended sediment provenance, demonstrated the wide geographical variability in source type contributions between catchments (Collins and Walling 2007, Smith and Dragovich 2008). Thus, the adoption of a catchment-specific fingerprinting approach would prove to be of most value to catchment managers in creating targeted management strategies for sediment control within their catchments.

5.2 Background and technique history

The general application of the sediment source identification began as a means to understand the processes of sediment erosion, transport and fate and to aid the creation of sediment budget models (Dearing et al 1990, Walling et al.1993) It has also found practical application as a means for sediment and pollution control (Walling 1993, Minella et al 2008).

Previous methods to assess sediment sources and budgets have been through the use of direct monitoring methods such as with erosion pins and troughs which estimated the of rate soil erosion (Davis and Gregory 1994, Stott 1999). Potential source identification via photographs and field observations (Jackson 1986) has also been used. However, these direct methods proved too costly and time consuming relative to data quality produced, to remain viable research methods (Loughran 1985, Peart and Walling 1988).

Investigations into sediment 'fingerprinting' began with attempts to retrace certain properties found in suspended stream sediment back to potential sources within each catchment by means of those defined properties or 'tracers' which were unique in some way to a potential source.

Sediment tracing techniques have evolved over the past three decades from single-tracer qualitative studies to the more robust multi-parameter quantitative methods used today. A brief description of the progression and refinement of what became the sediment fingerprinting technique is presented below.

Efforts to link land-derived sediment to streams began in the 1960's and were based on sediment colour properties. Moore (1961) looked at the colour variations in lake sediment cores in order to help identify their origin of (post-glacial) deposition. Grimshaw and Lewin (1980) used colour to identify between channel and non-channel sediment sources in a Welsh catchment. Peart (1993) used colour as a tracer in two Hong Kong catchments, but reported that they could not differentiate sources well enough to define provenance. Other tracer properties that have been used include the magnetic (Walling et al. 1979, Dearing et al 1985,) chemical and isotopic (Walling and Kane 1984, Peart 1993), Radionuclide (Walling and Woodward 1992) organic and biogenic (Brown 1985, Santiago et al. 1992) and physical (De Boer and Crosby 1995).

However, concerns have been raised regarding the intrinsic reliability of single-tracer methods (Oldfield and Clarke 1990, Walling et al 1993, Collins and Walling 2002). Two main issues have been expressed:

(1) The likelihood of tracer alterations during particle transport or within the aquatic environment – (either physical or geochemical) which may result in their redundancy as reliable tracers.

(2) The potential for erroneous source-sink matches due to certain source combinations falsely resembling an individual source type. A simplified example of this is illustrated in figure 6.1 below.

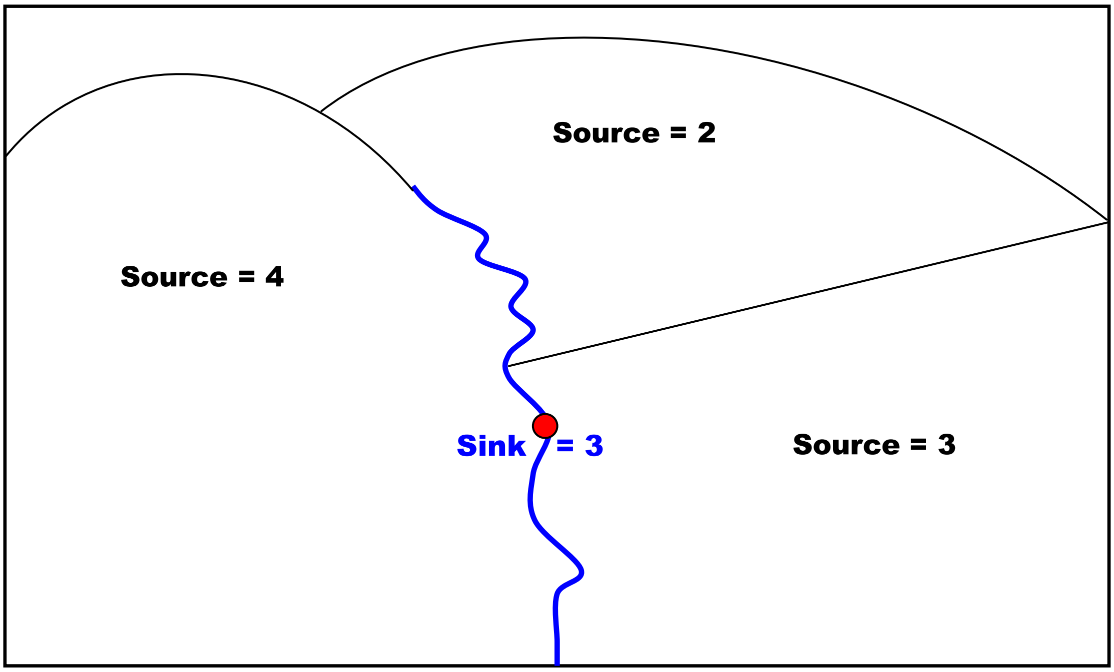


Figure 5.1 A riverbed 'sink' sample with three potential source types. Single-tracer values are assigned to each of the sources and to the sink.

Fig 5.1 illustrates the potential for source identification confusion using the single tracer method. In this example, the sink's value is 3 and may be assumed to have come from the source with a value of 3, but could also be the product of equal proportions of the sources with values of 4 and 2, or equal proportions of all three sources.

For these reasons, the idea of using composite or 'multivariate' properties as tracers was proposed. By using multiple tracers, a more robust and definitive match can be made between river sink samples and their potential sources.

Walling (1993) and Collins (1997) propose the use of fingerprinting properties taken from a diverse range of property categories (Chemical, radionuclide, isotopic, biogenic) to ensure an optimal (and statistically valid) source differentiation capacity. This would in turn improve the accuracy of source contribution estimates in the later stages of calculation.

Multivariate fingerprinting techniques have been shown to be applicable up to individual catchment basin scale. The property suites which optimally define source contributions are liable to change from catchment to catchment. It is thought that this may be due to controlling factors such as underlying geology, and soil type (Wallbrink et al 1996, Collins et al 1998).

To arrive at a quantitative estimate of source type apportionment, two main stages of calculation are required. The first involves the selection of fingerprinting properties which will unequivocally differentiate between source categories, and the second involves comparison of in-stream sample(s) with the suite of chosen fingerprint properties.

The calculation of both the optimal fingerprinting suites and the contributing source proportions are achieved by means of a series of statistical procedures and multivariate mixing models which are carried out in sequence. The steps involved are described in further detail in methods section 5.4 below.

5.3 The study area

The Lugg catchment is an area of 1077km² with upland impervious headwaters rising in Powys Wales, before crossing the border to Herefordshire and graduating to a lowland catchment in the reaches below the town of Leominster; where the river flows SSE to its confluence with the river Wye at Mordiford (SO570374).

This study concentrated mainly on the upper and transitional reaches of the catchment above the town of Leominster, and includes the tributary Arrow which joins the Lugg just downstream of the town. The catchment area included in the study is 530 km² and the long- term annual mean rainfall in this upper catchment is 1048mm which generates approximately 395mm of runoff (Marsh and Lees 2003).

5.3.1 Geology

Impermeable Silurian shales form the bedrock in the upper catchment headwaters with more permeable old red sandstones of Devonian age dominating as the river flows across the Welsh-English border. Some overlying gravels and glacial drift increase its capacity as an aquifer (Wade 2007). It is thought that these glacial clays, gravels and the permeable sandstone moderate the river's high flow peaks to some extent, and its base flow index is 0.66 which indicates the presence of groundwater (Lazar et al 2010).

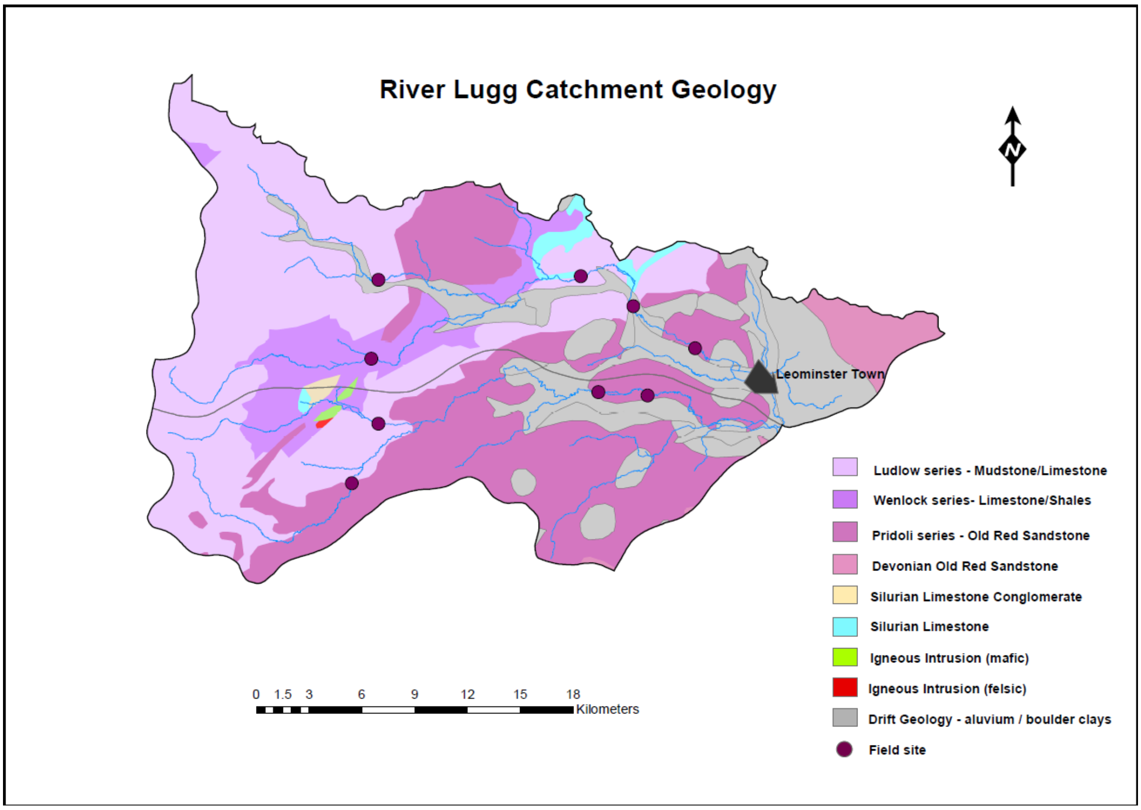


Figure 5.2. River Lugg - Upper-catchment geology

5.3.2 Land use

The Lugg is a predominantly rural catchment, with woodland and grassland and production of cattle and sheep in the upper parts of the catchment, and increasing arable and cattle grazing in the lower reaches. Agriculture is important in the catchment, with distributions of 0-82% upper; 28–82% in middle; and 14–86% in lower areas (Lazar et al. 2010).

Land-use for the catchment area upstream of Leominster (Butts Bridge Gauging station) and for the Arrow sub-catchment is presented in table 5.1 below:

Land use	Lugg % cover	Arrow % cover
Woodland	12.3	10.6
Arable & horticulture	17.5	5.6
Grassland	63.3	70.7
Mountain, heath, bog	5.0	12.1
Built-up areas	1.5	1.1
Water (inland)	0.3	0.1

Table 5.1 Land-use for Lugg sub-catchment above Butts Bridge (Data from Land Cover Map 2000, CEH Monks Wood)

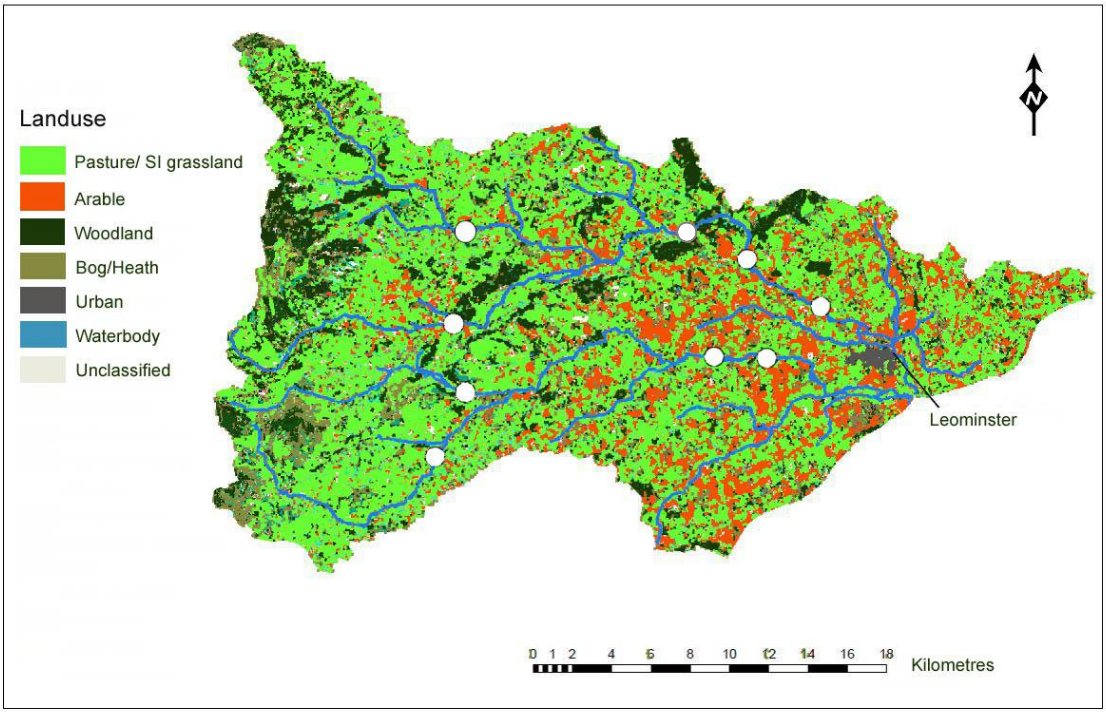


Figure 5.3 Land-use map of the study catchment area (Data derived from CEH Land cover map 2000 with field site locations. Orange areas denote arable land, light green areas, grazed turf and dark green areas denote woodland - which is more prevalent in the upper area of the catchment.

Natural vegetation is also significant throughout (upper: 18–100%; middle: 16–57%; lower: 13–86%). In the upland parts of the catchment however, slopes are steeper and grazing can place pressure that potentially decreases the vegetation cover and may result in higher erosion rates (Lazar et al. 2010). Within the main river channel, many of the river banks at the field site locations were actively eroding and so deemed a potential contributor to redd sediment (Hooke and Redmond 1989, Russell et al 2001).

5.3.3 Sediment yield

The INCA-Sed model (Lazar et al 2010), an Integrated Catchment Model for Sediments which is a dynamic, process-based daily time-step model was used to link sediment delivery from the landscape to the changes in-stream sediment changes on the Lugg. Results indicated that the most important sediment generation process is diffuse soil loss, and simulated sediment delivery to the river varied between 3 and 1102 kg ha−1 year.

An Environment Agency survey (River Lugg Catchment Wet Weather Sediment Mobilisation and Delivery Study 2006) was carried out between December 2005 and May 2006 in order to measure water quality at 19 locations throughout the catchment. For 36 spot samples retrieved during this period, 66% of them were above the EC Freshwater Fish Directive of 25mg/l as an annual average target for suspended solids, and 47% had SS levels that were classed as high or very high (i.e. between 2 and 4 times the target value).

The PSYCHIC model (Phosphorus and Sediment Yield CHaracterisation In Catchments) -a DEFRA funded project (Project PE0202), was applied to the Lugg catchment (Davison et al. 2008) and figure 5.4 below features the areas most susceptible to erosion according to model. This evaluation was based on land–use, soil type and characteristics and whether the land was under-drained or not.

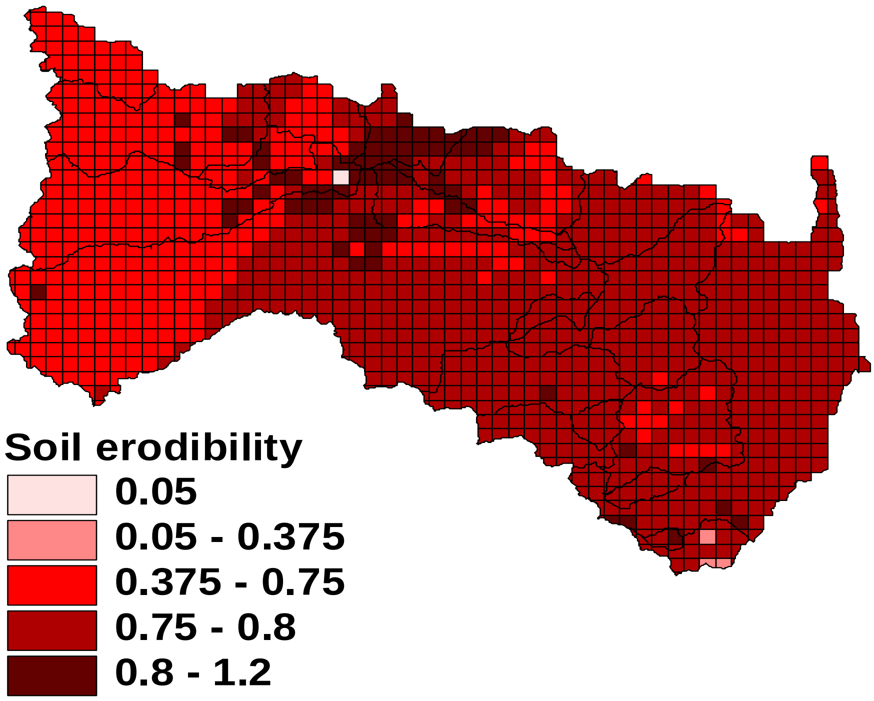


Figure 5.4. PSYCHIC model soil erodibility in the Lugg subcatchment

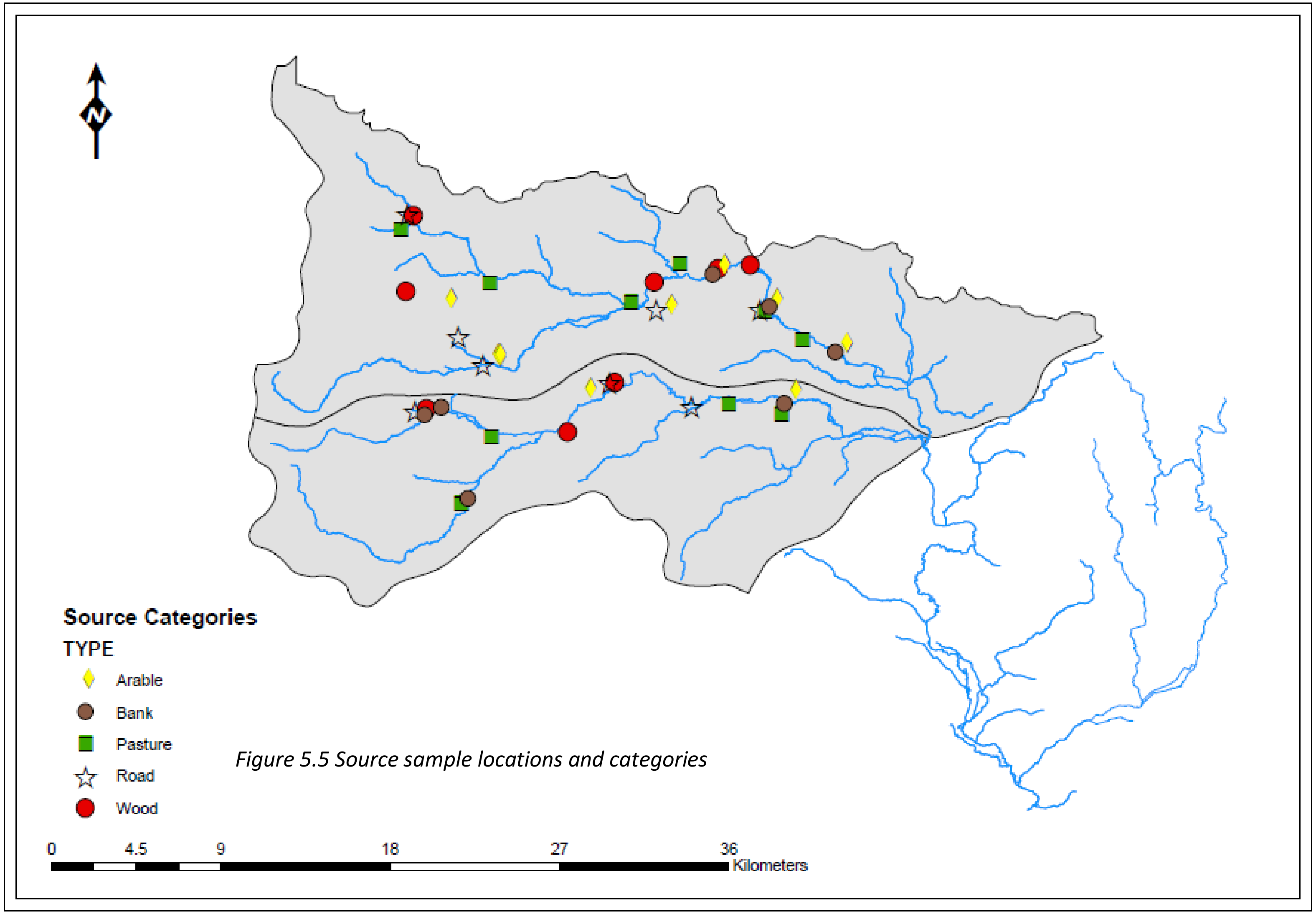


Figure 5.5 Source sample locations and categories

5.4 Methods

5.4.1 Overview of the composite fingerprinting technique

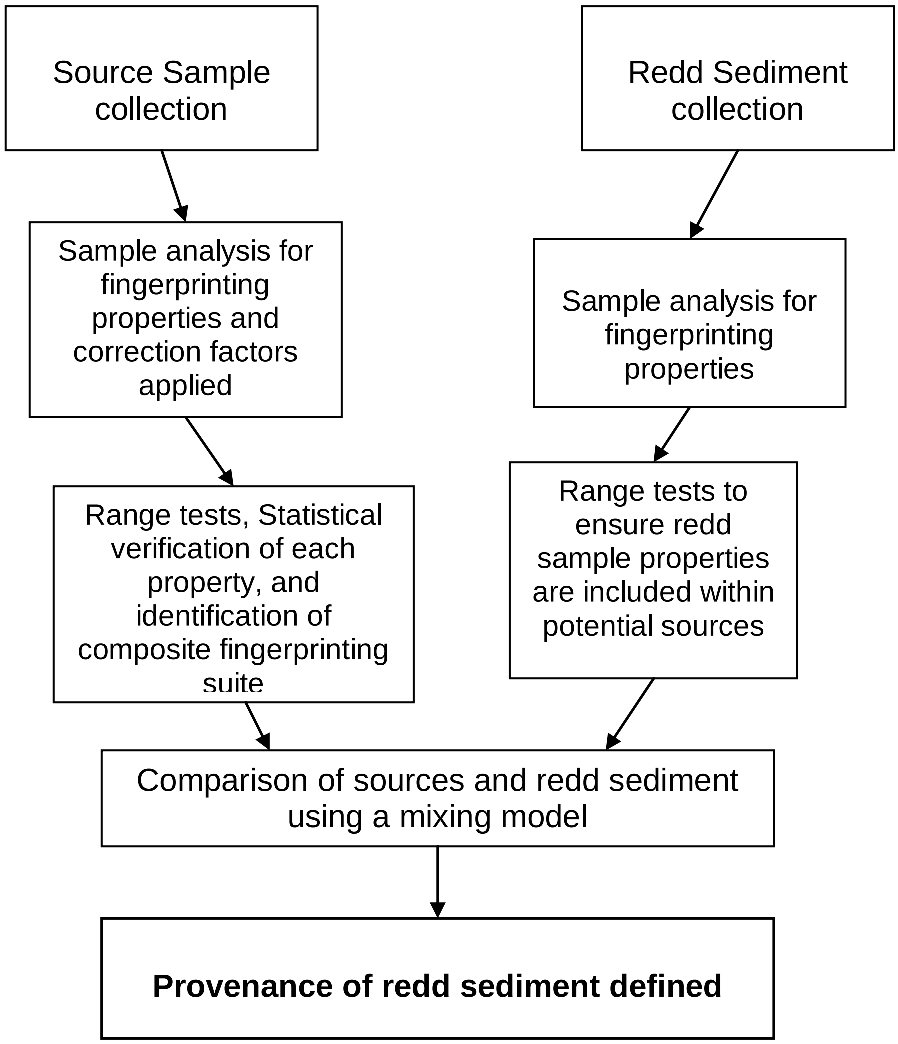


Figure 5.6 The procedure for fingerprinting of redd sediment source (adapted from Collins and Walling 2007).

5.4.2 Sample collection and analysis

50 source samples were collected in total. This represented between 8 and 10 samples from each of 5 principal land use types as well as 9 channel bank samples within the catchment as listed below and illustrated in figure 5.5.

1. Woodland
2. Arable
3. Pasture
4. Road Verges
5. Channel bank

Source samples were retrieved from areas that represented likely areas for mobilization by erosion. Samples were taken from areas within 50m of the river.

For each source sample, 1kg of surface sediment was collected; each of which constituted a number of smaller samples taken from disparate parts of the site to ensure the representativeness of each sample.

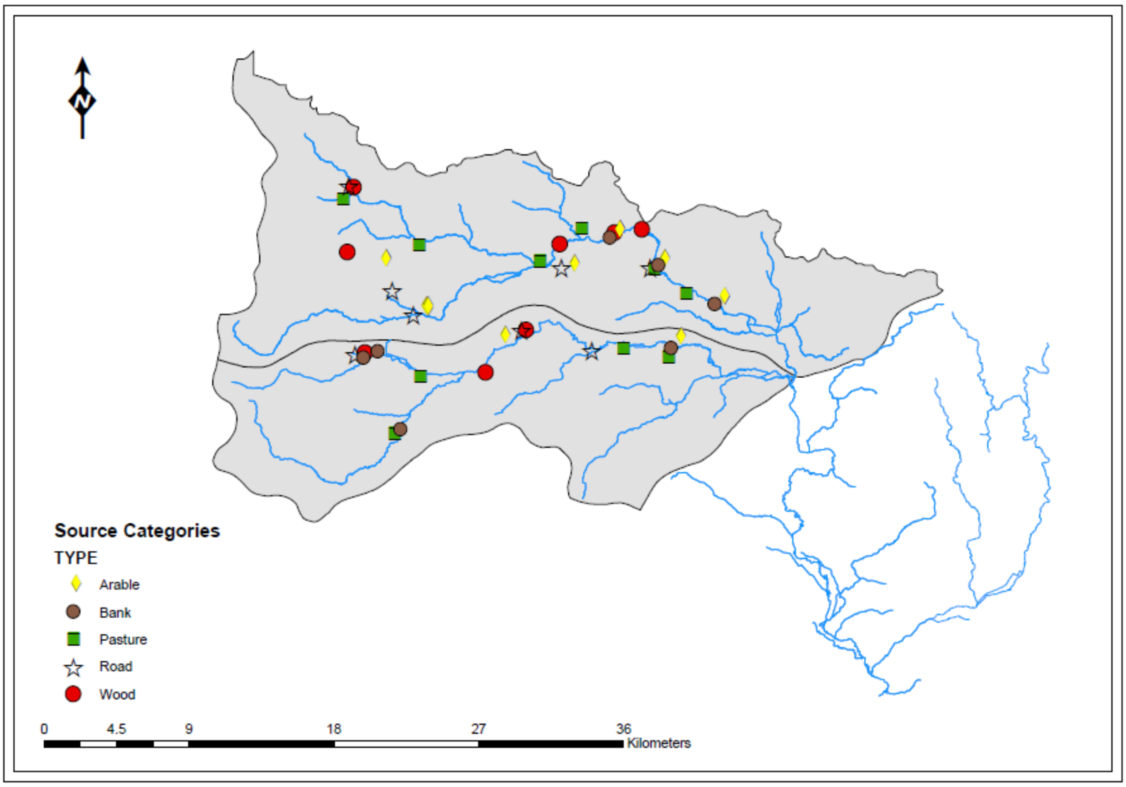


Figure 5.5. Source sample locations.

The redd sediment samples were retrieved from each of the artificial redd sites as illustrated in figure 5.7 below. Some samples were retrieved periodically at certain sites over the course of the incubation period in order to ascertain any differences in source contribution between early and late samples. Comparisons in source contribution were also made inter-annually between the spawning seasons 2008 and 2009.

Additionally, suspended sediment samples were collected by means of time-integrated Isokinetic samplers (Phillips et al 2000) which collected suspended sediment throughout the duration of the field seasons.

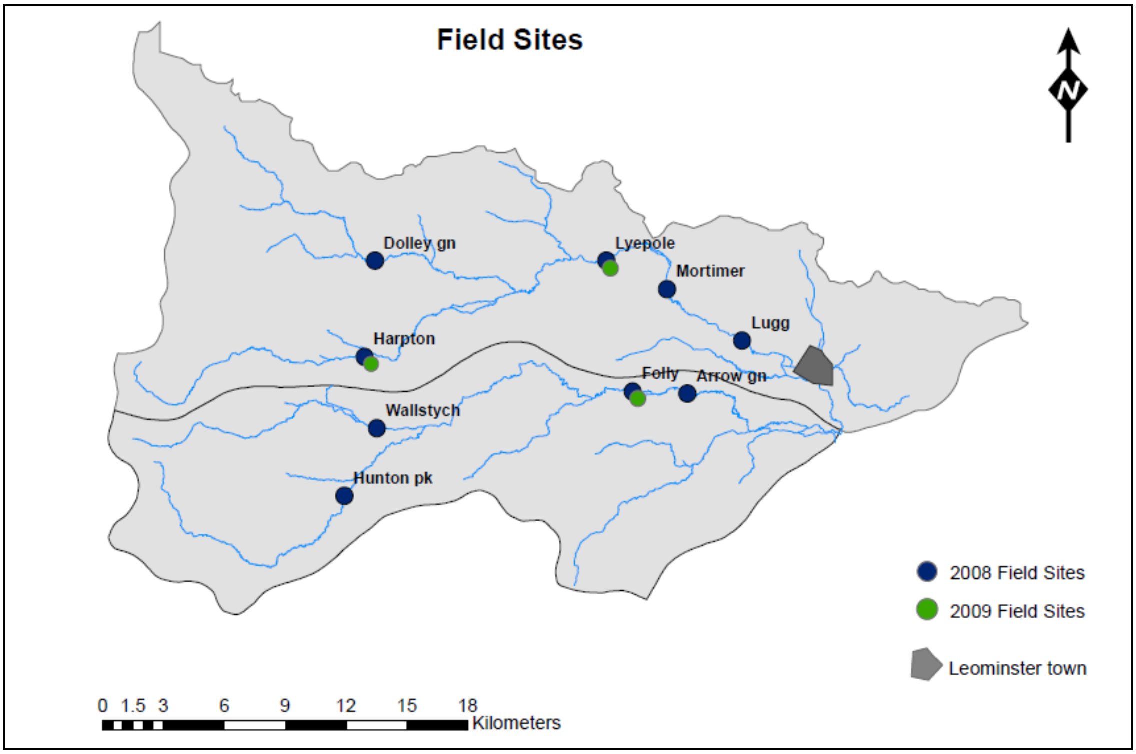


Figure 5.7 Redd sediment sample locations from the Lugg (north) and Arrow (south) sub-catchments. Sites featuring additional green dots are those for which inter-annual comparisons were made and from which periodic intra-spawning season samples were taken.

5.4.3 ICP-MS Sample analysis

All samples were initially sieved to a grain-size of <63µm using stainless steel sediment sieves to ensure processing of a representative fraction of the samples and ensure comparability.

4 grams of each of the soil and redd sediment samples were microwave digested using 10ml concentrated nitric acid - HNO_3 and a laboratory grade microwave to isolate acid-extractable elements and enable analysis via ICP-MS (Inductively-coupled plasma mass spectrometry). The method for sample preparation and procedure is outlined in EPA document 3050a (2007).

The ICP-MS unit combines a high-temperature ICP (Inductively Coupled Plasma) source with a mass spectrometer. The ICP source converts the atoms of the elements in the sample to ions. These ions are then separated and detected by the mass spectrometer. Figure 5.8 below outlines the process graphically.

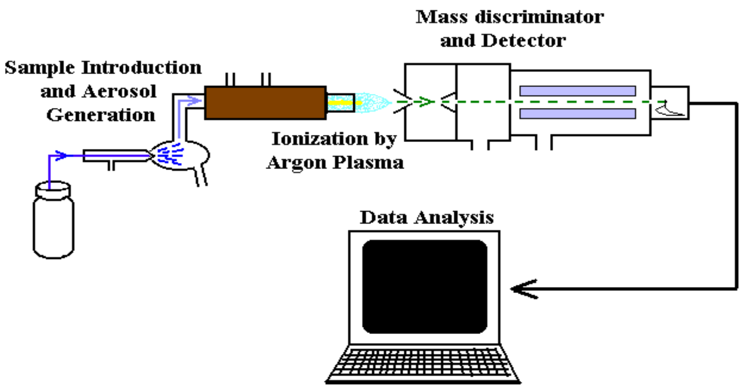


Figure 5.8. Elemental analyses via ICP-MS (Diagram courtesy of S. Kvech)

The samples were analysed for concentrations of 42 Elements as listed in table 5.2 below:

Alkali and Alkaline Earth Metals	*Other Metals*	*Non-metals*	*Transition Metals*	*Rare Earth Elements (REEs)*
Li, Na, Cs, Rb, Mg, Ba	Al, Ga, Sn, Sb, Tl, Pb, Bi, In	As, Se	Tl, V, Cr, Mn, Co, Ni, Cu, Zn, Hf, Re, Y, Zr, Mo, Cd	La, Ce, Pr, Nd^{144}, Nd^{146}, Sm, Eu, Gd, Tb, Dy, Ho, Yb

Table 5.2 Elements analyzed by ICP-MS

5.4.4 Grainsize analysis

Both soil and redd samples were also analysed for characteristic grain-size distribution and specific surface area using a Coulter Counter LS 130. Each sample (approx. 5g) was analysed in liquid form - <63 fraction suspended in distilled water, and 2 drops of Calgon to 50ml of sample were used to ensure optimal dispersal of sample particles. The solution was fully agitated to ensure representativeness. Approximately 2ml of sample was pipetted into the coulter sample cell and tested via laser diffraction for an optimal range of 10-12% obscuration. Addition of further sample or added water ensues if the optimal range is not achieved.

The samples were measured via laser diffraction form a grainsize range of 0.1µm - 90 µm. The mean surface area was calculated on the assumption that particles were non-porous and spherical in shape. These data were used as a correction factor for the absolute concentrations during the fingerprinting study.

5.5 Source discrimination

The ICP-MS elemental data were ordered according to source land-use type and redd sediment samples and a series of statistical tests were carried out.

A two-stage statistical procedure as described by Collins et al (1997) was carried out to ascertain the suite of elements which was capable of discriminating between source categories (land-use type), and would thus provide the composite fingerprint capable of redd sediment source apportionment.

5.5.1 Range Tests

Range tests were carried out to ensure that the redd samples to be analysed were fully represented by the source samples collected. Redd sediment elements whose concentrations are outside the range of the collective source sample concentrations are excluded from any further stage of the analysis.

Within the range tests, particle correction factors were employed to take account of higher concentrations possible in redd sediment due to smaller overall particle size diameter. Grainsize reduction occurs in riverine systems due to transport instream and overland. Grainsize analysis was carried out for all samples using an LS 1300 Coulter counter which measured grain size distributions from 0.1µm to 900µm diameter and also found the specific surface area which was used to compute the adjustments to concentration based on an average value for each land-use type.

Elements which failed the range tests and were excluded from further analysis were: Ti, Cu, Zn, Se, Mo, Cd.

5.5.2 Kruskal-Wallis tests

The first stage of statistical analysis involved a non-parametric kruskal-wallis h-test for the analysis of variance for each element, between the source sample groups (Kruskal and Wallis 1952). This was done to ascertain whether the element might successfully be used as a discriminant property between the 'land-use type' groups. Ideally, to obtain a high degree of distinction between the groups, the within-group variability will be low, and the between group variability, high. Elements that did not pass the Kruskal-Wallis test were eliminated for further stages of the analysis. Elements that passed the test obtained a p-value of <0.05 with a corresponding H-value lower limit of 9.50.

Results of the kruskal-wallis tests for distinction between groups are presented in table 5.3 below:

Element	P value	Significant
Li	0.012*	*
Na	0.81	
Mg	0.04	*
Al	0.003*	*
V	0.000*	*
Cr	0.05*	*
Mn	0.813	
Co	0.213	
Ni	0.04*	*
Ga	0.424	
As	0.05*	*
Rb	0.000*	*
Y	0.002*	*
Zr	0.154	
In	0.019	
Sn	0.640	
Sb	0.260	
Cs	0.003*	*
Ba	0.18	
La	0.05*	*
Ce	0.03*	*
Pr	0.03*	*
Nd144	0.02*	*
Nd146	0.04*	*
Sm	0.01*	*
Eu	0.01*	*
Gd	0.006*	*
Tb	0.008*	*
Dy	0.005*	*
Ho	0.004*	*
Yb	0.001*	*
Hf	0.05*	*
Re	0.124	
Tl	0.00*	*
Pb	0.01*	*
Bi	0.04*	*

*Table 5.3. Results of the Kruskal-wallis tests. Asterisk * denotes p-values at or above the 95% confidence level. A total of 25 elements passed the test.*

5.5.3 MDA - Multivariate Discriminant Function Analysis

Subsequently, a multivariate discriminant function analysis (DFA) was performed to define a suite of properties that together provided optimal discrimination between the source group categories. The SPSS program was used to carry out the analysis.

In DFA, the source categories act as the dependent or grouping variables, and each of the properties act as the independent or discriminating variables. The discriminant functions, or canonical roots, are created as a linear combination of independent / discriminating variables, where the first function maximizes the differences between the values of the dependent variable. Subsequent functions are orthogonal to it (uncorrelated with it) and maximize the differences between values of the dependent variable.

A forward stepwise algorithm was used, where at each step; the minimization of Wilks' Lambda provided the means to manually build the composite fingerprint which provided the discrimination. Starting with 2 potential properties, additional properties were added incrementally and either kept or discarded depending on whether the Wilk's Lambda value was improved or not. A lambda value of 1 occurs when mean values of all groups are equal, and a lambda nearing zero occurs when inter-group variability is small as compared to total or within group variability.

Initial efforts to discriminate between all 5 source categories were hampered by the fact that the arable and pasture categories were very similar (i.e. the ratio of inter-group to within-group variability was low. While all other groups could be clearly defined, some overlap of arable and pasture categories remained. This was thought to be due to the prevalence of rotation of agricultural land-use in the area, where land previously used as pasture may seasonally become arable land, and vice-versa.

To circumvent this issue, arable and pasture categories were merged to form one larger group termed ‘Agricultural land’. The statistical procedures were then repeated from the Kruskal–wallis test onwards. The K-W test results presented in table 6.3 above, reflect the testing done on this later, 4-group matrix. The groups are represented by the following numbers - Woodland (Group1), Agri-land (Group 2) Roads (Group 4), and Channel bank (Group 5).

Three additional channel bank samples were also eliminated from the DFA as they were found to resemble arable and pasture groups and impeded clear discrimination between source groups. It is thought that these samples may have been collected from surface horizons in the channel banks and thus were too similar in composition to adjacent agricultural land.

The progression of the stepwise classification process is presented graphically (after Collins and Walling 2007) in figures 5.9 (a) to 5.9 (d) below, where the source sample groupings are initially overlapping and not well defined. With the incremental addition of further properties, the discrimination between source categories improves until our final fingerprint emerges where 100% classification is achieved and there is no overlap between categories. The final composite fingerprint comprises 12 individual properties and correctly classifies 100% of the source samples (Figure 5.10). In terms of cross-classification and verification of groupings, 90% of groups were classified correctly, with Wood, Arable, Roads and Channel bank yielding cross-classified results of 80%, 95.2%, 100% and 77% respectively. The uncertainty associated with these figures should be considered in the context of the mixing model output in subsequent stages.

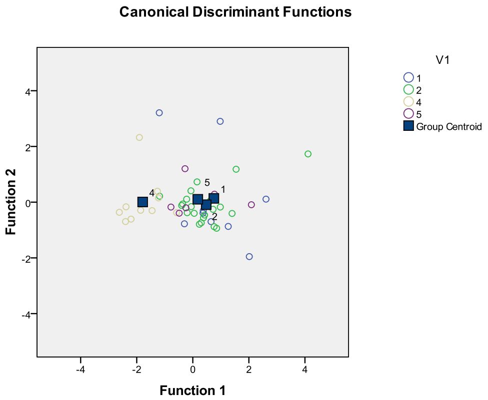


Figure 5.9 (a) Tl, Cs

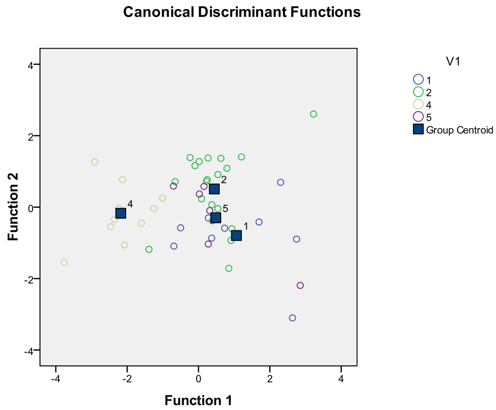


Figure 5.9 (b) Tl, Cs, As,Ni

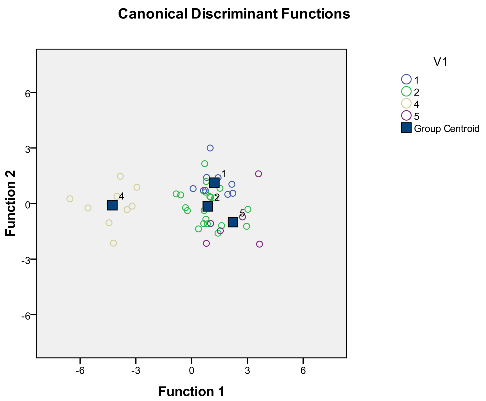


Figure 5.9 (c) Tl, Cs, As, Ni,Nd146, Mg

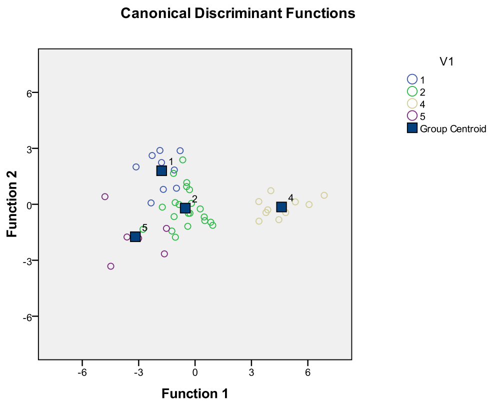


Figure 5.9 (d) Tl, Cs, As, Ni,Nd146, Mg, Al, Y

The progression of the cumulative effects of each of the 12 fingerprint properties on Wilks' lambda values and percentage correct classification are presented in table 6.4 below.

Tracer Property	*Wilks' Lambda*	*Cumulative % of source samples correctly classified.*
Tl	**0.502**	**60**
Cs	**0.495**	**60.9**
As	**0.427**	**60.9**
Li	**0.319**	**65.2**
Ni	**0.294**	**67.4**
Nd146	**0.237**	**69.6**
Mg	**0.083**	**76.1**
Al	**0.053**	**80.4**
Y	**0.029**	**91.3**
Rb	**0.019**	**95.7**
Hf	**0.014**	**97.8**
Pb	**0.010**	**100**

Table 5.4 : The optimum composite fingerprint for source type discrimination.

It was this fingerprint which was brought forward to the next stage of the process, where application of the fingerprint to the mixing model allowed the relative proportions of the 4 source categories within the redd sediment samples to be defined.

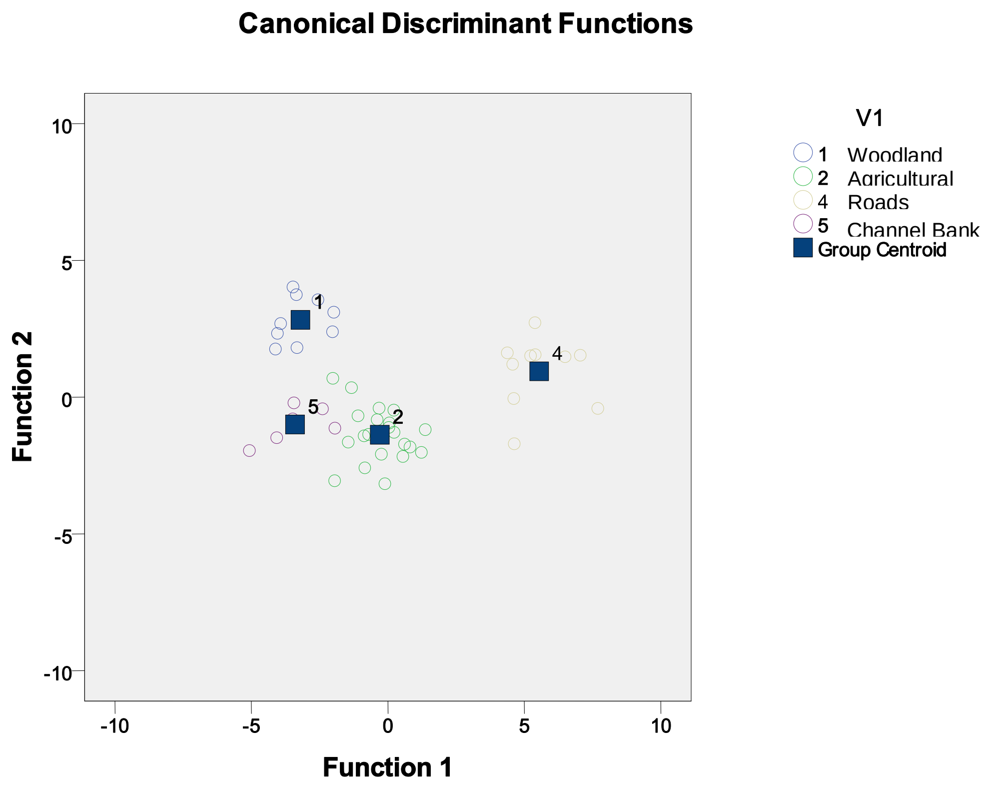


Figure 5.10 Final classifications with 12 fingerprint properties. (Tl, Cs, As, Ni,Nd146, Mg, Al, Y, Rb, Hf, Pb).

5.6 Source apportionment

5.6.1 Grainsize correction

Particles transported from the land surface may undergo physical changes during transport – in particular a decrease in overall particle size. Since this would affect the overall surface area available for adsorption of elements, and in turn the concentration of elements present in a sample (Stone and English 1993, Collins et al. 1998, Russell et al. 2001, Walling et al. 2002). In order to accurately compare the source concentration with those of the redd sediment in the framework of the mixing model; we need to take account of any changes in particle physical form which may have taken place during transport.

As described in section 6.4.4 above, an LS 1300 Coulter counter was used to measure grain size distributions of both source and redd sediment samples. All samples had previously been sieved to <63µm and so particle size distribution from 0.1µm to <63µm diameter was measured. The mean surface area was also extracted from this data, from which the particle size correction factors were computed. The ratios of mean particle size of redd sediment to the mean particle size of each land-use type to were used to calculate the correction factor and are displayed in table 5.5 below.

Land-use type	***Correction factor***
Wood	1.12
Agriculture	1.248
Road	1.023
Channel Bank	1.233

Table 5.5 Particle size correction factors for each land-use type

These correction factors were incorporated into each mathematical phrase of the linear equations within the mixing model to take account of changes in concentration due to particle size decrease in transport. Additionally, a tracer–specific weighting was applied at the end of the statement as explained below.

5.6.2 Tracer specific weightings

Tracer specific weighting were used in the mixing model to take account of the variation in measurement precision of each of the fingerprint properties. Since all data came from the ICP-MS process, the weightings would be established by computing the variance involved in replicate measurements for each element. The reciprocal of the square root of this variance was used as the weighting factor in the mixing model equations.

The specific tracer weightings for the Lugg fingerprint are presented below:

Tracer Property	***Weighting***
Tl	0.75
Cs	1.12
As	0.65
Li	1.17
Ni	1.14
Nd146	1.31
Mg	1.29
Al	1.22
Y	1.34
Rb	1.25
Hf	0.54
Pb	1.41

Table 5.6 Specific tracer weightings for each fingerprint property

5.6.3 Mixing model

A multivariate mixing model after that used by Collins and Walling (2007) was used to estimate the relative contribution of source groups to a particular river sample or grouped river sample means.

For each of the tracer properties in the composite fingerprint, a linear equation is constructed which relates the concentration of the property in the sample to that in the mixture; representing the sum of the contributions from the different source groups. Thus, the composite fingerprint is represented by a set of linear equations – one for each fingerprint property.

A least-squares method was applied for each of the linear equations where the proportions derived from individual sources (s) were estimated by minimizing the sum of the square of the residual 'R' for the 'n' tracer properties and the 'm' source groups involved. The model is described below:

$$R_{es} = \sum_{i=1}^{n} \left(\frac{C_i - \left(\sum_{s=1}^{m} P_s S_{si} Z_s \right)}{C_i} \right)^2 W_i \qquad (1)$$

Where,

R_{es} - Residual sum of squares

C_i = Concentration of tracer property 'i' in the 'sink' sample (ie: redd sample)

P_s = Relative contribution of the source category 's'.

S_{si} = Mean concentration of tracer property in the the source group 's'.

Z_s = Particle size correction factor for source category 's'.

W_i = Tracer specific weighting

n = Number of fingerprint properties

m = Number of bed sediment source type categories

The model also required two constraints to be satisfied:

1. The contribution from each source must lie within the range 0 to 1.

$$0 \le P_S \le 1 \qquad (2)$$

2. The sum of the contribution from all sources is equal to 1.

$$\sum_{s=1}^{m} P_S = 1 \qquad (3)$$

An example of a linear equation within the mixing model for a particular tracer property, and for 3 source categories: Top soil, Road verges and Channel Bank, is shown below:

The linear equation for the tracer Potassium (K) for the source categories will be :

=((F2-((F4*0.72*A15)+(F5*0.63*B15)+(F6*0.59*C15)))/F2)^2*1.5

Where F2 is the concentration of potassium in the redd sediment sample,
F4 is the mean concentration for the Topsoil category
F5 is the mean concentration for the Road verge category
F6 is the mean concentration for the Channel bank category

The numerical factors within the central set of brackets are the grainsize correction factors relative to each of the source categories.

A15, B15 and C15 are relative proportions of each source category, and the model setup starts off with them being equal – in this case a value of 0.33 each.

A linear equation such as this was constructed for each of the (13) tracer properties, and the source apportionment provided by minimization of the sum of squares of the weighted relative errors.

5.6.4 Monte Carlo Framework

In order to quantify the uncertainty involved in the estimate of source contributions produced by the mixing model, a Monte-Carlo approach was used (Collins and Walling 2007, Rowan et al. 2000).

A Monte-Carlo approach generally involves: (a) the definition of prior probabilities for the parameters of the model in question; (b) multiple simulations of the outcome(s) of the model by randomly sampling the parameter space according to the pre-defined probability distributions; and (c) the definition of the frequency distribution of the outcomes (New and Hulme 2000).

This was carried out using recreated normal distributions for each fingerprint property for each source, which compensated for the small sample size for each of the source sub-groups. A simulated series of 3000 potential values was created by means of a random number generator which used the mean and standard deviation of each property and source category. For this study, 12 fingerprint properties and 4 source categories gave rise to 48 columns of data which were used by the model to repeatedly (3000 iterations) solve the model giving source proportion data. The repeat iterations were used to obtain confidence limits for the relative source-type contributions to each redd sediment sample and were calculated from the standard error of the mean associated with the 3000 solutions.

5.7 Results and Discussion

Several scenarios which were run through the model are presented in Table 6.7 below. The first scenario reports on runs for individual sites in both years of the field study and the second reflects the mean values for all redd sediment samples for the years 2008 and 2009 and represents the most general evaluation of sediment apportionment available with this dataset.

Other scenarios represent both temporal and spatial variations and comparisons detected from the redd samples and a list of the various mixing model runs performed are listed in table 5.7 below.

Scenario #	***Redd groupings***	***Aim***
1	Individual sites	General assessment
2	All Redd samples	General assessment
3	2008 samples	Inter-annual variation
4	2009 samples	Inter-annual variation
5	Lugg samples	Spatial variation
6	Arrow samples	Spatial variation
7	Upstream samples	Spatial variation
8	Downstream samples	Spatial variation
9	Time-series – Lyepole Bridge site	Intra-season temporal variation
10	Time-series – Lower Harpton site	Intra-season temporal variation
11	Isokinetic samplers	Suspended sediment measure

Table 5.7 Redd sediment combinations run through the mixing model

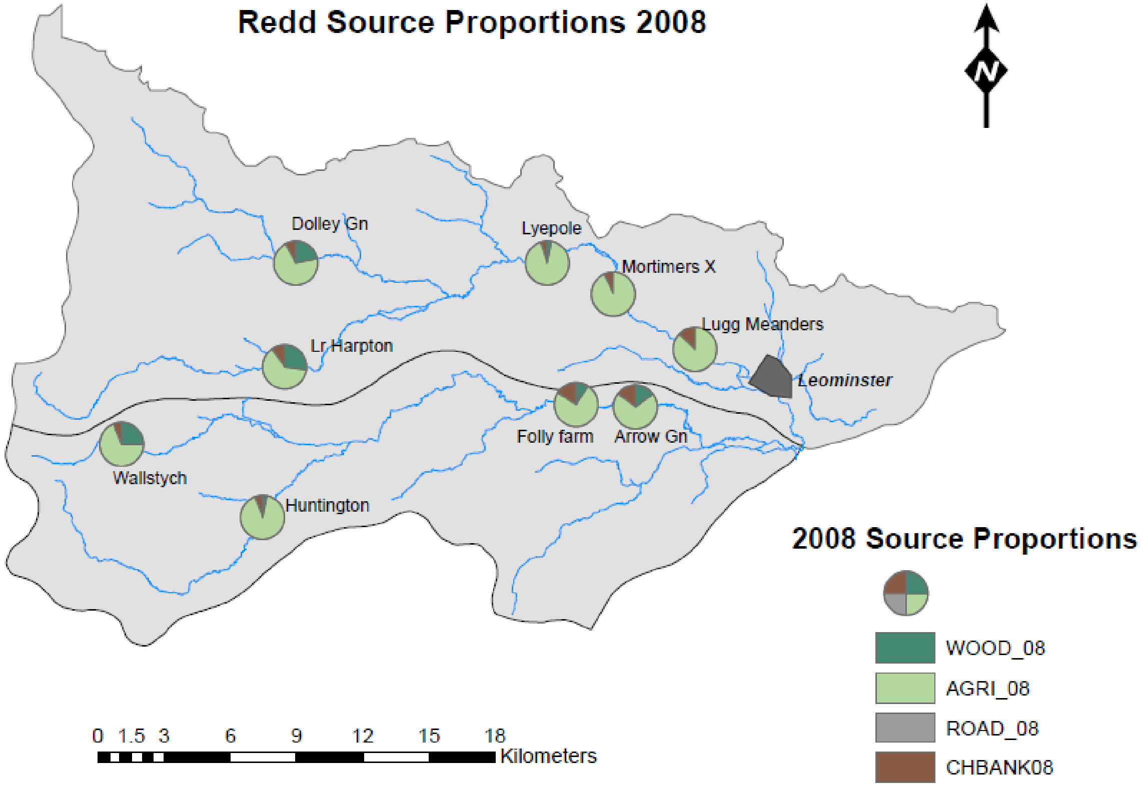


Figure 5.11 Source proportions at individual sites for the field season 2008

%	Hunt'on	Wallstych	Lower Harpton	Dolley Green	Folly fm	Arrow Green	Lyepole	Mortimers Cross	Lugg Meanders
Wood	***3*** ± 0.73	***25*** ± 1.98	***27*** ± 1.98	***23*** ± 2.02	***8*** ± 1.16	***15*** ± 1.47	***3*** ± 0.68	***1*** ± 0.23	***1*** ± 0.29
Agri	***91*** ± 1.82	***68*** ± 1.82	***63*** ± 2.02	***70*** ± 1.82	***75*** ± 1.88	***70*** ± 1.78	***92*** ± 1.74	***92*** ± 1.39	***86*** ± 2.0
Road	***0*** ± 0	***0*** ± 0	***0*** ± 0	***0*** ± 0	***0*** ± 0	***0*** ± 0	***0*** ± 0	***0*** ± 0	***0*** ± 0
CB	***6*** ± 1.59	***6*** ± 0.88	***10*** ± 1.29	***8*** ± 0.88	***16*** ± 1.29	***16*** ± 1.06	***5*** ± 1.53	***7*** ± 1.74	***13*** ± 1.82

Table 5.8 Percentage source proportions at the 2008 sites with associated confidence intervals as derived from the Monte-Carlo runs.

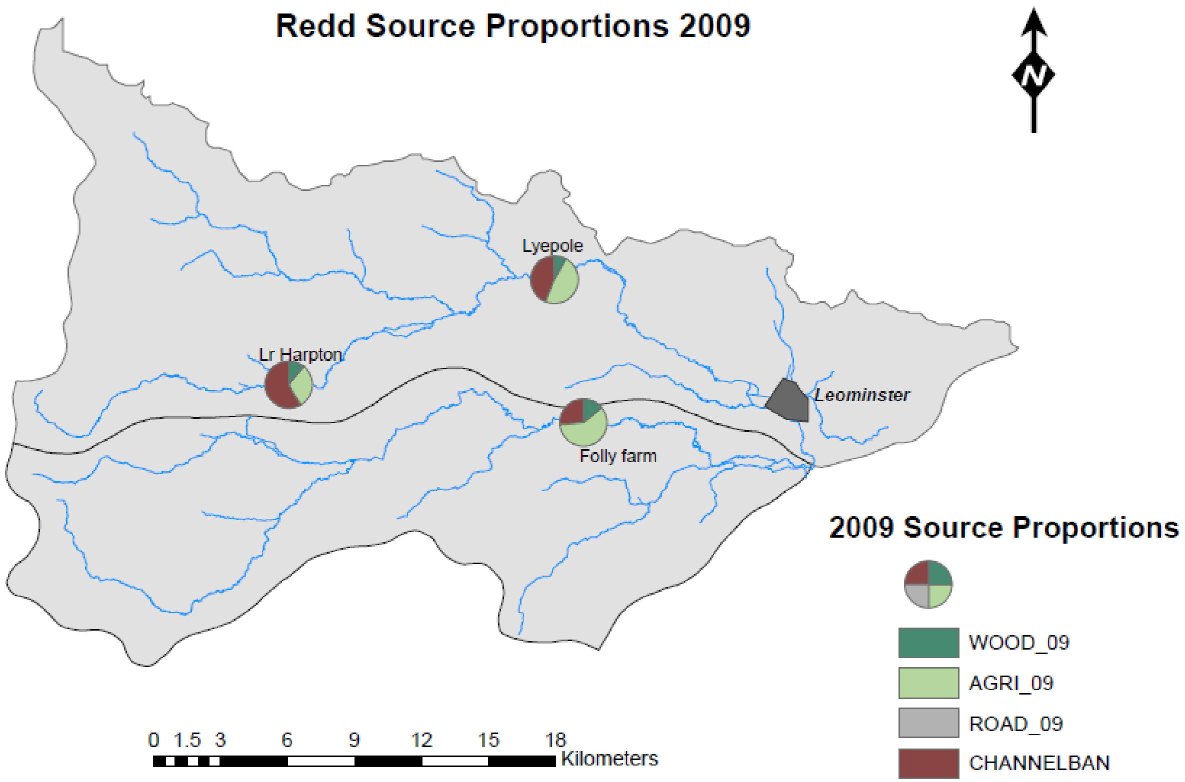


Figure 5.12 Source proportions at individual sites for the field season 2009.

%	Lr Harpton	Lyepole	Folly farm
Wood	**10.5** ± 0.96%	**8** ± 0.98%	**13.8** ± 1.41%
Agri	**30** ± 2.88%	**48** ± 2.66%	**59.5** ± 2.31%
Road	**1.3** ± 0.2%	**0** ± 0%	**1.5** ± 0.19%
Ch Bank	**58.3** ± 2.76%	**43.3** ± 2.47%	**25** ± 1.90%

Table 5.9 Percentage source proportions at the 2009 sites with associated confidence intervals as derived from the Monte-Carlo runs

Figure 5.13 below presents the mean source contributions to the mean property values of the redd sites sampled over the years 2008 and 2009.

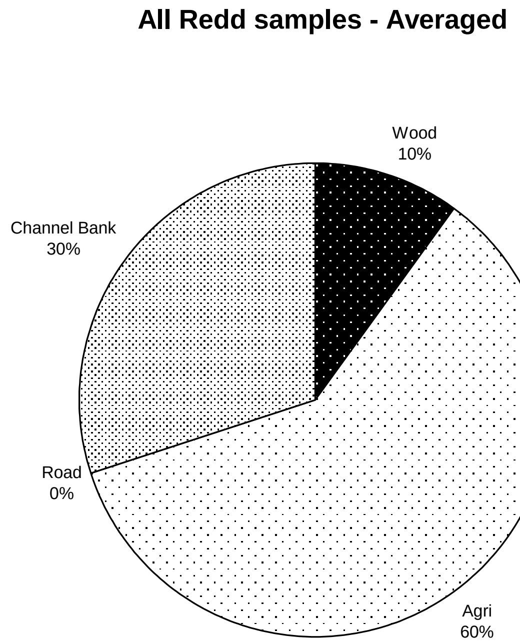


Figure 5.13 Model output for averaged values of all redd samples.

The initial results of the mixing model calculations show a significant contribution from land surface sources, and in particular agricultural land (Pasture and Arable) comprising 60% of the total sediment content. Woodland was shown to contribute 10% leaving the final contribution of 30% to channel bank sources. Roads sources were not shown to contribute to the sites sampled in the Lugg catchment.

These figures broadly agree with some studies previously carried out in nearby catchments – such as that by Collins et al. (1997) on the Plynlimon catchment which shows respective contributions for the Hore sampling site to be Pasture 63.7%, Forest 11.8% and Channel Bank 25.5%.

Other studies carried out within the area (Grusowski et al. 2003, Russell et al. 2001) report smaller contributions for channel bank within their specific study areas (8% and

11% respectively), but the difference may be due to the fact that these studies looked at the contribution of subsoil/field drain sources which were not addressed in this study and may act as a confounding factor when assessing channel bank/subsoil sources.

However, many other studies have highlighted channel banks as significant contributors to suspended sediment in agricultural catchments (Walling and Woodward 1995; Bull 1997, Collins et al. 1997a, Walling et al. 1999; Slattery et al. 2000).
Walling et al's 2003 reconnaissance survey on sediment provenance of fine sediment within salmonid redds reported a wide range of variation in source provenance – dependant on the region in question. They looked at a total of 18 salmonid rivers – among them; the Wye, for which they reported a surface sediment contribution of 58% and a channel bank/subsurface contribution of 42%. This is broadly in agreement with the above data found for its tributary, the Lugg which from figure 5.13 above is shown have overall contributions of 60% agricultural land to 30% channel bank. Overall, the land-use proportions of the Lugg in particular and the Wye in general, are similar.

The report produced from the Psychic model project (Davison 2008) which assessed both sediment yield and phosphorus input in to the Wye catchment and some of its tributary basins report estimated that between 40-55% of the sediment in the Wye catchment comes from banks/ in-channel sources beds.

In terms of the reflected land-use percentages on the contribution of each source type, comparison of land-use apportionment to the model output may elucidate whether any agreement or significantly disproportionate source is evident. Arable land-use for the entire Lugg catchment is 26%, but for the upper part of the catchment (above Leominster) where this study took place, arable represents only 17% to a 63% allocation of grassland/pasture in the upper Lugg. Both categories combined account then for 80% of land use in the catchment, with ~10% allocated to woodland and a further ~10 % to upland/mountain/heath. On initial appraisal, it would seem plausible that the above source contributions may be realistic given that they broadly match those of general land-use patterns. However, a quantification of the relative contributions of arable and pasture separately would be of interest in order to ascertain any disproportionate effects in contributions from either category.

5.7.1 Inter-annual variability

With a view to assessing any inter-annual variation in source apportionment, the mixing model was run for two contrasting groups of redd sediment - one for the combined values from the 2008 field season and one from the 2009 season.

The resulting source contributions are displayed in figure 5.14 below.

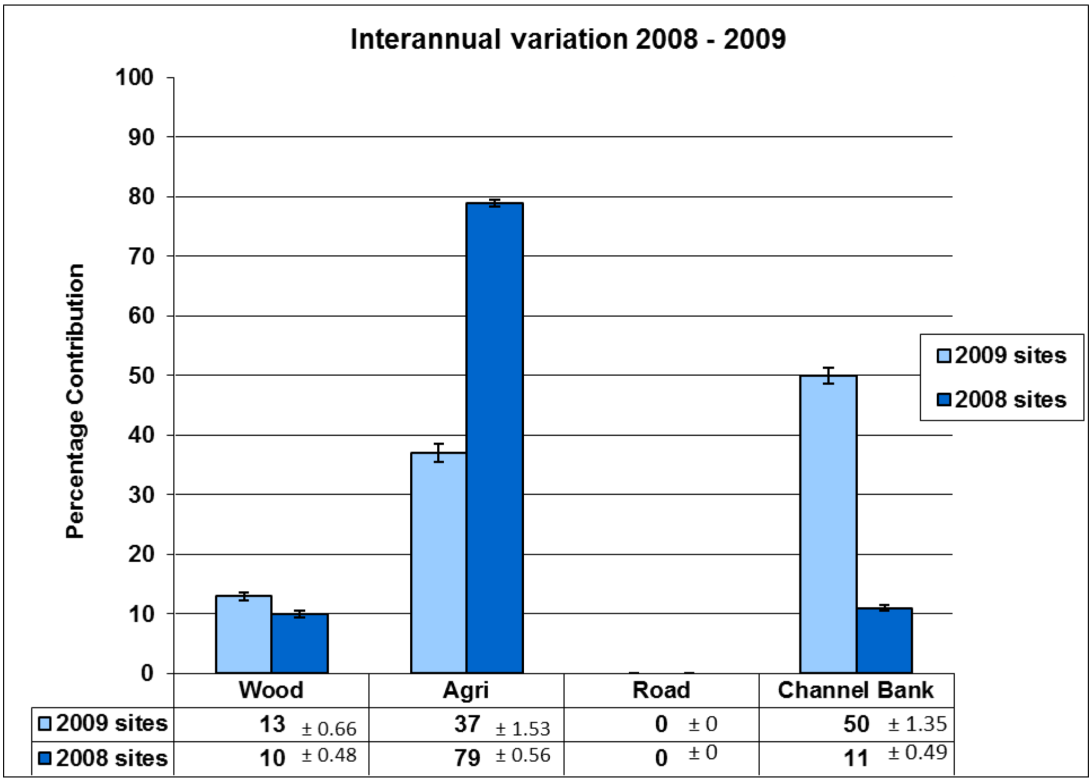


Figure 5.14 Mixing model results for grouped sets of redd samples from the end of each of the field seasons 2008 and 2009.

A significant difference in response was seen between 2008 and 2009 where, in 2008 a 79% contribution from agricultural sources was seen and a channel bank contribution of 11%, and in 2009 a 37% agricultural contribution and a 50% channel bank contribution in redd sediment samples.

This variability in response may be related to discharge and spate events within the catchment, which were also varied markedly between the 2008 and 2009 seasons.

Stream hydrographs for both seasons are featured in figures 5.15 and 5.16 below and reflect a high-discharge, multi-event season during the 2008 campaign, and a contrasting low-flow 2009 season with few major events.

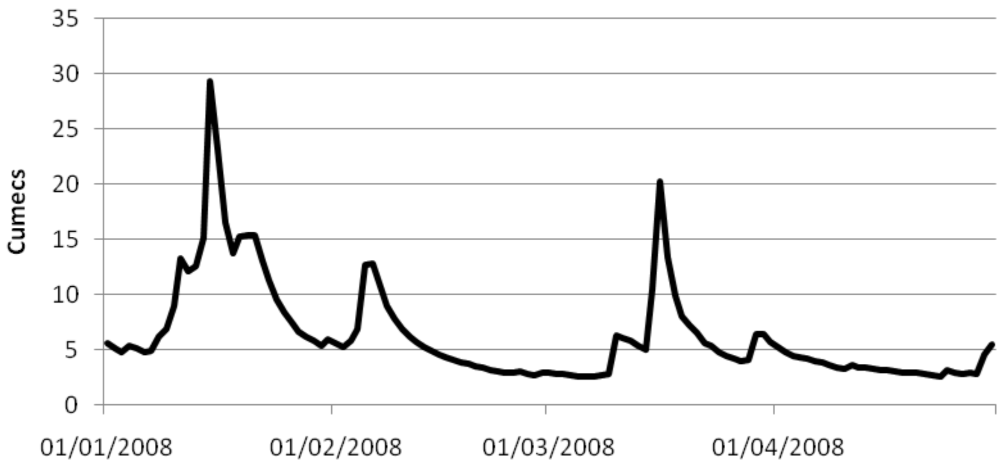


Figure 5.15 Daily mean flow hydrograph for the Lugg at Byton for field season 2008

2008 was a spate year with at least two major transport events and increased sediment yield overall. Flows shown in figure 5.15 are daily mean flows which could potentially have been exceeded within the daily 24 hour window. On average, sediment infiltration levels during 2008 season exceeded those of the 2009 season by 40%.

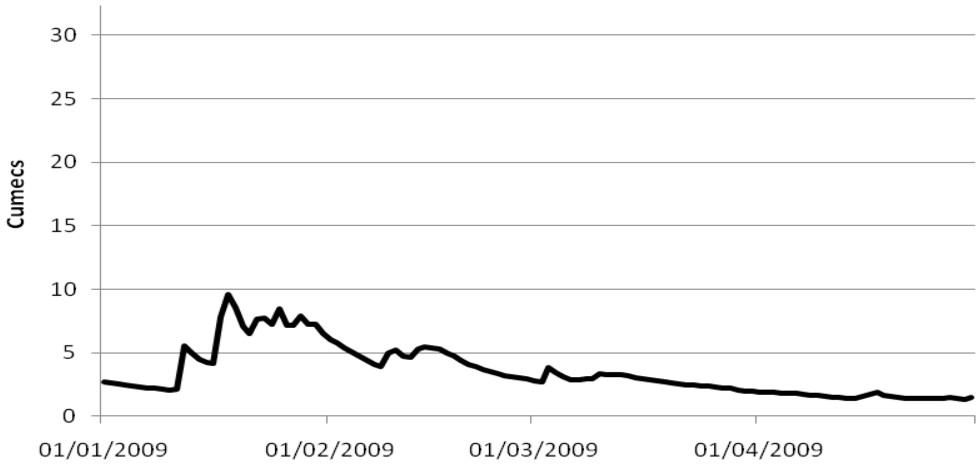


Figure 5.16. Daily mean flow hydrograph for the Lugg at Byton for field season 2009

It is widely accepted that suspended sediment yield has a positive relationship with discharge, since sediment yield is in part controlled by energy conditions (Walling 1977, Rondeau 2000, Baca 2002) where:

$$C = aQ^b \qquad (4)$$

C being the suspended sediment concentration in mg/l, Q the water discharge in m^3/s and a and b are empirically derived regression coefficients.

While it is generally thought that increased discharge will have a positive effect on suspended sediment yield, and lower discharges an increased incidence of sediment storage, factors other than discharge magnitude – such as sediment availability, also exert an influence on the concentration of sediment recorded in a stream, and that the idea of seasonal loops controlling successive cycles of transport, exhaustion and supply of sediment were also at work (Walling 1974).

However, the controls on variability in sediment source distribution during different seasons, weather conditions and discharges are less clear.

Field observations have highlighted the increase in connectivity between pasture and arable fields during wet weather events due to increase mobilization of waterlogged soils (Collins et al. 1997, Russell et al. 2001, Oeurng et al. 2010).

Collins and Walling (1997b) looked at seasonal and inter-storm variability in suspended sediment source contributions in two UK catchments and found significant variation from one storm event to the next – with changes in contribution from cultivated land, woodland and channel bank apparent. It was also thought that seasonal variations in source contributions underlay this data.

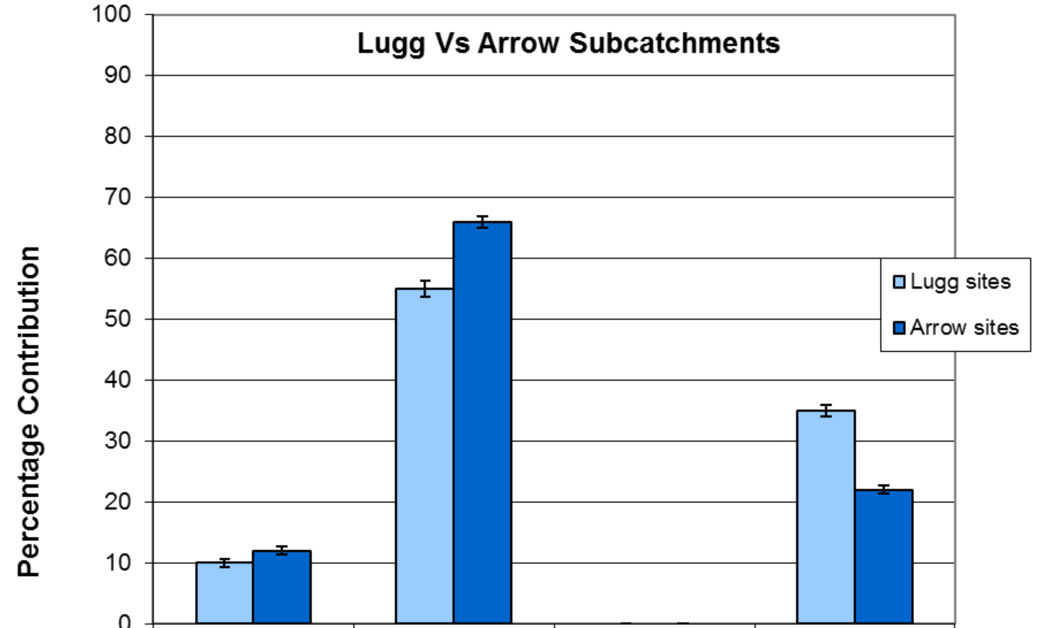
Although this study focuses on the assessment of redd sediment gravels it is also apparent that inter-annual variations are present and may be due to the dominant flow regimes in force at the time or to antecedent conditions on land that influence the availability of sediment for mobilization during a given spawning season.

Russell et al. (2001) observed that many areas of pasture which were situated within the riparian area were frequently waterlogged and liable to increased runoff and thus sediment transport. This may be a factor at play here where increased runoff from pasture during wet weather events, cause the distribution of source apportionment to change. As mentioned in section 5.1 areas devoted to arable land can also cause increased mobility of sediment (Chambers et al. 1992, Evans 1996, Stoate et al. 2001).

With this in mind, it will be of interest in the context of future work on this catchment to separate the two sources and calculate their individual proportions within the redd gravel and thus ascertain whether either pasture or arable is the dominant contributor within the Lugg catchment.

5.7.2 Spatial variability with the catchment

Part 1: Lugg sub-catchment vs. Arrow subcatchments



	Wood	Agri	Road	Channel Bank
Lugg sites	10 ± 0.65	55 ± 1.25	0 ± 0	35 ± 0.88
Arrow sites	12 ± 0.67	66 ± 0.96	0 ± 0	22 ± 0.64

Figure 5.17 Lugg and Arrow sub-catchment source contributions

When the redd sites were grouped into their respective sub-catchments, the Arrow sub-catchment was found to have a higher contribution of agricultural land sources than the Lugg; (66% as opposed to 55%), and a lower contribution of channel-derived sediment (22% to 35%).

This may be in part due to higher area given over to grassland and pasture within the Arrow catchment, or may be due to higher use of riparian areas for pasture/ arable which may increase the connectivity of these sources with the river, however this is difficult to quantify. Also, the generally higher channel bank structure present on the main Lugg channel may indicate that bank erosion is more prevalent here and affect the source contribution balance in this way.

Part 2: Upstream versus downstream sites

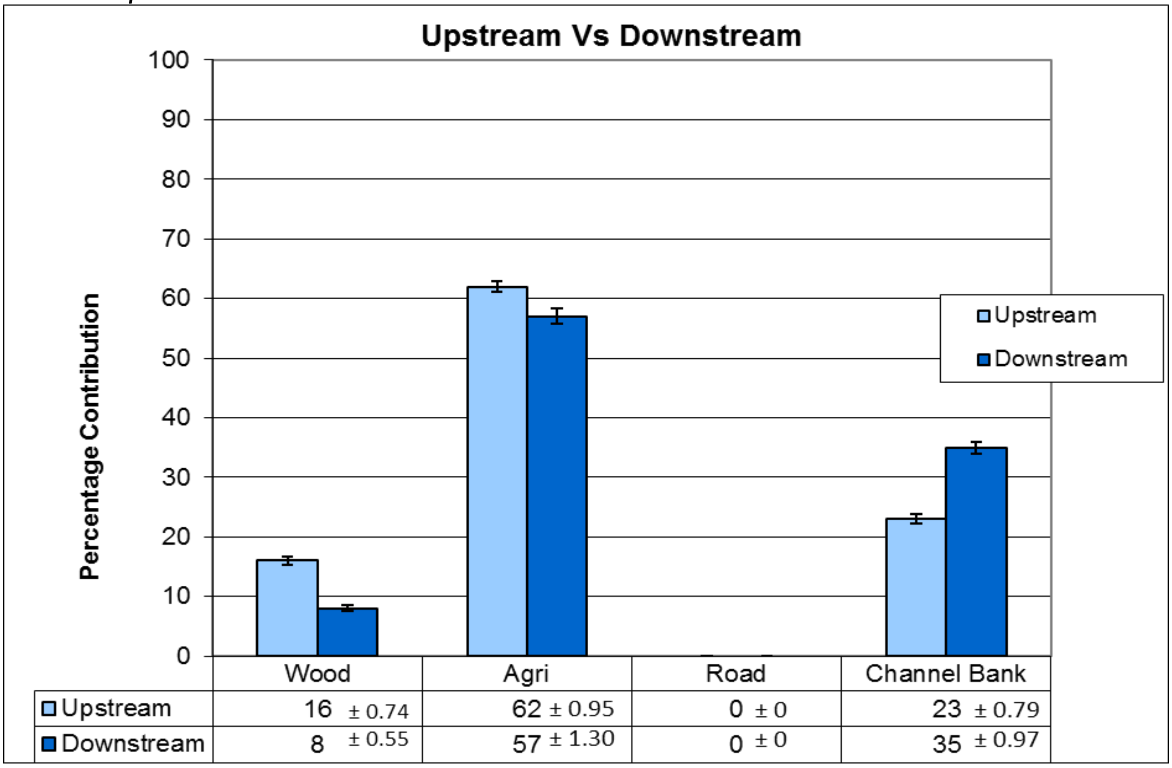


Figure 5.18. Comparison of source contribution between upstream sites and downstream sites within the catchment.

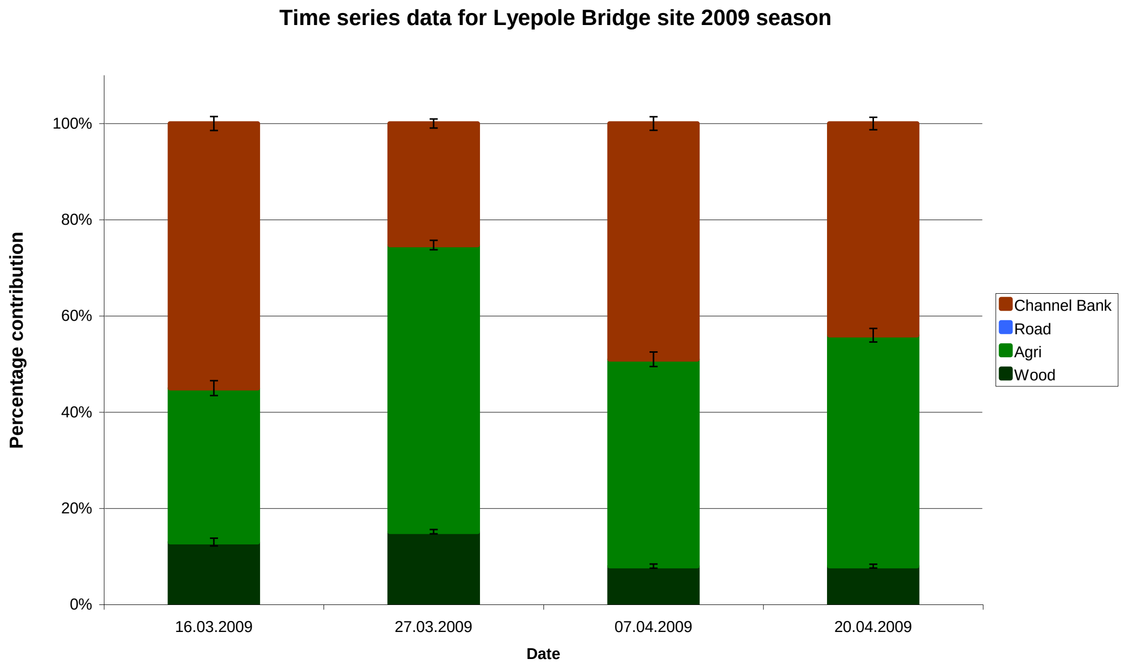
Upstream versus downstream trends showed little variation in terms of agricultural contribution overall (62% Upstream to 57% downstream), but both woodland and channel bank responses did show some intra-catchment contrast. Channel bank sources comprised 23% and 35% of upstream and downstream sites respectively, and woodland showed the opposite trend with a higher (16%) contribution from upstream sites to an 8% contribution at the downstream sites. The trend in higher input from woodland sources is in general agreement with the overall distribution of land-use within the catchment as the higher concentration of wooded areas are in the upstream and upland parts of the catchment- for both the Lugg and Arrow river channels (see figure 5.3).

5.7.3 Intra-seasonal variation

Source apportionment over the field season

Investigation of the short-term variations which may be present a particular site over the egg and larval incubation time, periodic samples of redd sediment, retrieved over the course of one field season were run through the mixing model. The samples were retrieved on the following dates; 16/03/09, 27/03/09, 07/04/09 and 20/04/09 which approximated to 10-day intervals over the incubation period.

Samples from three separate sites – one upstream (Lower Harpton) and one downstream (Lyepole Bridge) on the Lugg, and one site on the Arrow (Folly Farm) were run through the model to gauge temporal response in source contributions as well as inter-site variation.



Confidence Intervals	*Wood %*	*Agri %*	*Road %*	*Bank %*
16/03/2009	*±0.79*	*±1.54*	*±0*	*±1.44*
27/03/2009	*±0.46*	*±0.97*	*±0*	*±0.93*
07/04/2009	*±0.43*	*±1.52*	*±0*	*±1.4*
20/04/2009	*±0.4*	*±1.42*	*±0*	*±1.28*

Figure 5.19. Intra-seasonal variation in source contributions from potential sediment sources at the Lyepole bridge site 2009

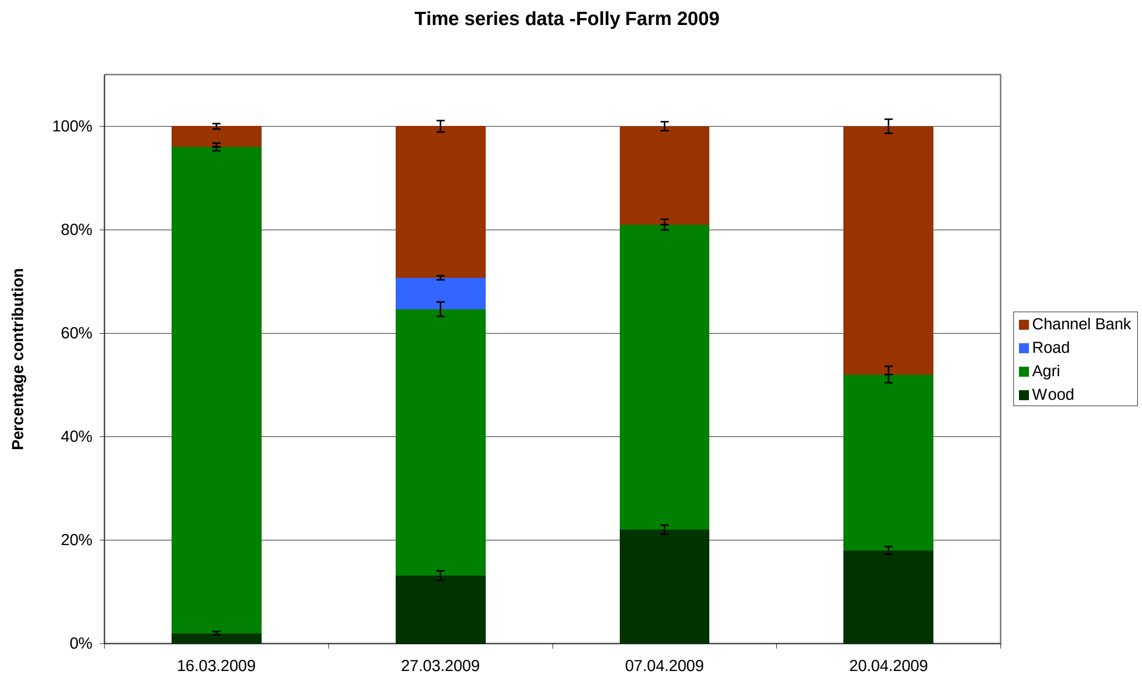
At the Lyepole bridge site, the range of source contributions over the incubation period varied from 32% Agricultural topsoils and 55% Channel Bank on 16/03/09 to 59% Agricultural topsoils and 25% Channel Bank on 27/03/09. The distribution on the later sampling dates of 07/04/09 and 20/04/09 indicated a more even distribution between agricultural and channel bank sources, at ~ 45% each on both dates.

Confidence Intervals	Wood %	Agri %	Road %	Bank %
16/03/2009	*±0.67*	*±1.43*	*±0.21*	*±1.49*
07/04/2009	*±0.44*	*±1.52*	*±0*	*±1.38*
20/04/2009	*±0.37*	*±1.47*	*±0*	*±1.37*

Figure 5.20. Intra-seasonal variation in source contributions from potential sediment sources at the Lower Harpton site on the Lugg main channel 2009

At the upstream Lower Harpton site, the variation observed ranged from 24% Agriculture and 59% Channel bank on 16/03/09, to 41% Agriculture and 51% Channel Bank sources. The final sample on 20/04/09 indicates high channel bank input of 65%. It is at this site the first incidence of Road sources are detected, at 4% on 16/03/09 only.

The Folly Farm site located on the Arrow gave the most varied response; with 94% Agricultural sources observed for 16/03/09 ranging back to 34% Agriculture and 49% Channel Bank sources in the final sample of 20/04/09. It was at this site that the highest levels of input for woodland sources were found – at 22% on 07/04/09. This coincides with some clear felling of a copse of trees located within the riparian zone near the site, so could be indicative of contributions from those works.



Confidence Intervals	*Wood %*	*Agri %*	*Road %*	*Bank %*
16/03/2009	*±0.32*	*±0.74*	*±0*	*±0.52*
27/03/2009	*±0.91*	*±1.36*	*±0.37*	*±1.1*
07/04/2009	*±0.88*	*±1.03*	*±0*	*±0.87*
20/04/2009	*±0.77*	*±1.59*	*±0*	*±1.38*

Figure 5.21 Intra-seasonal variation in source contributions from potential sediment sources at the Folly Farm site on the Arrow, 2009

There are presently no examples available for direct comparison of these results to other similar studies, but Nicholls (2001) compared the intra-storm variation of river-bed sediment to land-use sources at the river Torridge, Devon and found a substantial variability in the contribution from four sources – Woodland, Channel bank, Cultivated land and Pasture. In particular, contributions from Cultivated land were found to vary from 0% to 70% over a 3-month period and for Pasture, contributions of between 10%

and 60% were observed for a period of similar length. Channel bank contributions from a similar period varied between 20 and 50%.

It should also be mentioned that observed % variation in source proportions are relative values that may reflect changes in the magnitude of other sources, rather than a change in the absolute concentration of one particular source, and that total fine sediment mass accumulated within a redd sample should also be considered in this context.

5.7.4 Suspended sediment source apportionment

Suspended sediment samples collected by means of time-integrated Isokinetic samplers (Phillips et al 2000) throughout the duration of the field seasons and collected at the end of each season were also run through the model to ascertain the relative suspended sediment source contributions, which are displayed graphically in figure 5.22 below.

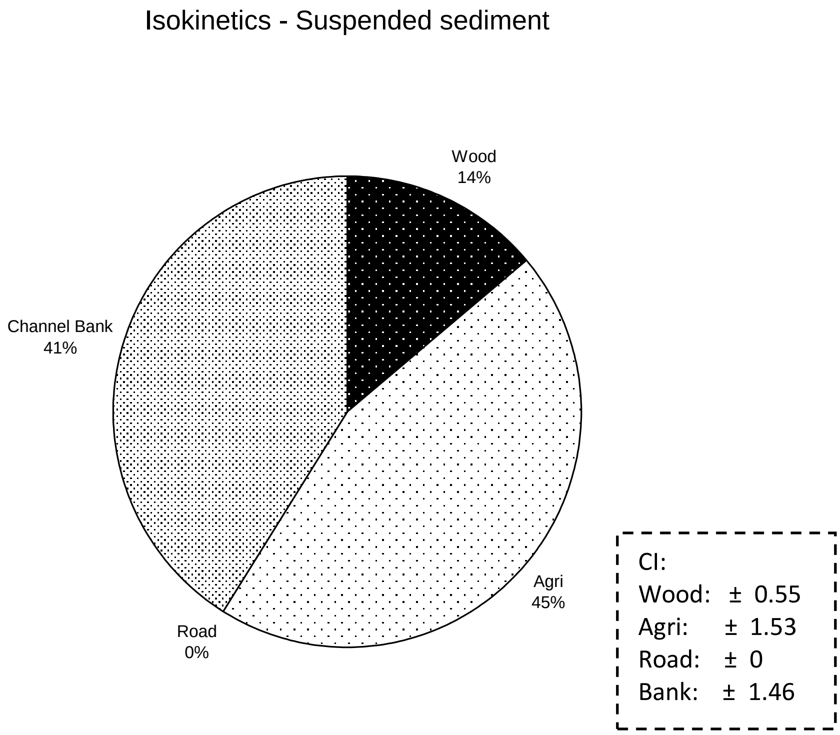


Figure 5.22 Average suspended sediment source contributions for field seasons 2008 and 2009, with confidence intervals for each source category.

Suspended sediment contributions were broad samples retrieved at the end of the field season and represented suspended sediment contributions for the entire salmon spawning period from January to late April. The above results indicate a broad match between averaged source contributions for redd sediment and suspended sediment source contributions, with 45% agricultural sources, and 41% Channel Bank. Woodland sources contribute 14% while Road sources were not detected at all. This observation is also consistent with average redd sediment proportions.

5.8 Conclusions

Detrimental effects of fine sediment infiltration into Salmonid spawning gravels have been well documented and are of increasing concern in certain UK catchments.

Mitigation efforts informed by knowledge of the provenance of that sediment may facilitate catchment management efforts to minimise land-derived input due to anthropogenic activities. Minella et al. 2008 demonstrated the effects of improved land use management on catchment sediment yield using the fingerprinting approach where the difference in relative source contributions from field surfaces and unpaved roads decreased post-treatment to 54% and 24% respectively, from a pre-treatment average of 63% and 36% respectively.

The results of this study show that contribution of Agricultural and channel bank sources were most important (32%-94% and 4%-65% respectively) and that roads and woodland were of least importance (0%-6% and 2%-22% respectively) in the Lugg catchment. This observation is in general agreement with other studies carried out in the region such as that by Collins et al. (1997) on the Plynlimon catchment which shows respective contributions for the Hore sampling site to be Pasture 63.7%, Forest 11.8% and Channel Bank 25.5%. Also Walling et al. (2003) reconnaissance survey on redd sediment provenance reported a surface sediment contribution of 58% and a channel bank/subsurface contribution of 42% on the river Wye.

Estimates of land derived sediment from this study amounted to an average value of 70% (combined agricultural and woodland sources), with a maximum input of up to 94%. A large degree of annual variation in input was observed with increased agricultural input during high flow years which coincided with increased overall sediment yield within the redds.

As mentioned, the relative channel bank proportions will be dependent on the amount of agricultural and other land-derived sediment reaching the river bed during a particular season or event. Additionally, the variability in inputs of bank-derived sediment may be related to the natural variability inherent in bank erosion rates as well as the complex relationship between runoff and sediment stores. The nature of different flood events will also affect channel bank inputs; since during some floods minimal bank erosion may occur resulting in larger proportions of sediment derived from catchment sources, whereas during other events large-scale failure may occur, contributing large amounts of sediment to the river beds (Bull 1997).

A comparison of 2008 fine sediment mass with the proportions of sediment source contribution for that year highlights that at the sites where sediment yields are higher overall, (eg: Lyepole, Mortimers Cross, Huntington) the agricultural component tends to be high also.

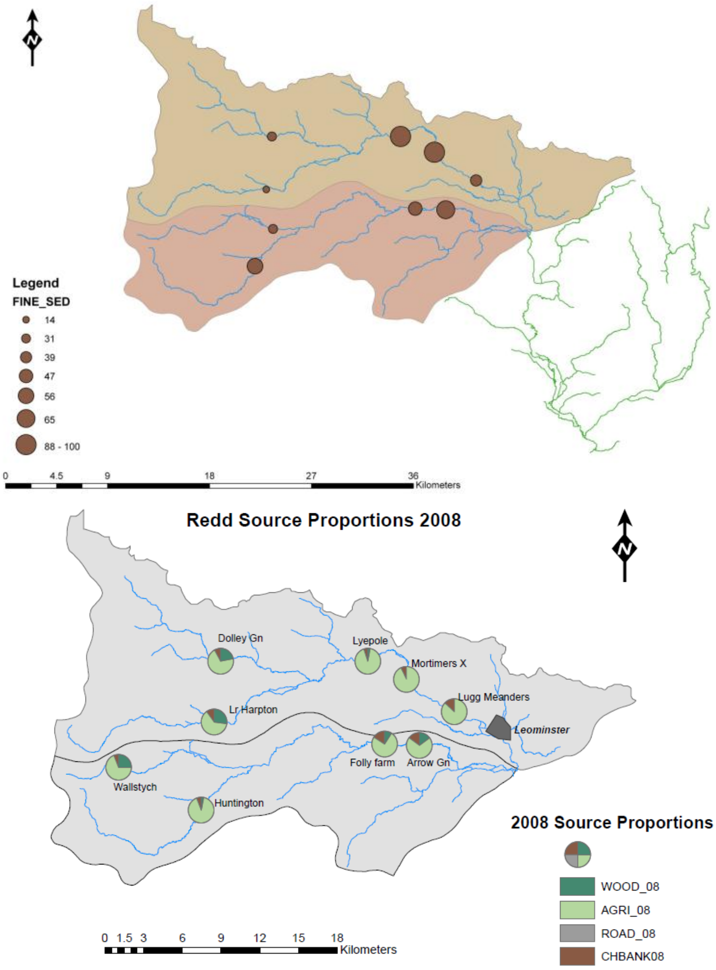


Figure 5.23. Fine sediment (<1mm) mass in redds as compared to redd source proportions for the 2008 field season.

Bearing figure 5.4 in mind (reproduced below) on the psychic model soils erodability within the Lugg catchment, it is evident that the areas with higher erodability coefficients coincide with higher contributions of both sediment and agricultural input as seen from the 2008 model and sediment analysis results in this study.

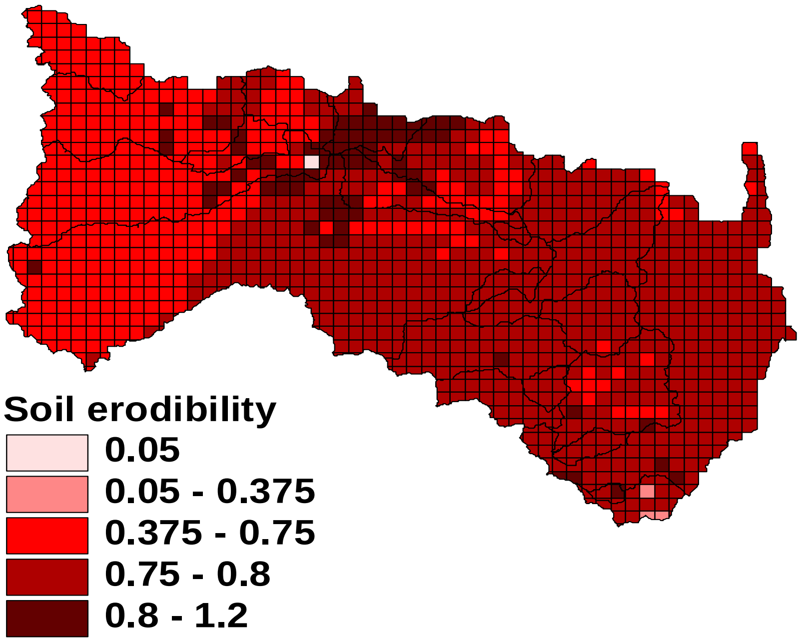


Figure 5.4. (repeated) PSYCHIC model soil erodibility in the Lugg subcatchment

Lugg specific land-use recommendations should thus bear in mind the likely 'hot spots' that may contribute to overall higher yield and contributions from agricultural land. From awareness of the erodability – based on slope and geology, to implementation of measures designed to mitigate against sediment transport to water courses where risks are higher than usual. For example, respect of over winter crops, sediment management during tree felling operations (e.g. figure 5.21), reduction of track wheelings in farms which can act as sediment conduits and ensuring that crop planting orientation is parallel to river courses, can all reduce the amount of agricultural input. River basin management plans can make use of the evidence from sediment sourcing studies such as this to inform decisions on best practice and to minimize detrimental impacts of sediment to water courses; such as width of buffer zones and other mitigation measures based on the susceptibility of that land.

Lastly, it would be of further use for catchment management efforts to separate the Agricultural land use category to elucidate the relative contributions of Arable and Pasture sources and the spatial and temporal variability of these sources within the catchment. In future studies, investigations into land that has had minimal or no recent turnover of use – (i.e.: rotation between grazing and arable use) may ensure more geochemically distinct samples to be collected, enabling stronger individual fingerprints to be identified and thus better differentiation between Arable and Pasture categories.

Chapter 6 Incubation Environment

6.1 Introduction

This chapter provides details on experiments which investigated the physical and chemical redd environment and the recorded response in terms of embryonic survival recorded over two field seasons.

There has been an increasing trend in the literature towards a recognition that interdisciplinary approaches to salmonid habitat studies and remediation are the way forward and that studies stemming from one sole perspective – be that purely physical or biochemical/biological are liable to overlook the complexity of interactions between the disciplines and the resultant effects on larval survival due to multiple interactive causes (Chapman 1988, Reiser 1998, Wu 2000, Crisp 2000, Greig et al 2005).

This chapter highlights and supports the hypothesis of multiple drivers in the redd environment. While sedimentary infiltration may impact upon redd habitat quality, it is the interactions of this sediment with other key environmental factors which best explains the degradation in incubation habitat.

Additionally, alternative causes may be implicated in effects on larval survival such as the effects of the infiltration of groundwater into the redd zone (Soulsby et al 2001, Malcolm et al 2003, 2005) or the effects of synthetic chemicals on larval development (Finn 2007). These effects may be compounded with sedimentation impacts - often exacerbated by certain land-use practices in the riparian zone (Walters 1995, Owens and Walling 2002, Krishnappan et al 2009). All of the above factors in turn have an overriding driver – discharge velocities (Q), under whose influence they respond and interact.

Oxygen availability within the redd zone has been regarded widely as one of the key factors influencing incubation success (Hayes et al 1951, Koski 1966, Turnpenny and Williams 1980, Ingendahl 2001, Malcolm et al 2003, Grieg et al 2005).

Investigations have been varied in the approach they take on oxygen limitation within the egg zone, with some studies focusing on the deposition of fine sediment and associated blockage of interstitial pore spaces limiting oxygen within redd zone (Chapman 1988, Bjornn and Reiser 1997, Heywood and Walling 2007).

Alternative studies have looked at the oxygen demands of intruded sediment which may be rich in oxygen-depleting compounds, which in turn impact on interstitial oxygen concentrations within the redd (Chevalier and Carson 1984, Rex and Petticrew 2006), while others have looked at groundwater-surface water interactions which can alter the oxygen concentration with the hyporrheic zone if groundwater masses are oxygen-depleted. If the egg zone falls within this area of interaction, hypoxic conditions may impact on developing embryos (Soulsby et al 2001, Malcolm et al 2003, 2005). Localized groundwater infiltrations, depending on residence time and bedrock chemistry, can have effects on redd environment through the impact of hypoxic (long residence) water on small spatial (and temporal) scales (Malcolm et al 2005, 2008). Due to the heterogeneous nature of these interactions, assessment is necessary in conjunction with any study of sedimentary controls on spawning habitat to ensure accurate appraisal of a particular reach in terms of spawning habitat quality.

These avenues of research highlight the importance of oxygen concentrations to investigations of the redd zone and the multiple ways in which limiting conditions may occur.

Additionally, the build-up of metabolic waste products can cause toxic reactions in developing larvae if not cleared efficiently from the egg zone (Meehan 1997). High levels of metabolic waste can also further deplete oxygen levels due to oxidation reactions with the nitrogenous waste. This is a good example of the interaction of multiple factors – a possible scenario being low intragravel flows created by fine sediment infiltration and associated lowered oxygen levels due to respiration and other reactions compounded by toxic waste product effects, with limited replenishment of fresh water to the redd zone.

Related to this, stream water quality also remains an issue and pertinent to catchment management targets. Land-use influences on stream water quality will have effects on incubation zone quality and also needs to be addressed. Thus during the 2009 season, water quality tests were carried out on the redds to attempt to address the excess metabolite and water quality issues.

Thus, given the breadth of potential controls on the incubation zone, any comprehensive study into spawning habitat quality needs to address these and query the particular suite of influencing factors at play within the catchments in question.

Sublethal effects on emergent fry should also be considered in the context of recruitment success and future population health on at risk catchments. Studies on sublethal effect have recently been advocated and use of fry noted as high quality, more detailed indices of spawning habitat quality (Kondolf 2008, Youngson 2004, Buss et al 2009).

In chapter 7, I address how intragravel environmental degradation may sub-lethally affect incubating larvae, and present results of a comparative study on sibling larvae from differing redd sites. This study illustrates how fry condition can be reflective of compromised incubation conditions and act as an indicator of spawning gravel quality.

6.2 Methods

6.2.1 Redd construction and assessment of survival

Methods and equipment used during the field campaigns are described in detail in chapter 3, but for clarity, will briefly be described in the following section.

Artificial redds were constructed during the 2008 field campaign at each of the 9 field sites. Two redds were constructed at each and percentage survival was recorded at the estimated time of emergence relative to water temperature. Estimated emergence time was calculated on the basis of development/ temperature growth curves as employed by Crisp (1992) and Gorodilov (1996). Eyed eggs were supplied from the Wye and Usk hatchery at Painescastle and a control batch retained at the hatchery so any natural variations in the survival rates could be accounted for in the field site survival results.

6.2.2 2008 Setup

Figure 6.1 outlines the setup at each of the nine field sites during 2008 field campaign. At each site two redds were installed containing the sediment baskets and egg baskets contained within. A standpipe enabling periodic measurement of oxygen, intragravel flow and conductivity was located just below the baskets, on the downstream side.

At the Lugg Meanders 2008 supersite – multiple baskets were installed in a single redd so that developmental and survival rate could be established periodically throughout the incubation period.

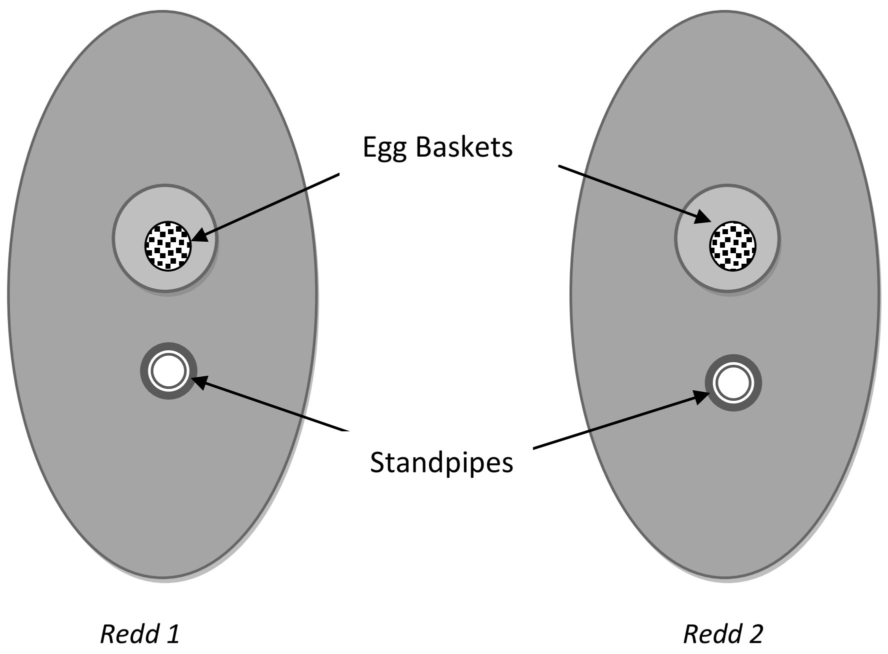


Figure 6.1. Diagram of the redd setup at the 2008 sites

Dissolved oxygen

Periodic measurements for dissolved oxygen and temperature were carried out using the YSI (model 250) probe via the in-situ standpipe.

Additionally, an Anderaa probe (model 4175) was installed at the Lugg Meanders supersite to record dissolved oxygen concentrations within the redd zone. This provided high- resolution data to complement the periodic site measurements. The Anderaa probes are not oxygen consuming and are able to record continuously without depleting oxygen in the environment. These were connected to Delta-T dataloggers programmed to sample DO (µmol) and temperature at 1 minute intervals and log average values over 10 minutes. Prior to installation, DO optodes were cross calibrated in the laboratory at a range of O_2 concentrations and temperatures showing agreement to within 1% O_2 saturation and 0.1°C.
The probes were located in the egg zone (0.2m depth into Redd) and at 0.3m from the leading edge of the Redd hump.

Intragravel flow

As described in chapter 3, section 3.4.4, intragravel flow velocity was measured via the conductiometric standpipe technique (Carling and Boole 1986) during periodic visits to the field sites. The intragravel flow was calculated based on the rate of dilution of a saline/alcohol solution. Post-sampling comparison of the exponent of the decay curve with calibrated dilution curves (Grieg 2004) allowed estimation of intragravel flow velocities.

Conductivity measurements

Conductivity measurements were used to compare the concentration of dissolved solids within the water column and the incubation zone. Since groundwater frequently contains a higher concentration of dissolved solids which is indicative of weathering processes, any difference between conductivity of the redd zone and that of the stream water may be an indication of groundwater-surface water interaction.

6.2.3 2009 Setup

Three main sites were installed during the 2009 season, two of which contained higher resolution monitoring probes and were classed as 'supersites'. An additional upstream site at Dolley Green was installed with two redds containing one single basket and recorded survival uniquely. This was done chiefly as a positive control for the season, since the Dolley Green site had been the most successful site during the 2008 season.

For the three main sites, (Lye, Lower Harpton and Folly Farm), multiple baskets were installed in the main redd and one basket retrieved at intervals of 10 days throughout the incubation period. This was in order to assess larval development and condition at the sub-lethal level and to enable a series of tests for larval fitness. This experiment is explained in further detail in Chapter 7. The second redd (redd 2) held just one basket containing 100 eggs which was assessed for survival rate on retrieval at predicted emergence time.

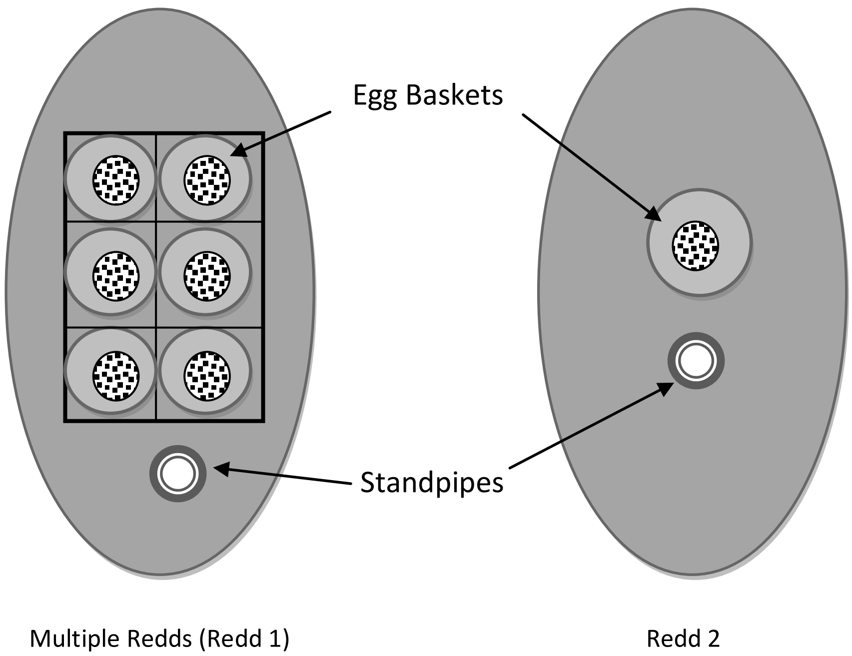


Figure 6.2. Redd format and setup at the 2009 sites, showing a Redd 1 multiple-basket redd and Redd 2 single basket format.

Salmon eggs were sourced from the Environment Agency hatchery at Cynrig, Wales and were of single parentage with the aim of minimizing any inherent variation in response – in terms of both survival and measures of sublethal effect (Verspoor et al 2007).

Dissolved oxygen and conductivity measurements

Periodic measurements (approximately weekly) for dissolved oxygen, temperature, intragravel flow and conductivity were carried out via the in-situ standpipe in the same way as for the 2008 sites.

At the two supersites, an Anderaa probe was installed within the multiple redds adjacent to the baskets and measured dissolved oxygen and temperature at 10-minute intervals. Environment Agency sondes were deployed at each of the field sites, which measured dissolved oxygen, pH, turbidity and temperature at 15 minute intervals throughout the incubation period.

Groundwater upwelling

In order to investigate the possibility of groundwater upwelling at redd sites, both supersites were installed with a piezometer setup which involved two upright tubes each holding a pressure-sensitive device. A Schlumberger™ mini diver was placed at 50cm depth beneath the river bed surface and was coupled with a small pressure transducer placed at the gravel bed–stream water interface. Both devices logged data related to pressure variations at and within the stream bed relative to water depth. Thus, any detected difference between the two probes that deviated from the predicted pressure-depth gradient suggested changes in hydraulic head and indicated either upwelling or downwelling within the stream bed. After correction for barometric pressure changes in the mini-diver (an absolute transducer), the data was compatible for comparison with data from the river-bed pressure transducer (gauged type).

Water quality measurements

Additionally, nalgene™ tubes were installed into the multiple redds at all three main sites. The tubes were perforated at one end to ease extraction of water samples during the weekly field site visits over the incubation period. From the samples, field tests of dissolved oxygen, conductivity, nitrate/nitrites and ammonia were taken to check for any variation in water quality.

6.2.4 2010 study set-up

During the field season of 2010, an experiment investigating dissolved oxygen concentration and temperature at a range of depths was carried out at Lyepole bridge. This was done to complement information on piezometric readings for groundwater – surface water interactions at the same site. The probes were positioned in a metal mesh tube as illustrated in figure 6.3.

Egg baskets containing 50 eggs each were enclosed in fine mesh baskets to minimize sediment intrusion. While it was recognized that the depths at which two of the baskets were placed did not reflect egg depths in naturally occurring redd systems, they were intended to act as a gauge against the high-resolution dissolved oxygen levels.

The metal tube was placed in an oversized constructed redd, and subsequently secured by infilling of the excavated gravels.

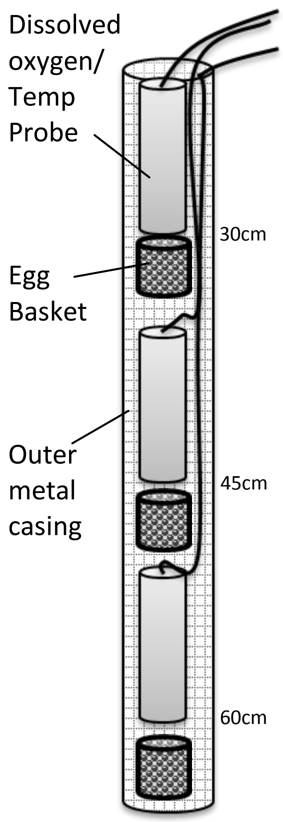


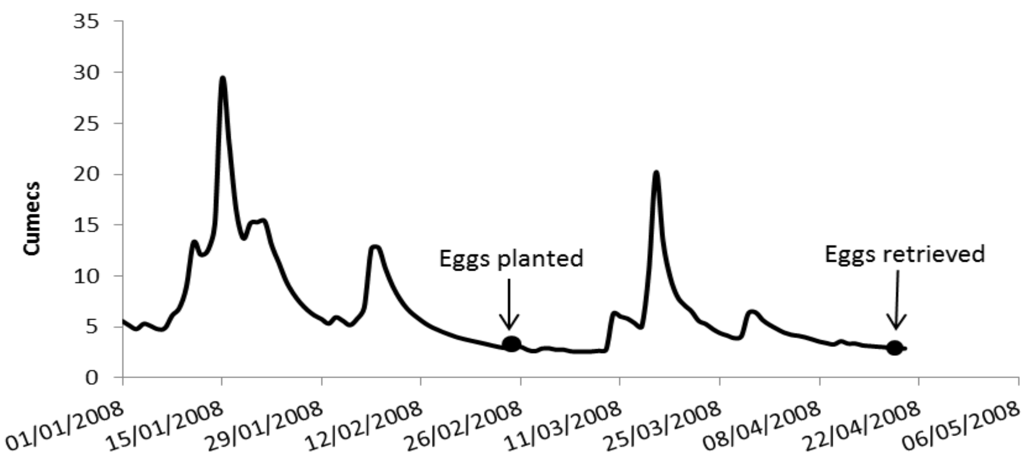
Figure 6.3. 2010 Probe tube set-up with high resolution probes and adjacent egg baskets.

A Piezometer set-up as described in chapter 3 was placed in proximity to the redd zone by the river bank, to monitor hydraulic gradient over the field season.

6.3 Results of incubation experiments

6.3.1 Overview of hydrological regime

To enable contextualization of each field season and the relative hydrological regimes operating during those times, hydrographs of each of the incubation field periods – 2008, 2009 are displayed in figure 6.4 below. From this, it is evident that 2008 was a comparatively wet year with spate event occurring mid-spawning season (Mean discharge for period 6.5 cumecs). 2009 was much drier with average discharges of 2.49 cumecs well below the annual mean discharge of 3.96 cumecs.



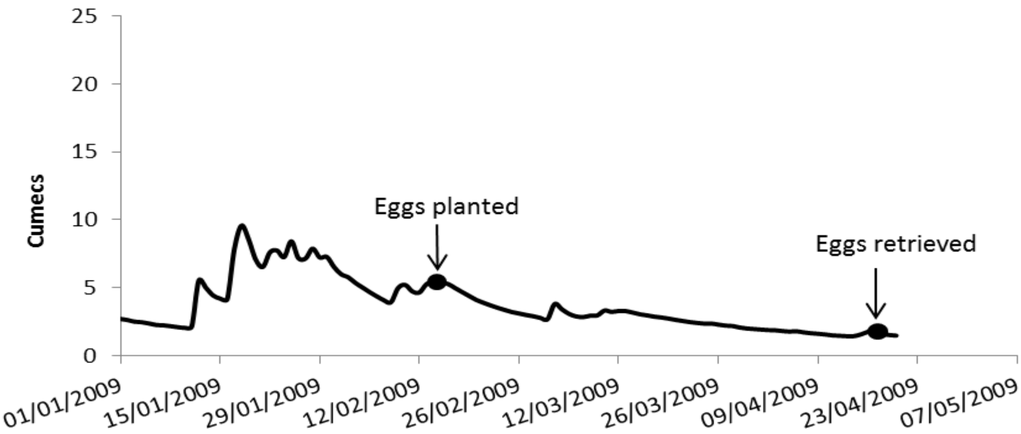


Figure 6.4 Discharges during and previous to the incubation period of the eggs during field seasons 2008 and 2009.

6.3.2 Survival

Table 6.1 below shows the percentage survival recorded for each of the redd sites for both field seasons. These rates were compared against control batches at Painescastle hatchery where survival was found to be 98% to hatch and 96% to emergence. The survival rates recorded at the field sites can thus be held as representative of conditions within the gravel alone and not reflective of naturally high rates of mortality within that cohort of eggs.

2008 Sites	Redd 1	Redd2 (early retrieval)
Huntington	28	35
Wallstych	34	40
Lower Harpton	42	48
Dolley Green	57	70
Folly Farm	33	29
Arrow Green	31	28
Lyepole Bridge	35	38
Mortimers Cross	37	43
Lugg Meanders	12	-

Table 6.1 Percentage survival recorded at the 2008 field sites

Baskets were retrieved from the Redd 1 positions at estimated emergence time on 15th April 2008. Redd 2 baskets had been retrieved at approximated hatch time to ensure some data on survival was obtained during this first field season, where uncertainty regarding scour and spate event survival required preparation for these potential risks.

Minimum survival was recorded at the lowest site, Lugg Meanders with 12% survival recorded at emergence. Maximum survival was recorded at the upstream Lugg site at Dolley Green with 57% survival at emergence and 70% recorded at approximated hatch time at the same site. Variation in survival rates is reflected in a standard deviation of 13.77 across all sites.

Survival for the 2009 field season was recorded for both redds at estimated emergence time; the 21st April 2009. Survival was high at all sites, with maximum survival again recorded for the Dolley Green site with 92% and 88% survival respectively. The Lyepole bridge site recorded the lowest survival rates - at 82% and 76% respectively. Variation between the 2009 sites is reflected in a standard deviation value of 4.69.

2009 Sites	Redd 1	Redd2
Dolley Green	92	88
Lower Harpton	81	93
Folly Farm	78	90
Lyepole Bridge	82	76

Table 6.2 Percentage survival recorded at the 2009 field sites

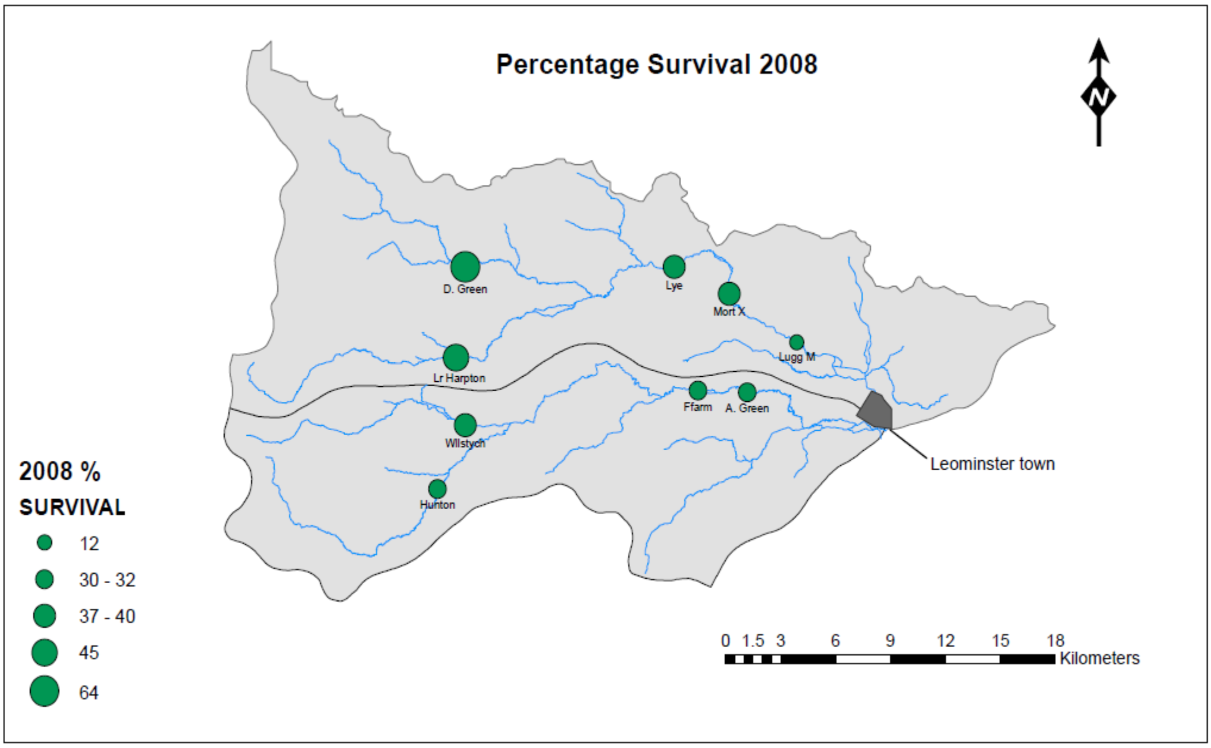


Figure 6.5. Percentage Survival for the 2008 field season at nine sites

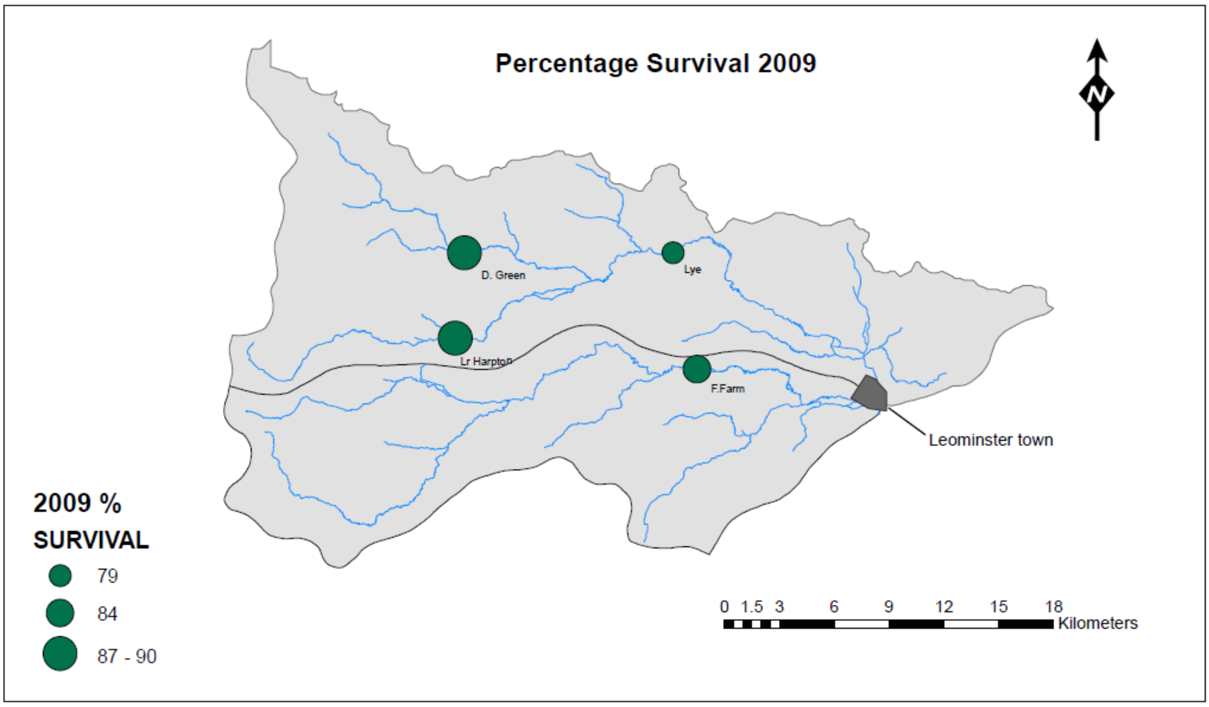


Figure 6.6. Percentage survival for 2009 field season at four sites

No survival data was available at the 2010 Lyepole Bridge site, as all eggs were dead (as eggs) on retrieval at approximated emergence time. While it is acknowledged that two thirds of the eggs were planted at depths and conditions not normally associated with salmon spawning habitat and as such were not included with the incubation studies analyses of 2008 and 2009, it is likely that hypoxic conditions detected at the reach during the field season was the key driver operating during this time. This is further discussed in section 6.4.4.

6.3.3 Dissolved oxygen

High flows during the 2008 field season prevented access to the lower Lugg and Arrow sites - Lyepole bridge, Mortimer's Cross, Lugg Meanders and Folly farm (Arrow) for the visit scheduled on 18th March. Thus standpipe measurements (DO, intragravel flow and conductivity) were not feasible at those field sites for that date.

There is a general decline in oxygen concentrations with time, and minimum concentrations recorded at emergence for most sites. The three lowest Lugg sites show a differing trend, with minimum oxygen concentrations recorded just after the spate event – when the sites were newly accessible following the spate event, with an increase in levels recorded for the final measurement at emergence time.

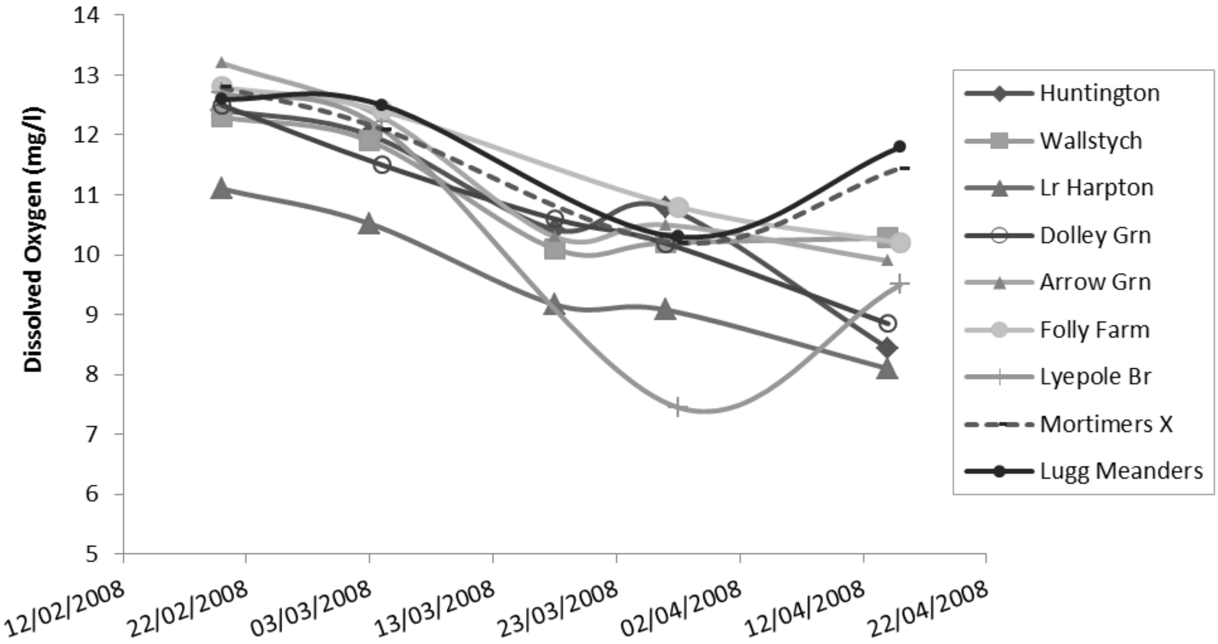


Figure 6.7. Dissolved oxygen concentrations as sampled during periodic visits for field sites during 2008 season

For the 2009 sites, dissolved oxygen concentrations were more stable, with no clear marked decline over the course of the incubation period, as had been observed during the 2008 season. This may reflect the lower flow conditions experienced during the 2009 season and the attendant lack of related external influences due to higher flow conditions, which had been experienced during the 2008 spate year.

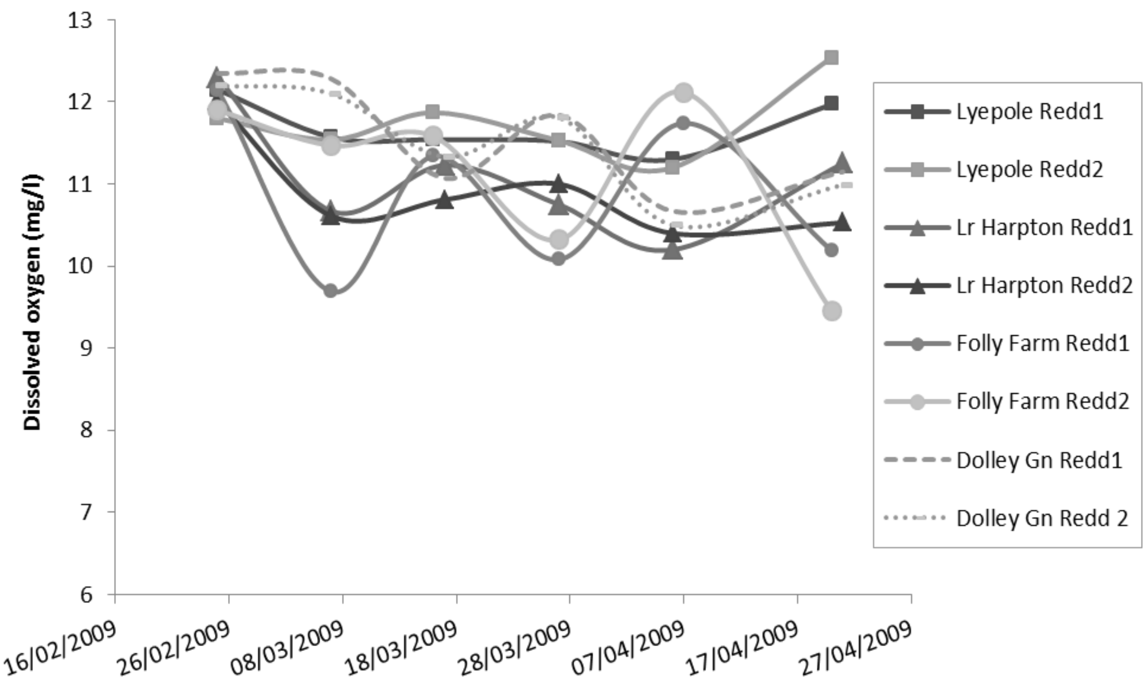


Figure 6.8. Dissolved oxygen concentrations as sampled during periodic visits for field sites during 2009 season

6.3.4 Intragravel Flow Velocity

As mentioned above, during 2008 there was an interruption in the collection of intragravel data due to the mid-March spate event. Thus data from the lower inaccessible sites is omitted from the below graph representing the progression of intragravel flow velocities with time.

Generally, intragravel flow velocities tended to decline with time over the field season, with initial velocities ranging between 2884 cm/hr^{-1} and 1359 cm/hr^{-1} and end-of-season velocities ranging between 818 cm/hr^{-1} and 326 cm/hr^{-1} .

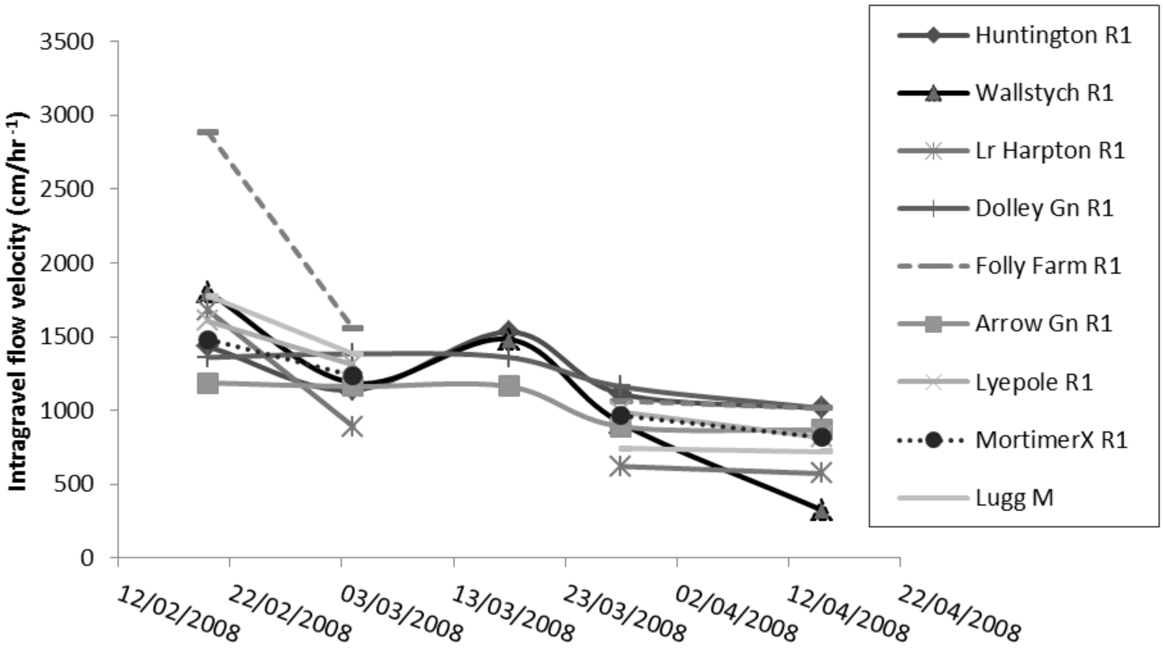


Figure 6.9. Intragravel flow velocity as sampled during periodic visits for field sites during the 2008 season. Access was not possible at some of the downstream sites due to the spate event which occurred on 16th March 2008.

The 2009 intragravel velocities recorded did show a slight decline over the course of the field season, with initial velocities ranging between 1556 cm/hr^{-1} and 1236 cm/hr^{-1} and end-of season velocities of between 1384 cm/hr^{-1} and 990 cm/hr^{-1}.

The Redd 1 Folly farm site showed a sag in intragravel velocities halfway through the season with a slight increase evident on the final periodic visit. This was not reflected in the second redd at this site, and may point to reach scale variations in intragravel flow, due to differences in hydraulic gradient or GW-SW interactions on a small scale.

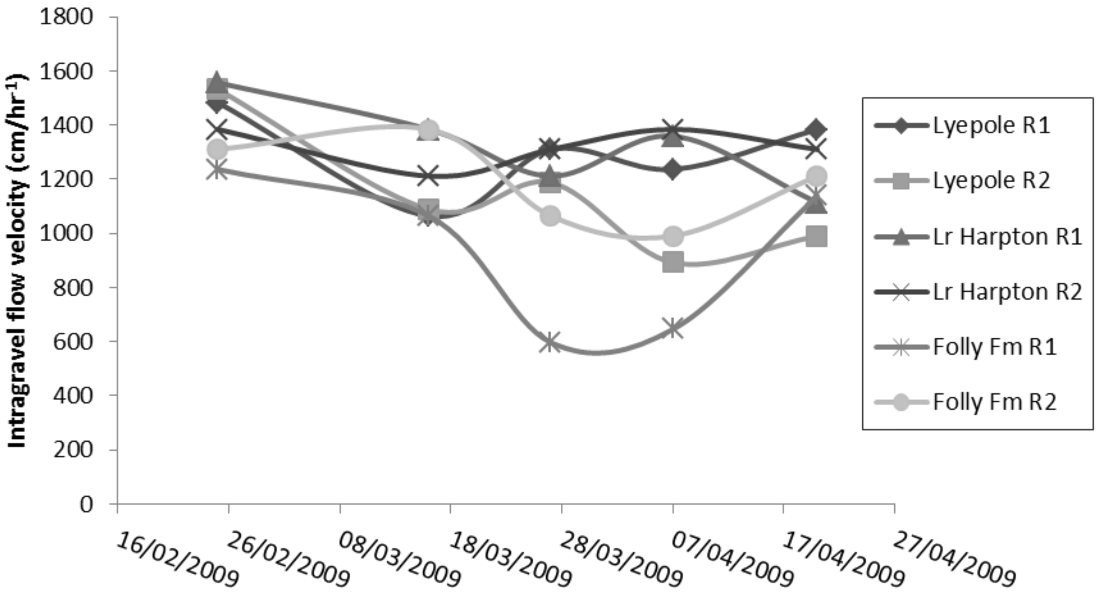


Figure 6.10. Intragravel flow velocity as sampled during periodic visits for field sites during the 2009 season.

6.3.5 Spatial and temporal variation in the catchment

The intra-site spatial variation in survival, intragravel flow and dissolved oxygen is represented by the standard deviations recorded over each field season in table 6.3 below.

In terms of temporal variation over the two field seasons, standard deviations are higher for all three parameters during the 2008 season as compared with 2009, showing a higher variability of response during the higher-flow year. Standard deviations are highest for all three parameters when both field seasons are calculated together.

	2008	*2009*	*Field seasons combined*
End of Season Standard Deviation IGF	230.9	142.11	278.94
Maximum Standard Deviation IGF	468.27	292.05	-
Average Standard Deviation IGF	241.23	196.86	-
End of Season Standard Deviation DO	1.13	0.97	1.14
Maximum Standard Deviation DO	1.13	0.97	-
Average Standard Deviation DO	0.61	0.66	-
Standard Deviation in Survival	12.74	6.65	25.79

Table 6.3. Summary of spatial and inter-annual variation at the Lugg study sites for the 2008 and 2009 field seasons. The standard deviations are based on the variation between study sites for each periodic sampling date.

As a means of investigating the relationship between dissolved oxygen concentration and intragravel flow, paired data collected from each site visit over the two field seasons were plotted against each other. For the 2008 field season, a positive relationship is evident with a trend towards higher oxygen levels in gravels experiencing higher flows. Regression models explained 31% and 35% of the variation in the sites using linear and polynomial models respectively.

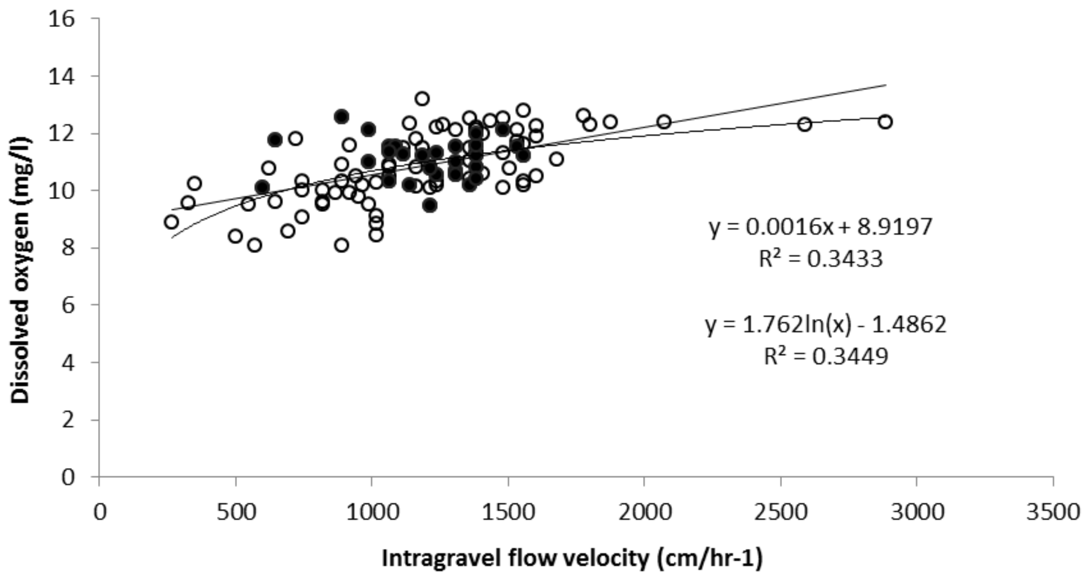


Figure 6.11. Intragravel flow velocities plotted against oxygen concentration for all field sites. White dots represent 2008 sites and black dots, the 2009 sites.

However, for the data plotted for the 2009 data series, there seems to be no real link between dissolved oxygen levels and intragravel flows experienced. This may signify the high level of site-specificity present within the catchment particularly during low-flow years, or the coarse resolution of the instruments and sampling methodology which hindered detection of fine scale variations.

6.3.6 Oxygen flux thresholds

It had been widely documented that there is a critical limit of oxygen concentration required by incubating embryos, below which mortality is likely, due to failure to support respiratory needs. There is however much discrepancy in the literature regarding exactly where this limit is, and the 'critical' range varies from 5mg/l (Wickett 1954, Davis 1975) to 8.0mg/l (Alderdice et al 1958) and as high as 11mg/l (Silver 1963) for stress-inducing sublethal oxygen concentrations.

It has also been proposed however, that these critical values are co-dependent on the velocity of the intragravel water flowing through the redd system; thus delivering fresh water with replenished oxygen supplies to the eggs (Silver et al 1963, Carling 1984, Greig 2004). In his work on observed effects of varying oxygen concentrations and intragravel flow velocities to developing embryos, Silver et al (1963) reported that intragravel flows of 700 cm hr^{-1} coupled with oxygen concentrations of 6mgl, provided similar incubation conditions as 6cm hr^{-1} velocity, with 11mgl dissolved oxygen.

The product of the oxygen concentration in the egg pocket and the intragravel flow velocity, termed the oxygen 'flux' is calculated as:

$$O_2(flux) = C_0(v \times a_{egg}) \qquad (1)$$

The calculated flux must be greater than the oxygen consumption of the eggs for successful respiration and incubation to take place (Sliver 1963, Daykin 1965, Wicket 1975).

In his review of factors influencing the availability of oxygen to incubating embryos, Greig determined the oxygen flux required to support respiratory requirements of incubating Atlantic salmon. His calculations were based on the theory of mass transport as derived from work by Daykin (1965) and Wicket (1979) and validated against laboratory observations (Silver et al 1963, Hamor and Garside 1978, Sigurd 2003).

Application of the theory of mass transport provided a model to estimate the dissolved oxygen and intragravel flow requirements of incubating embryos by means of 1) calculating the rate of diffusion across the egg chorion –dependant on the concentrations outside and inside the egg in addition to other coefficients unique to each relevant species (egg radius/chorion thickness/diffusion constant) and 2) calculating the flux or supply of oxygen provided by the product of DO and flow velocity as described above.

In order to provide a means to define habitat quality, maximum rates of consumption - calculated within the first part of the model, were used to compare with oxygen supply to the egg and the below figure illustrates the calculated threshold values as calculated by Grieg for two different incubation temperatures.

Additionally, the Lugg sites end-of-season values for intragravel flow against dissolved oxygen for were plotted onto Greig's graph and for the most part fall above the critical thresholds at both 5° and 10°C. However, when considering the high resolution data for the three sites Lugg Meanders (2008), Lyepole bridge (2009) and Lower Harpton (2009) some differences in results were evident. The three sites had been fitted with high-resolution dissolved oxygen optodes which recorded data at 10 minute intervals and these data points were matched with approximately corresponding times of Intragravel flow sampling. Of the three sites, the Lugg Meanders 2008 site recorded a severe dissolved oxygen lag mid-season during and following the spate event which was not evident from the periodic measurements. Where this data could be matched with IGF measurements, a data point was produced and of these, 3 points are seen to fall below the threshold of minimum DO–IGF requirements and into the sub-optimal zone. The two sites (Lyepole and Lower Harpton) with high frequency data recorded from 2009, remained above the threshold limits.

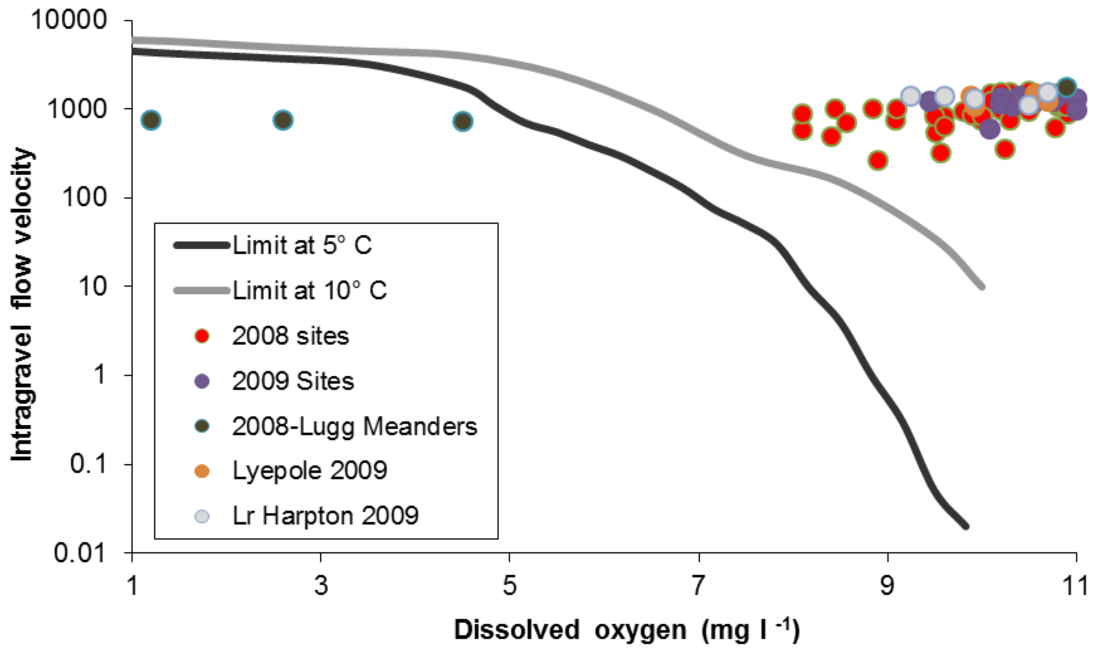


Figure 6.12 Threshold levels of dissolved oxygen against intragravel flow velocity as calculated by Grieg et al (2007), featuring the Lugg site values.

Additionally, a general guideline of derived velocities and oxygen concentrations feature in Grieg's paper (2007) as three categories – high, intermediate and low.

Habitat quality	Oxygen concentration (mg l^{-1})	Interstitial flow velocity (cm h^{-1})
Low	0–6	≤1
Intermediate	6–9	2–15
High	>9	>15

Table 6.4 (from Greig 2007) Oxygen concentrations and interstitial flow velocities classified into low, medium and high categories.

These values were also used for comparison with the Lugg site values for the 2008 and 2009 spawning seasons.

While some Lugg sites would have been assigned for some periods to the intermediate level for oxygen concentration, intragravel flow data generally plotted above 15cm h^{-1} and was therefore classed as within the 'high' category for habitat quality.

Intragravel flow and dissolved oxygen concentration from 2008 and 2009 Lugg and Arrow sites are plotted onto Grieg's derived values for co-dependent critical limits relative to both factors, and the sites generally plot above these critical limits, indicating good incubation conditions.

Nonetheless, although Oxygen and intragravel flow broadly equate with good quality habitat according to the DO/IGF model categories, survival in 2008 does not always reflect this, where sometimes moderate survival was reported, indicating that there may be further influences at work or that there were temporary fluctuations in habitat quality that remained undetected by the periodic field monitoring.

A series of Pearson correlation tests were carried out relating survival to intragravel flow, to final oxygen concentration and finally to oxygen 'flux' which is the product of intragravel velocity and dissolved oxygen concentration. Values reflect the correlation values from both field seasons combined. The results of the test are displayed in table 6.5 below.

Survival – DO (End of season)	Survival – DO (Minimum)	Survival – IGF	Survival - Flux
0.41	**0.63**	**0.69**	**0.72**

Table 6.5 Pearson correlations of potential survival determinants as calculated with Lugg site data

When the minimum observed values which had been collected from the high-resolution Anderaa probes were added to the dataset, there was a marked improvement in the predictive ability of dissolved oxygen.

However, similar to the findings of Grieg et al (2007), oxygen flux was found to be the better indicator of survival when compared to either dissolved oxygen or intragravel flow alone, with a Pearson value of 0.81 for the combined data set - all values included.

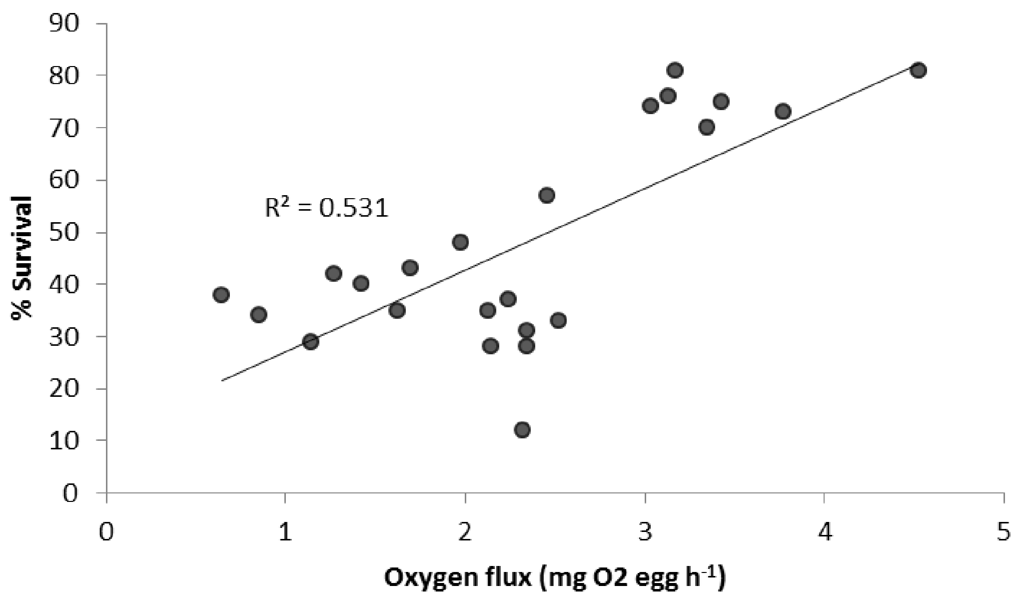


Figure 6.13 Survival –oxygen flux relationship for the Lugg sites

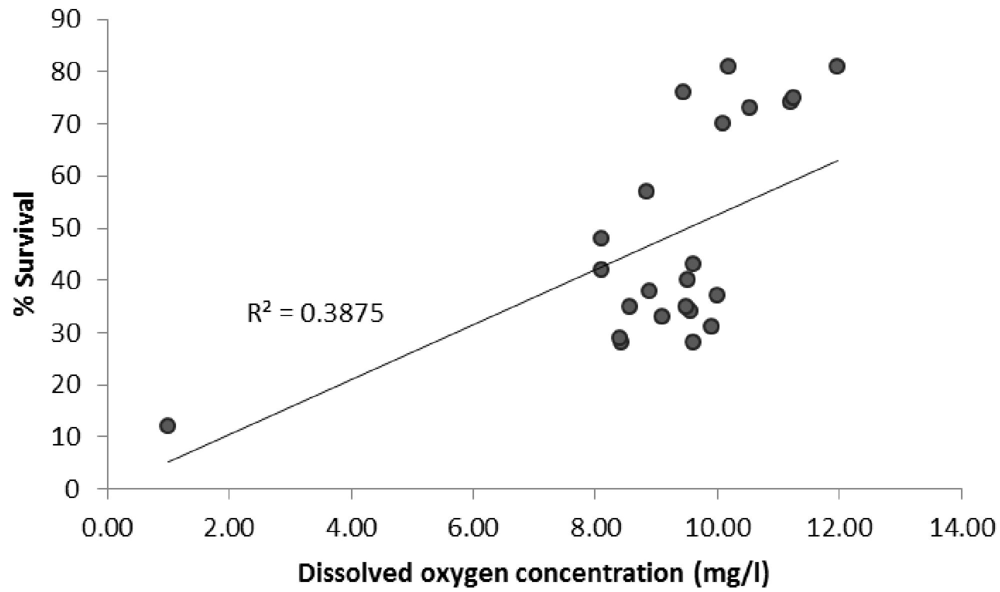


Figure 6.14. Survival – final oxygen concentration relationship for the Lugg sites

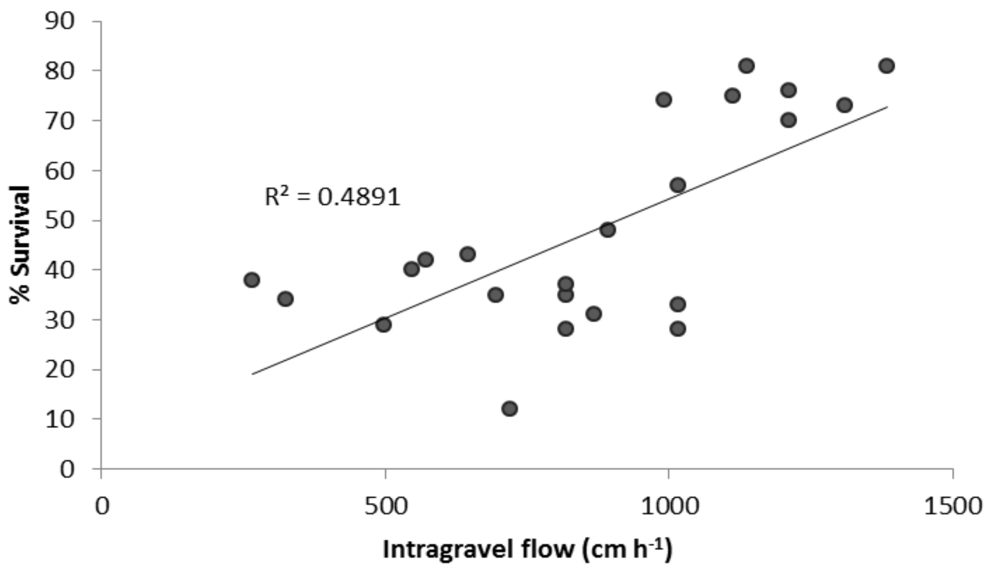


Figure 6.15. Survival – Final Intragravel flow velocity concentration relationship for the Lugg sites

While the statistical tests of survival against final oxygen 'flux' proved to be statistically significant for the parameters tested, it should be noted that there may be other influences at play here which are not accounted for. There were omissions of data for certain dates – during the spate periods and this was in part be supplemented by continuous DO readings when they were available. Intragravel flow measurements were not possible during these periods. Malcolm et al (2011) carried out a study looking at Intragravel flow as a predictor for survival and found that it did not perform well on a catchment with significant (hypoxic) groundwater upwelling finding rather that dissolved oxygen concentration measures were better indicators. Our contrasting results here may indicate the dominance of surface water influence in the Lugg catchment over the 2 field seasons investigated and the interrelated effects of sediment infiltration on intragravel flows and thereby dissolved oxygen concentrations. However, other sources of complexity should not be ruled out. The next section investigates the possibility of long residence groundwater as an alternative mechanism for decreased spawning habitat quality.

6.4 Results of groundwater - surface water interactions studies

There has been an increasing awareness in hyporheic zone studies of the influence that groundwater infiltration can have on the ecology of the habitat, and a recognition that fluctuations in the physical and chemical characteristics of the zone can impact on the nutrient cycling as well as the biota living within it, from microbial communities to invertebrates to incubating salmonids (Findlay et al 2003, Storey and Williams 2004, Malcolm et al 2004, 2006).

Studies of the hyporheic zone are chiefly concerned with the interactions of two different water bodies; groundwater and stream water. These bodies typically have different characteristics which can be represented by differences in alkalinity, conductivity and other elements depending on the geology of the underlying bedrock and drift deposits. Studies of one or more of these defining characteristics can help define the interactions between these two bodies on temporal and spatial scales. Additionally, the presence of reduced water – low in dissolved oxygen has also been associated with groundwater infiltration into the hyporheic zone, and all of these measures have been used to differentiate between the water bodies (Soulsby et al 2001, Youngson 2004). Soulsby et al (2001) found that higher levels of conductivity were periodically found within salmonid redds, and investigated this through tracer studies which indicated a reversed hydraulic gradient during the rising limb of higher flow events.

Recent studies (Malcolm et al 2006, Soulsby et al 2009) have highlighted the importance of high resolution sampling - particularly in relation to salmonid spawning gravels and review the relevance of how previous investigations into hyporheic exchange have been carried out, pinpointing the mis-match between the frequency of sampling regimes investigating the hyporheic environment and the highly variable nature of the hyporheic environment.

Malcolm et al (2006) related the results of a study on hyporheic dynamics within a catchment using high resolution dissolved oxygen and piezometers to measure hydraulic head. They showed that there was significant mixing between the two water bodies especially around the time of higher flow events, with a positive hydraulic gradient apparent during the rising limb followed by a negative gradient shortly after - notably during the recession limb of an event.

Observations of dissolved oxygen fluctuations within the hyporheic zone, and particularly within salmon egg deposition zone over very fine temporal scales compound and renew traditional concerns of the impacts of hypoxic conditions on incubating salmonid embryos and larvae (Chapman 1988, Ingendahl 2001, Malcolm et al 2003, Grieg et al 2006).

It was with this in mind that during field seasons 2008 and 2009, conductivity measurements were taken via the in-situ standpipes during each periodic visit and results are shown in figures 6.16 -6.19. Some redd zones appear to have slightly differing conductivities as compared to overlying stream water, sometimes higher but also lower in conductance. Given that these results on their own do not provide a definitive signal of upwelling groundwater masses, a further study during the 2009 season was carried out which looked at measuring the difference in hydraulic gradient through the use of piezometers at depths of 30cm.Additionally, in 2010, piezometers were employed along with oxygen sensors buried at a range of depths to further investigate GW-SW interactions and variations with depth, since survival indices had been variable at this site over previous seasons, and because it was considered a possible candidate for GW interactions given its constricted valley form and underlying glacial clays (Malcolm et al 2005).

6.4.1 Conductivity as a groundwater indicator

Measurements for electrical conductance were carried out during the field seasons 2008 and 2009 where possible, on periodic weekly/10 day visits. Figures 6.16 and 6.17 show the temporal variations in conductivity in both stream water and redd water through time. Each site is represented by a specific colour. Dashed lines indicate redd zone measurements and solid lines represent stream water values.

Despite limitations on access to some site during the 2008 spate event, a sharp decline in conductivity levels is evident around mid-march, coincident with the high precipitation levels and subsequent spate event. Conductivity thus varies with flow rate and appears to have an inverse relationship with turbidity (Bek et al 1994; Mitrovic et al 1995), which tends to restrict the addition of ions in the water column (Doltzman et al 2001).

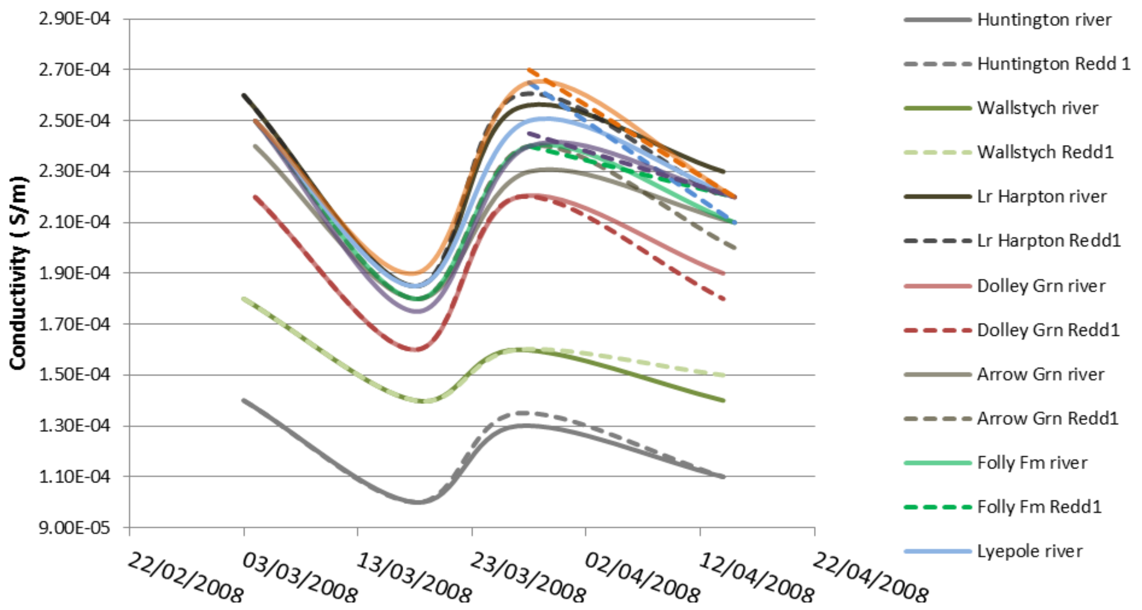


Figure 6.16. Conductivity in redd and stream water for the 2008 sites

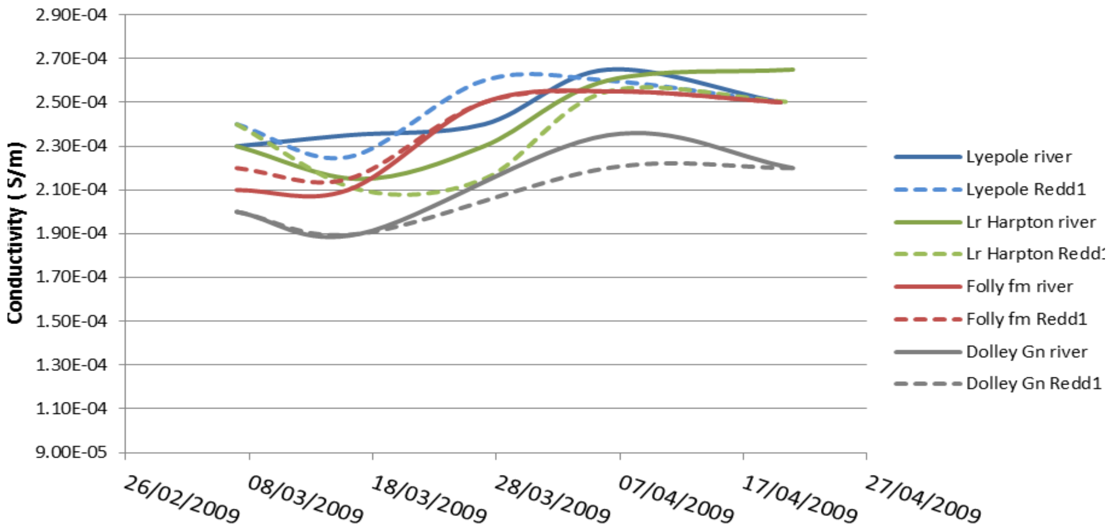


Figure 6.17 Conductivity in redd and stream water for the 2009 sites

In terms of indications of groundwater upwelling, slight differences in conductivity were evident for some sampling points between river and redd conductivity measurements, indicating the possibility of the presence of other water bodies. This is mainly evident during latter part of the 2008 field season and mid-season during 2009 as shown in figures 6.18 and 6.19 below. It should be noted that redd conductivity measurements at the downstream 2008 sites were not feasible during the higher flows. Nonetheless, for the observable conductivity differences, intragravel measurements deviated both positively and negatively from stream values depending on the site in question. Despite a narrower overall range in conductivity during the 2009 season, (with values between 1.9 x 10^{-4} and 2.65 x 10^{-4} as opposed to a range of 1.1 x 10^{-4} to 2.7 x 10^{-4} during 2008 field season), site-specific differences between stream-water and redd water were slightly higher during 2009.

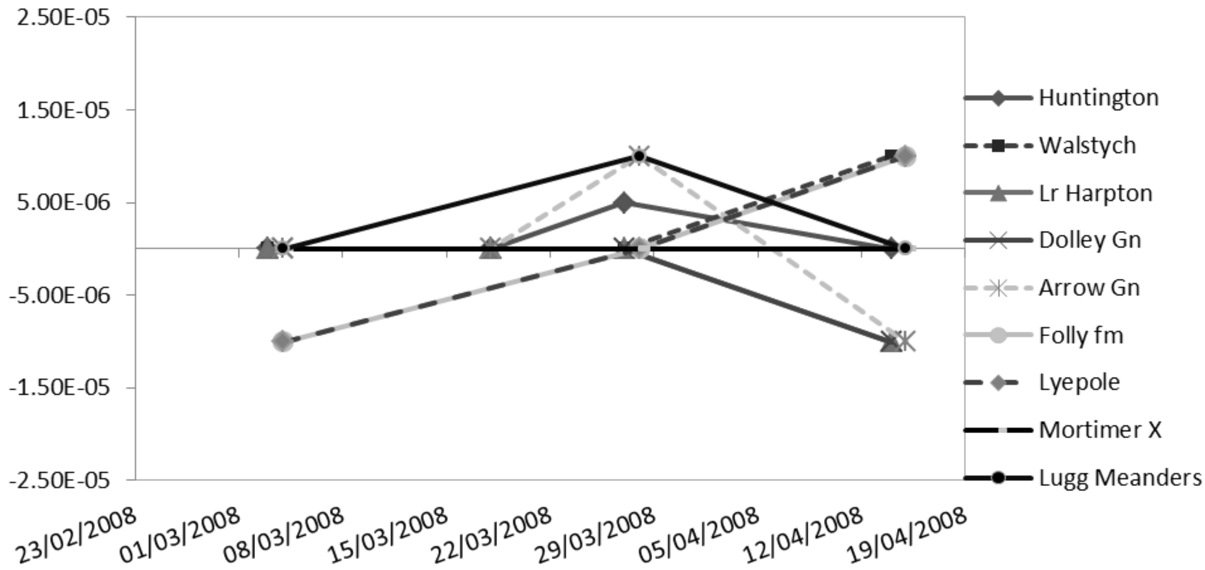


Figure 6.18. Difference in specific conductivity difference between redd water and stream water at the 2008 sites.

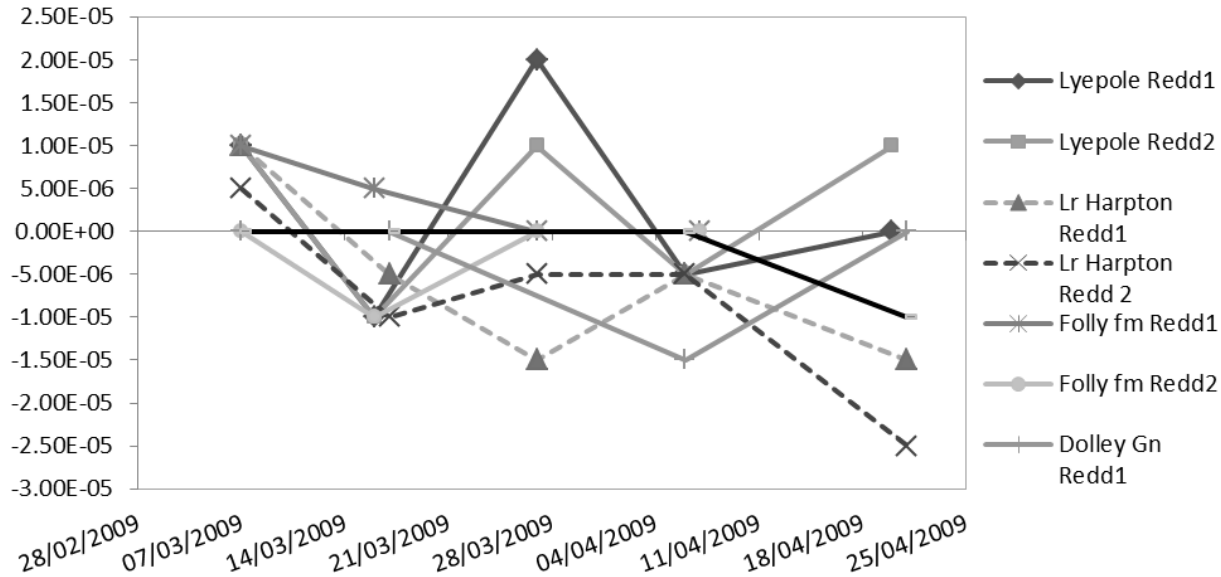


Figure 6.19. Difference in specific conductivity difference between redd water and stream water at the 2009 sites

From this evidence, it can be asserted that the possibility of differing water bodies / masses is present. However, evidence of directionality or dynamics of hyporrheic exchange is not conclusive, so investigations of further parameters were carried out in subsequent years.

As outlined in section 6.4 above, the main indicators of groundwater presence within the hyporheic zone of the stream system are low levels of dissolved oxygen in comparison to stream water (Boulton et al 1998, Malcolm et al 2003, Soulsby et al 2009), a positive hydraulic streamward gradient (Malcolm et al 2003, 2006), a more stable temperature regime (Webb and Walling 1993, Hannah et al 2008) and differing chemical characteristics when compared to stream water (Soulsby et al 2001, Krause 2009). Table 6.6 below outlines the main properties commonly used to differentiate ground water from surface water bodies.

Water body	***Temp***	***DO***	***Head***	***Conductivity***	***Alkalinity***	***Nitrate***	***Ammonia***
SW	Diurnal signal	Higher	Negative gradient	Lower	Lower	Higher	Lower
GW	More stable regime	Lower	Positive gradient	Higher	Higher	Lower	Higher

Table 6.6 Comparative summary of groundwater and surface water properties.

In addition to periodic conductivity measurements, high-resolution monitoring of three additional parameters was carried out to test for GW-SW interactions. Firstly, hydraulic head differences over a vertical plane within the river bed were recorded during 2009 and 2010. Secondly, high resolution dissolved oxygen sensors were installed within the river bed to record micro-scale fluctuations within the redd-zone and any indications of groundwater influxes. Thirdly, high resolution temperature data was investigated as additional evidence. Results of these investigations are presented in turn and discussed in the following sections 6.4.2 – 6.4.5.

6.4.2 Hydraulic head as an indicator of groundwater – surface water interactions

For the 2009 season, Schlumberger™ mini-diver piezometers were installed at the Lower Harpton and Lyepole Bridge sites at a depth of 30cm within a piezometer tube in the river bed. Additional pressure transducers were also installed at the same sites, level with the river-bed i.e.: 0cm. Measurement intervals of 15 minutes were set, and data from both loggers were compared at the end of the field season. The direction of water movement was derived from the difference in hydraulic head between the two; where positive trends signified upwelling from the bed and negative trends show streamwater infiltration into the riverbed.

The hydraulic gradient for the Lower Harpton site is shown in figure 6.20 below, and demonstrates the high temporal variability and fluctuations alongside discharge data for the same period. Despite the low flow conditions during this field season, hydraulic gradients indicate negative trends as discharge peaks occur; in particular on the 3rd and 9th of March. This is consistent with increased infiltration of river water into the stream bed as discharge increases. Conversely, increased upward movement of water can be seen as discharge levels decline e.g.: on 5th March and again on 14th March, where a positive upwelling trend can be seen as the hydraulic gradient increases briefly. This is presumably in reaction to temporarily increased groundwater inputs and lags slightly behind the discharge peak.

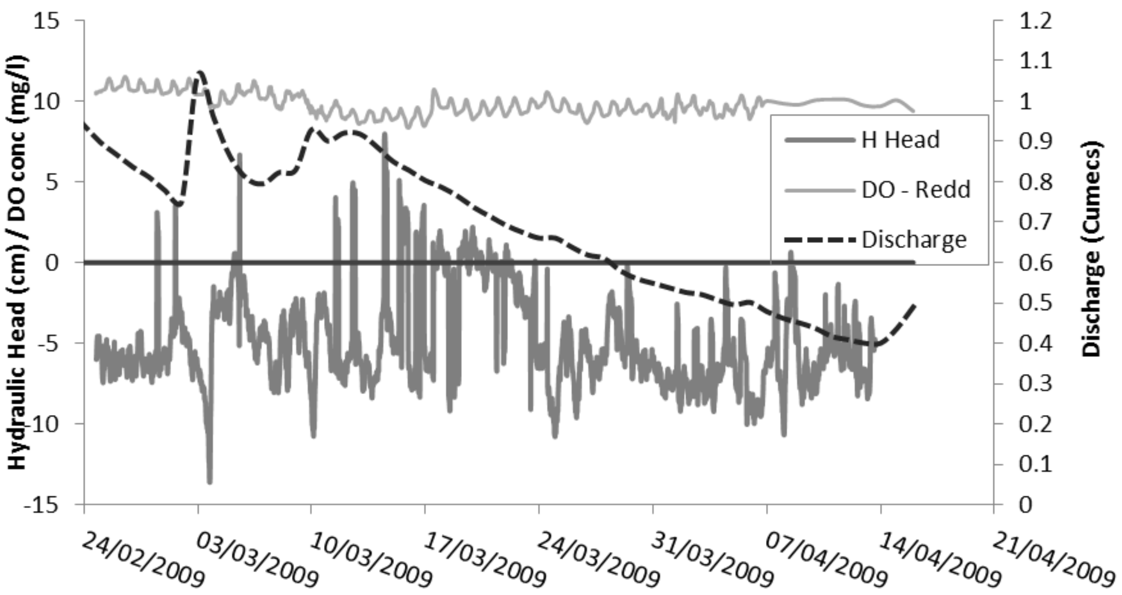


Figure 6.20. Hydraulic gradients at the Lower Harpton 2009 site as measured by difference in head between two piezometers (values on primary axis) with discharge and dissolved oxygen in the redd for the same period.

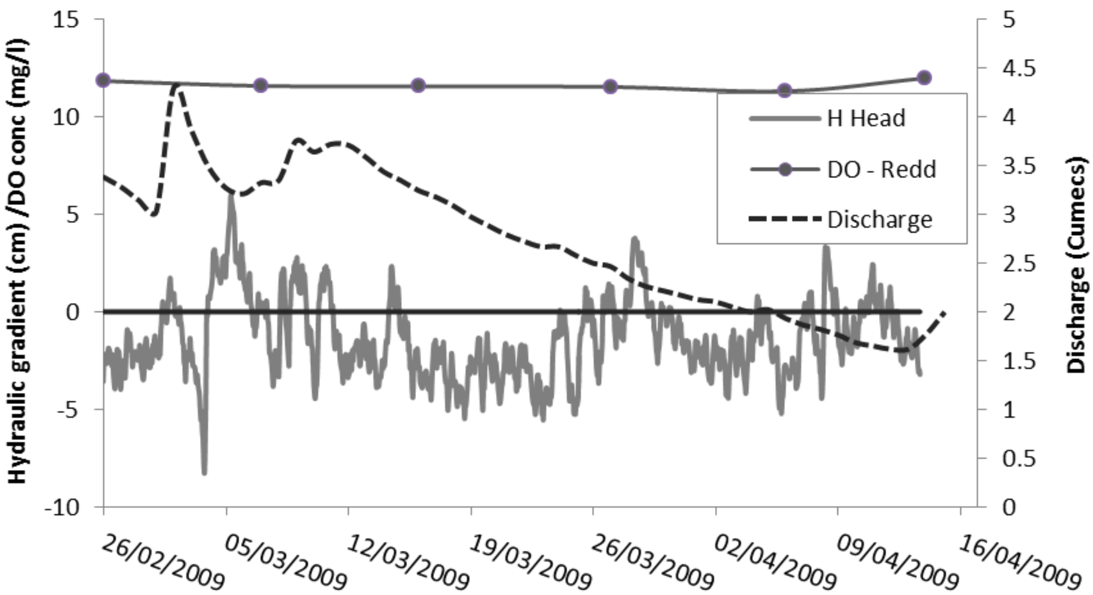


Figure 6.21. Hydraulic gradients at the Lyepole 2009 site as measured by difference in head between two piezometers (values on primary axis) with discharge and dissolved oxygen data in the redd for the same period (secondary axis).

At the Lyepole bridge site, the same pattern of hydraulic trends followed any rapid increase in discharge – again mainly around the peak flow of 3rd March, where a negative hydraulic gradient is seen, followed by a positive gradient (signifying upwelling) coincident with the falling discharge limb. The relatively dry nature of this field season however resulted in no dramatic peaks or troughs in head measurements with all readings of head differential within a 15cm vertical range.

Dissolved oxygen sensors for the two sites were initially high resolution probes, but due to technical difficulties at the Lyepole site, periodic oxygen measurements were deemed more reliable at that location. Data for both sites show dissolved oxygen concentrations remaining high for the entire incubation period, and unaffected by fluctuations in head or discharge.

In 2010, a similar piezometer setup as that of 2009, was installed at the Lyepole bridge site. Results are displayed in Figure 6.22 below.

Fluctuations in hydraulic gradient during this season inversely reflected discharge data very closely, with even small peaks in discharge mirrored by negative hydraulic gradients. In particular, a large negative hydraulic gradient was observed coincident with the increased discharge around the 2nd of April, indicating a downward flow component and a possible stream-water influx into the river bed at that time. Decreases in discharge are associated with positive hydraulic gradients and possible increased groundwater components at those times.

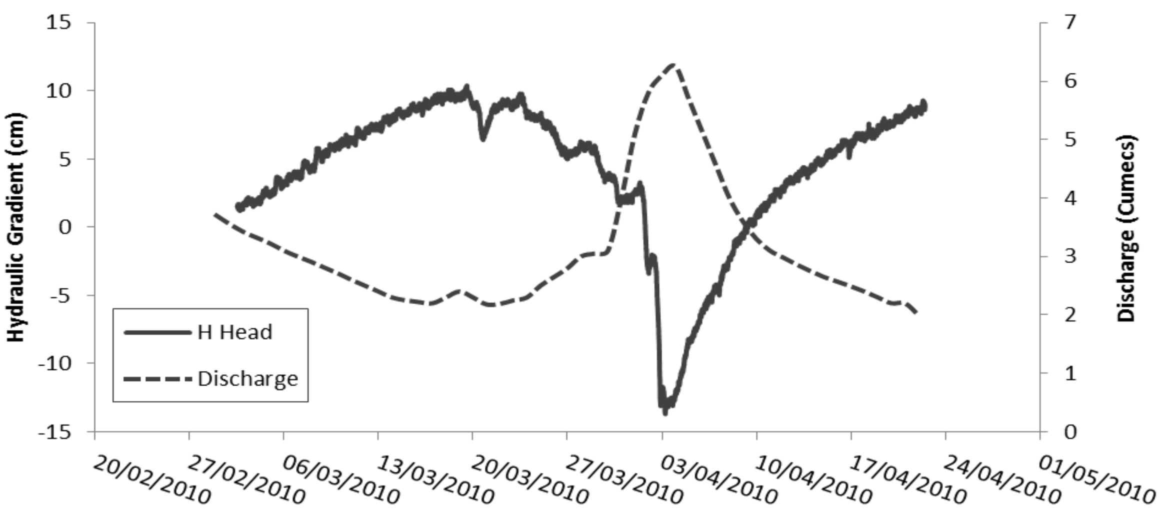


Figure 6.22 Lyepole 2010 Hydraulic gradients as measured by difference in head between two piezometers (values on primary axis) and discharge data for the same period (secondary axis).

In terms of the patterns in hydraulic gradient relative to discharge events, these findings are broadly in agreement with the previous study by Malcolm et al (2006) and Soulsby et al (2009), where event peaks were associated with increasingly negative hydraulic gradients on the rising limb of events, frequently followed by more positive gradients on the falling limb of an event as upwelling groundwater emerges stream-ward.

6.4.3 Groundwater influences on temperature

Temperature data can be used to deduce the directionality and degree of GW–SW interactions (Silliman and Booth 1993, Evans et al 1995, Malcolm et al, 2004). Groundwater typically exhibits a more stable thermal profile than surface water - which is characterized by both diurnal and seasonal temperature fluctuations. Consequently, we can infer that differences between hyporheic and surface thermal regimes result from differences in local GW–SW interactions.

Surface water exhibits both seasonal and diurnal fluctuations due to its varied exposure to infrared radiation. In terms of diurnal fluctuations, the warmer periods will fall mid-afternoon with temperature troughs occurring around 4 -6am before sunrise. In terms of seasonal patterns, surface water will be at its warmest during the summer months, and coolest during the winter. Comparatively, ground water is generally cooler during the summer months, and warmer during the winter months, with studies showing periods of isoparity between the two bodies during March-April, and Sept-October (Winter 1999, Calvache et al 2011). Since the Lugg field investigations encompassed the March-April periods when seasonal differences between the two water bodies may be at a minimum, focus was applied to the lack of diel temperature fluctuations as an indicator of groundwater contribution.

Figure 6.23 displays the temperature fluctuations in stream and hyporheic zones at the 2009 Lower Harpton site. While there is a slight lag in temperature profile in the 30cm depth readings, overall temperatures follow stream temperatures very closely, and show the same diurnal patterns and those within the water column above. There are no clear indications here of GW-SW interactions and this is supported by data shown in figure 6.20 for the same location, where dissolved oxygen levels in the redd remain high with no clear positive peaks in hydraulic gradient. Thus evidence does not point to active GW-SW interactions within the redd zone at this site during 2009.

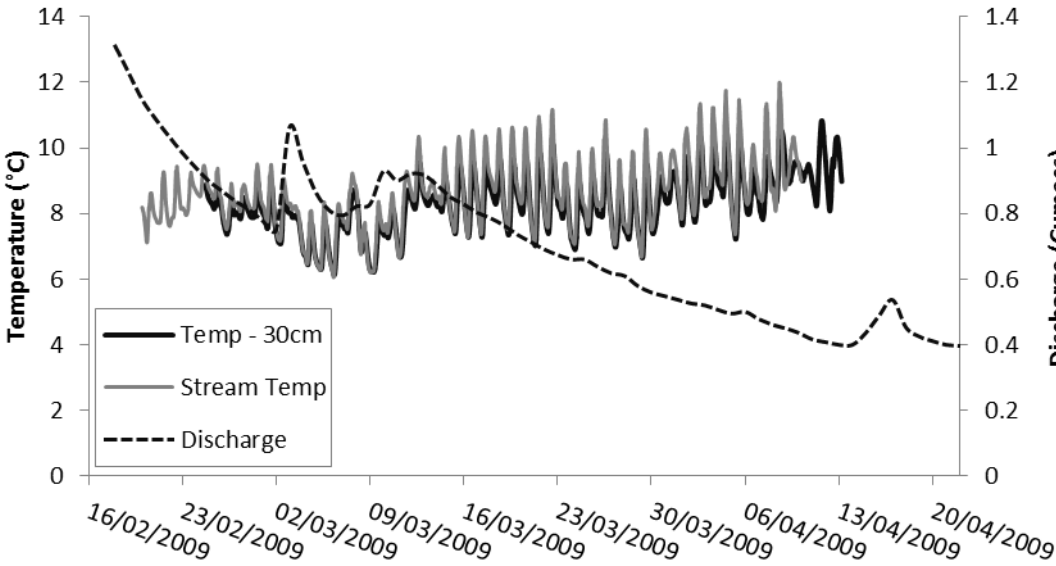


Figure 6.23. Temperature fluctuations at the Lower Harpton 2009 site

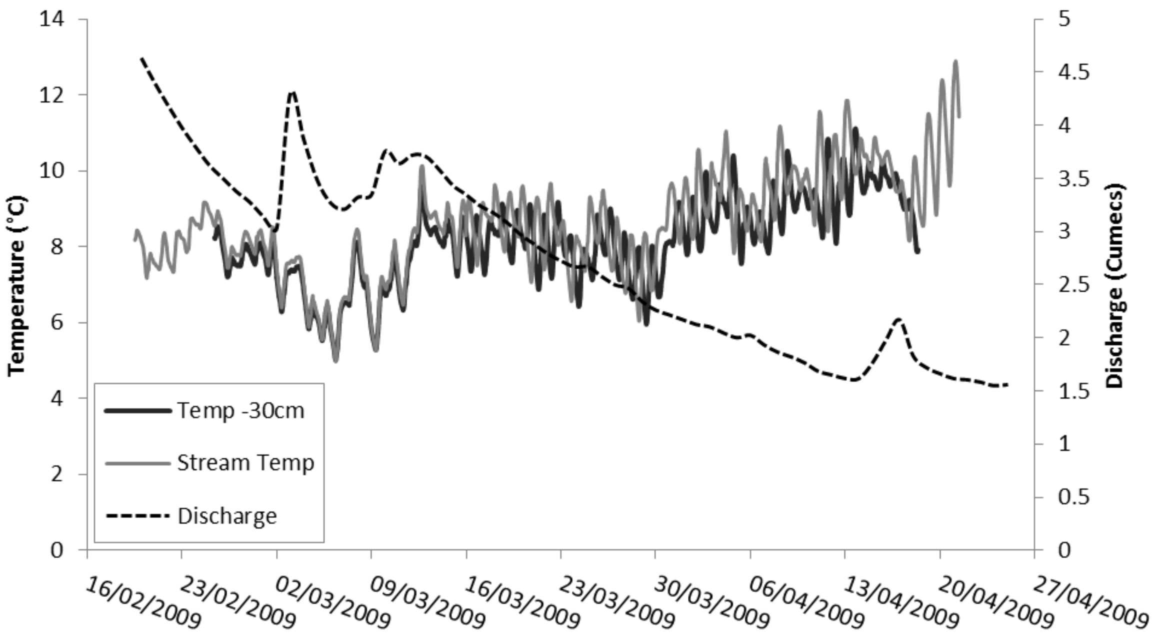


Figure 6.24. Temperature fluctuations at the Lyepole bridge 2009 site.

Similarly, at the Lyepole bridge site, temperature fluctuations again follow stream temerature very closely with only occasional lags in response at the 30cm depth. Again, grouped with the dissolved oxygen and hydraulic head data for this site (figure 6.21), there is no clear indication of groundwater influence at this site suring 2009.

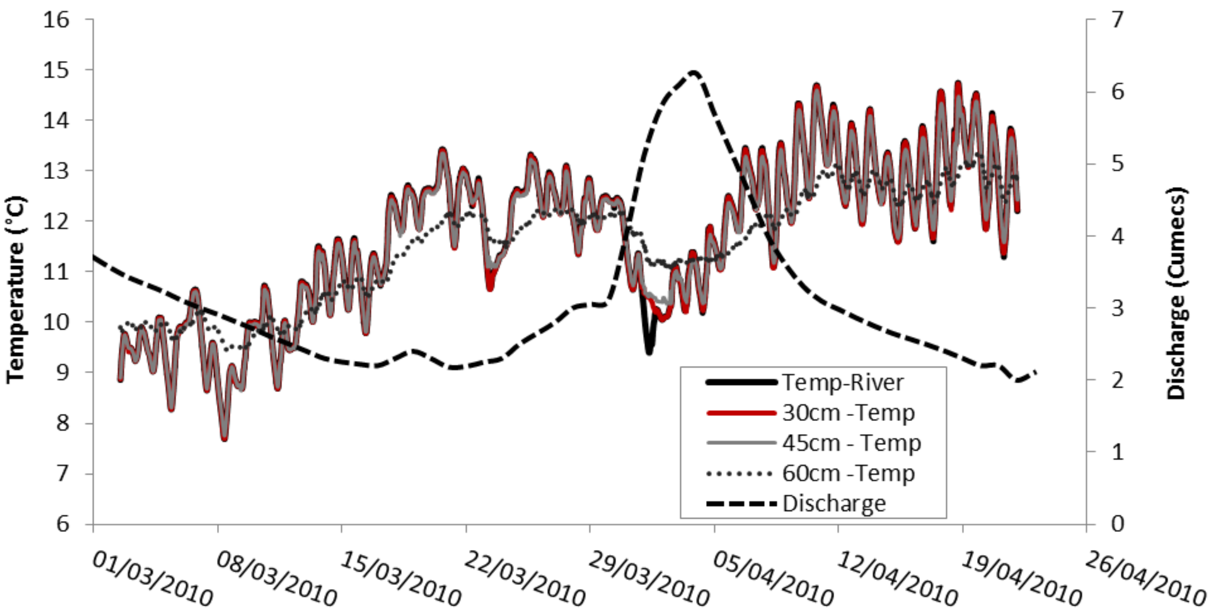


Figure 6.25. Lyepole 2010 temperature data

Temperature data was more detailed at the 2010 Lyepole bridge site; with temperature readings from depths of 30, 45cm and 60cm which could be compared to the stream temperature profile. The probe data from 60cm depth shows a clear difference in temperature regime and an almost complete lack of diel temperature signal. Other probes follow the stream temperature pattern fairly closely with a slight lag and a minor drop in amplitude with depth. Further dampening of the diel pattern can be seen during the high flow period around 30th March in the 45cm and 30cm probes, indicate possible GW-SW interaction at this time.

6.4.4 High resolution fluctuations in dissolved oxygen

Although there was no evidence for GW-SW interactions from 2009 dissolved oxygen levels as seen from figures 6.20 and 6.21, the Lyepole bridge site during 2010 revealed contrasting results.

During the 2010 season, multiple dissolved oxygen probes were buried and aligned vertically at 3 depths within the river bed at the Lyepole bridge site, in order that observations of temperature and dissolved oxygen could be made and compared with that of overlying stream water concentrations and with discharge.

Anderaa™ dissolved oxygen optodes (model: 3830) were buried at depths of 30cm, 45cm and 60cm and set to retrieve data at 10 minute intervals throughout the field season. Data was stored on Delta-T™ DL2e logger devices.

Data for the 2010 Lyepole bridge site is displayed in figure 6.26 below and exhibits highly variable dissolved oxygen concentrations, indicating the heterogeneity of the hyporheic zone and its wide spatial (vertical) and temporal variability.

On examination of the oxygen probes' data, a distinct decline in dissolved oxygen levels is coincident with a high flow event around the 2nd April. All three buried probes show a response at this time, but readings differ relative to depth. The probe at 60cm depth shows a slight initial decline in oxygen concentration around the 24th March when discharge levels begin to increase, but show a marked decline on the 1st April in correspondence with the steep rising limb of the high flow event. Oxygen concentrations remained near zero for a period of 4 days, before increasing to normoxic levels on the 7th April, which corresponds with the falling limb of the discharge event.

The probe at 45cm depth responds in a similar way, but remains at anoxic levels for a shorter time period that the deeper probe and reads normoxic levels after a period of 2 days.

The 30cm depth dissolved oxygen levels also show a decline around this time, but in a more erratic fashion, perhaps indicative of its higher connectivity with the stream water interface. Although dissolved oxygen levels never reached zero at 30cm depth, hypoxic levels were reached on several occasions throughout the period; corresponding with the rising limb of the higher flow event but also around the 17th of April, on the lower falling limb of the event.

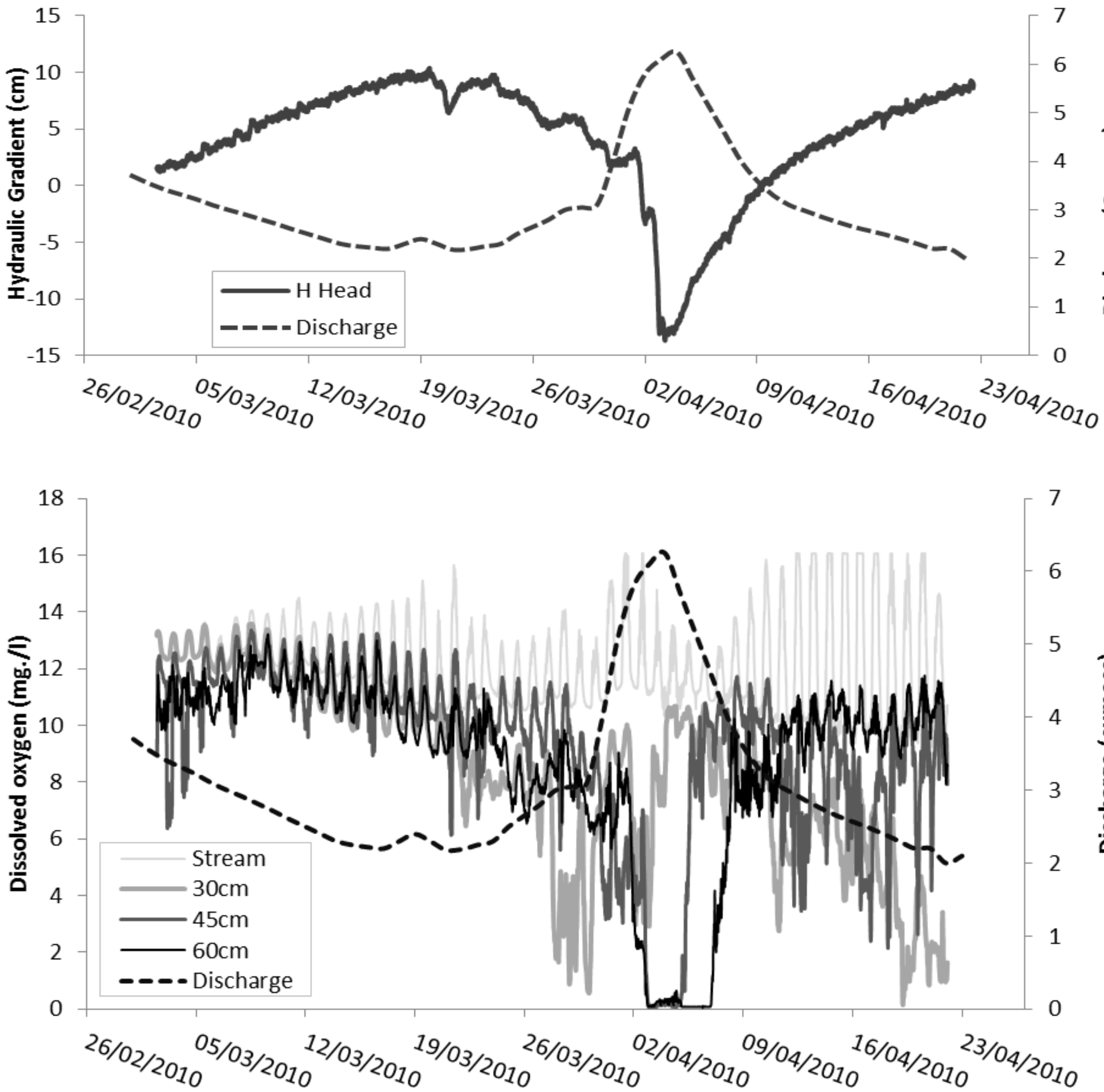


Figure 6.26. Dissolved oxygen data from four probes buried at various depths during 2010, here plotted alongside discharge data for the same period. (Hydraulic head data for the same period is featured above)

Previous studies by Malcolm et al 2006 and Soulsby et al 2009, also showed declines in dissolved oxygen levels which coincided with event peaks, but not for every event. They found that over the course of a number of events, successive catchment wetting resulted in lowered dissolved oxygen levels during the later events with more complex responses where prolonged wet conditions persisted. They found that this may partly be explained by increased water table elevation in response to groundwater recharge, and the subsequent rapid emergence of long-residence low oxygen groundwater at the hyporheic margin.

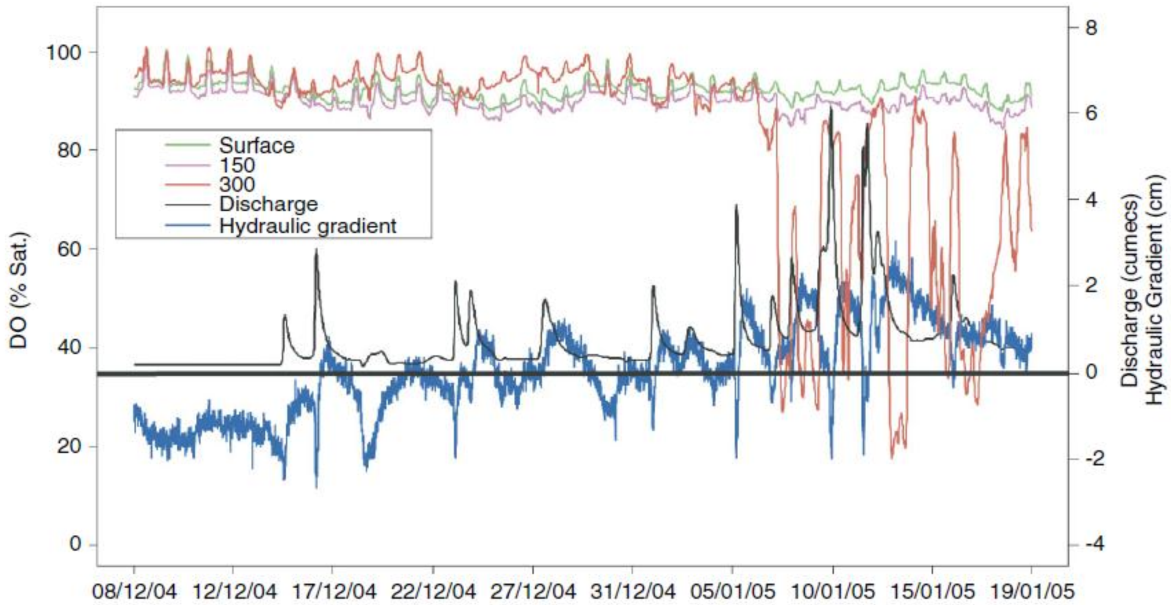


Figure 6.27. Malcolm et al (2006) Hydraulic head data with dissolved oxygen data for the period from 8th December 2004 to 19th January 2005 showing the complexity of DO response to catchment wetting.

In relation to the 2010 Lugg observations, it seems plausible that the rapid response of the dissolved oxygen levels to the March wet weather event may have been primed by high water table levels present since the previous spate event in late January 2010, during which discharge reached above 22 cumecs at its peak. Figure 6.28 below shows the daily mean flow data from the 1st Jan, and includes the larger January spate event.

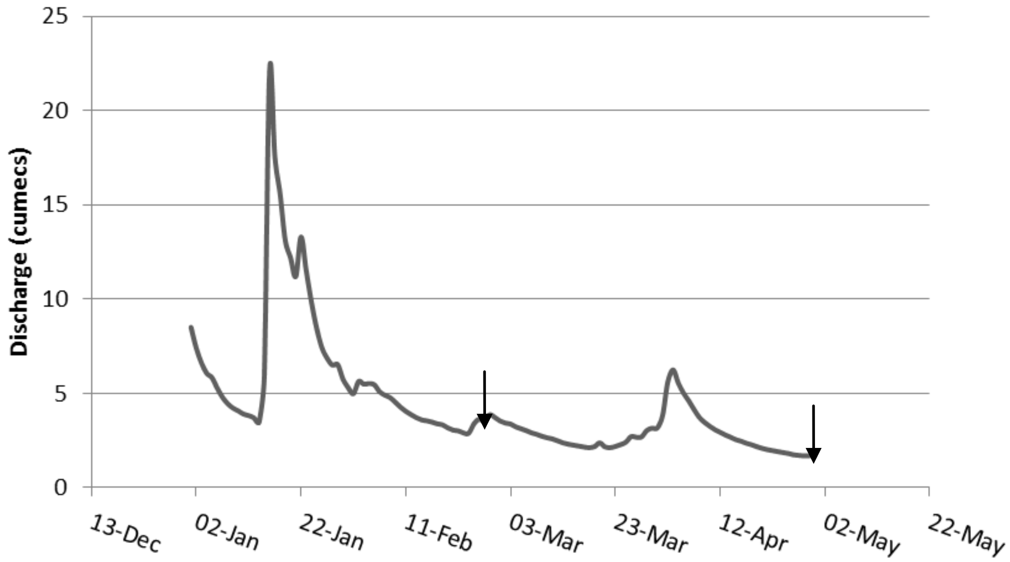


Figure 6.28. Discharge for the Lyepole Bridge site, January-May 2010 illustrating catchment wetting prior to the fieldwork period. Installation and retrieval of equipment is indicated by black arrows on the graph.

The above findings are broadly similar to those of others looking at GW-SW interactions on other catchments, where lowered dissolved oxygen levels were frequently associated with higher flow events, with levels recovering to near surface water DO concentrations during dryer spells. A similar finding is evident in the study by Soulsby et al (2009) where heightened discharges during a wet weather period coincided with severe drops in dissolved oxygen concentration at the 30cm depth (figure 6.29). Decreases in oxygen are evident mostly on the rising limb of the event with recovery to normoxic levels only after discharges returned to base level.

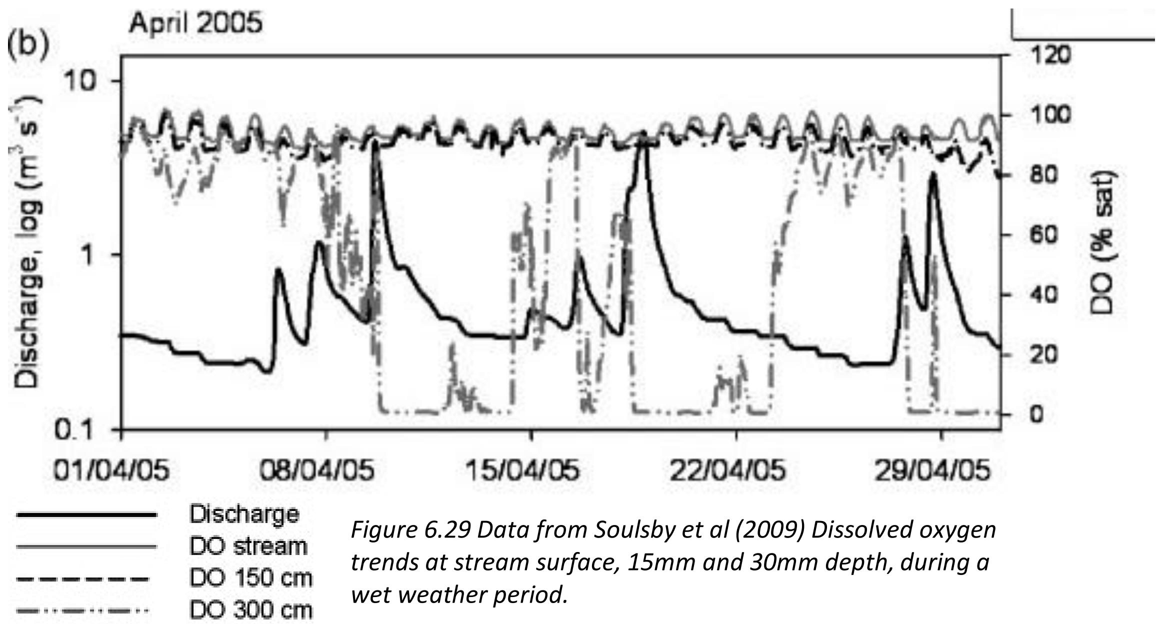


Figure 6.29 Data from Soulsby et al (2009) Dissolved oxygen trends at stream surface, 15mm and 30mm depth, during a wet weather period.

Below is a conceptual groundwater model proposed by Soulsby et al (2009) which aims to explain this association and its relevance to the needs of developing salmonid larvae. The sketch indicates groundwater dominance during the recession limbs of high flow events, and the possible low oxygen concentration of this water with attendant effects on incubation success.

Sketch (b) represents the general head reversals (as illustrated well in 2010 at the Lyepole bridge site) at the hydrograph peak, where streamwater infiltrates the hyporheic zone and oxygen levels remain high. (C) represents the baseflow minor interactions during dry periods, where hyporheic exchange is shallow in nature and oxygen content of the hyporheic zone will generally be high and thus capable of supporting embryonic incubation.

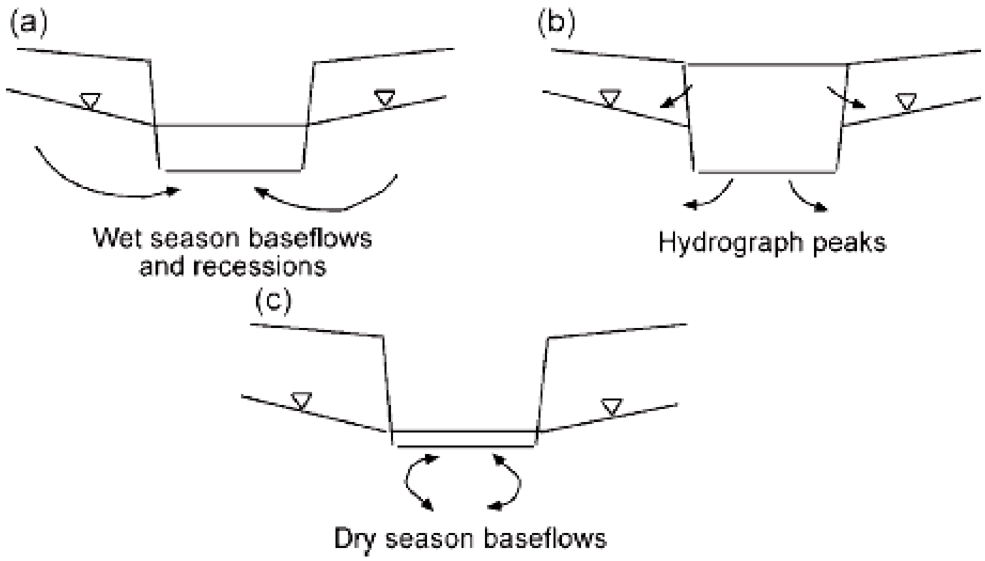


Figure 6.30. (From Soulsby et al 2009) Conceptual model of groundwater-surface water interactions.

The above model is a simplification of the GW-SW dynamics in a catchment. As mentioned above, Previous studies by Malcolm et al 2006 and Soulsby et al 2009, showed variability in Groundwater infiltration response to wet weather events, whereas Malcolm (2006) states “Events of similar magnitude can produce marked differences in hyporheic water quality due to state dependence on antecedent conditions”. Thus consideration of the broader recent history of catchment precipitation and seasonal spate events should form part of any study into hyporheic zone dynamics. Additionally, as can be seen in both Malcolm et al 2006 (figure 6.27) and the Lugg 2010 figure 6.26, positive hydraulic gradients do not always directly correspond to the depleted oxygen concentrations, but exhibit a more erratic behavior once a 'threshold' event has occurred.

An explanation for this behaviour may be due to the heterogeneity of GW-SW interactions locally. The single piezometer set-up measures only vertical flow beneath the streambed, and does not account for lateral groundwater flow within the hyporheic zone (Winter 1999, Kalbus et al 2006). A more in-depth set-up would involve a nest of piezometers spread spatially throughout the reach, and the hydraulic gradient calculated from the difference in hydraulic head and the horizontal distance. From this, vertically distributed piezometer data can be used to draw lines of equal hydraulic head for the construction of a flow field map showing the groundwater flow behaviour in the vicinity of a surface water body (Winter 1999, Baxter 2003).

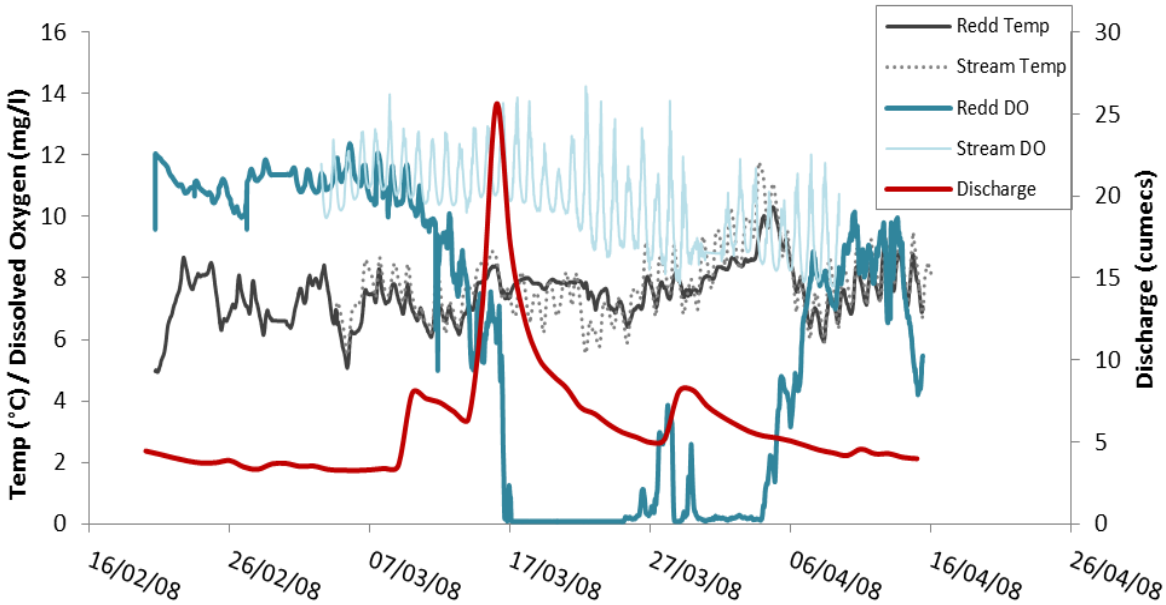


Figure 6.31. High resolution data from the Lugg Meanders 2008 site. Discharge is displayed on the secondary y axis

The above findings may go some way to explaining Lugg Meanders data during the 2008 spate event (figure 6.31 above), where sustained low dissolved oxygen concentrations were recorded and correspondingly low survival rates found (12% survival).

High resolution dissolved oxygen and temperature data from the 2008 supersite show a similar pattern to that seen during 2010 investigations. Although no head data is available for this field season, a period of low dissolved oxygen is coincident with the mid-season spate event once again – indicative of groundwater upwelling in an already wetted catchment. Figure 6.32 shows the previous spate history of the catchment prior to redd building and this is in agreement with Malcolm et al's observations of low DO signals occurring most frequently following multiple wet weather events.

Additionally, temperature signals from within the redd (30cm depth) exhibit dampened (diurnal patterns as when compared to stream temperatures for the same period. This compounds the evidence of groundwater effects on incubation habitat quality at this site.

In terms of situation of the field sites there is the possibility that the two lower sites; Lyepole bridge and Lugg meanders are more liable to GW influx as they are geographically situated on areas with underlying glacial drift and thus potential aquifers, whereas other areas of the catchment are based on sandstone or shale bedrock and may be less affected by groundwater with long residence, low oxygen characteristics. Additionally Lyepole Bridge site is located within a constricted valley – another factor which has been found to contribute to groundwater upwelling, especially when coupled with slow-draining glacial clays (Baxter and Hauer 1998) as is the case in the lower study sites.

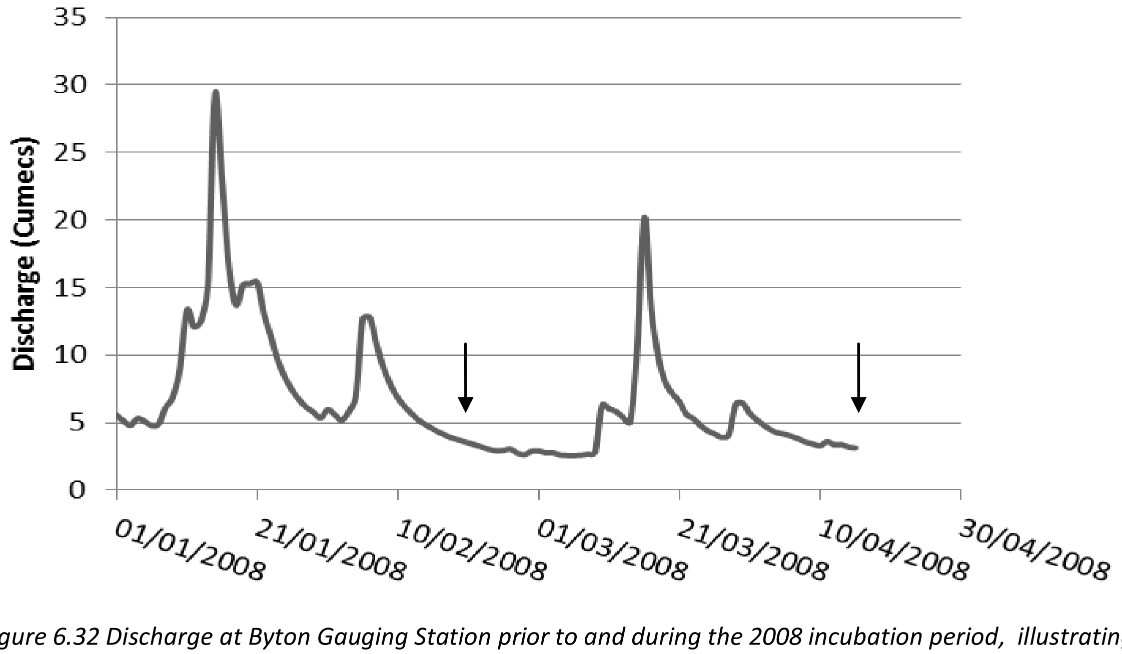


Figure 6.32 Discharge at Byton Gauging Station prior to and during the 2008 incubation period, illustrating the frequency of spate events and catchment wetting prior to egg incubation.

While the data retrieved during the dry 2009 season gave no indication of groundwater-surface water via hydraulic head, temperature or dissolved oxygen data, similar investigations during the following 2010 season showed increased likelihood of groundwater presence using the same measurement parameters. Discharge was higher during the 2010 season (max discharge 7-8 cumecs) and thus is proposed as the controlling mechanism for groundwater infiltration into the hyporheic and redd zone. The 2008 data, while lacking information on hydraulic gradient, supports this proposition and exhibits both dissolved oxygen and temperature reading that are indicative of groundwater presence and coincident with the largest spate event witnessed during the study –with maximum discharge measurements of 25 cumecs at its peak.

While it seems clear the discharge (Q) is a chief driver of hyporheic habitat quality; due in part to groundwater infiltration in areas where catchment wetness was sufficient to cause a 'tipping point' where groundwater swell reached redd level within the river bed. It remains unclear what the precise threshold values of catchment wetness are, which may then trigger groundwater upwelling during a high flow event (Malcolm 2006, 2009 Soulsby 2006). Also, while higher discharge events have been linked to groundwater upwelling they have also been linked to streamward flow around event peaks (thus reversing the flow direction and oxygenating the redds). It should also be noted that evidence for groundwater intrusion into the hyporheic zone is as yet limited, and probably a catchment-specific phenomenon controlled by underlying geology, soil type, land use and catchment wetness. This too would require empirical studies to determine hydrological response to catchment wetness relative to catchment typology.

Table 6.7 shows the suite of evidence collected which indicates the presence of groundwater in two of the three study sites investigated.

	Lugg Meanders 2008	*Lr Harpton 2009*	*Lyepole 2009*	*Lyepole 2010*
Hydraulic head	(no data)	✗	✗	✓
Dissolved oxygen	✓	✗	✗	✓
Temperature	✓	✗	✗	✓

Table 6.7. Summary of groundwater indicator results for the Lugg study sites investigations 2008, 2009 and 2010.

Indications of GW-SW interactions over the three field periods, as evidenced by temperature, hydraulic head and dissolved oxygen concentration data are strongest during periods of higher flow, and when the catchment is already saturated due to previous wet weather events. These conditions together create conditions of lowered habitat quality due to intrusions of hypoxic water into the egg zone.

Oxygen concentrations during the 2010 season at the 30cm depth fell below critical levels broadly reported in the literature (<~5mg/l) and for durations of up to 4 days. All planted eggs died during this field season. More severe oxygen sags were observed at this depth during the 2008 season – as seen in figure 6.31, with oxygen sags lasting up to 8 days during the mid-season spate event. Survival for this site was 12%. There is no precise consensus on the duration hypoxia tolerated by salmon embryos. Alderdice et al (1958) reported that eggs of chum salmon (*Onchorynchus keta*) could tolerate dissolved oxygen concentrations as low as 0.3mg/l for as long as 7 days, and silver et al (1963) found that Chinook salmon (*Onchorynchus tshawytscha)* could tolerate levels of 2.6 mg/l with mortality only occurring at 1.4mg/l. Other studies report much higher critical DO levels; Ingendahl (2001) reported a mean critical level of 6.9mg/l for brown trout and Malcolm et al cited (2003) a value of 7.6mg/l for Atlantic salmon. These findings add to the range of findings on dissolved oxygen tolerances of salmon embryos, and the 12% survival observed at the Lugg Meanders site is remarkable and outside any previously reported tolerance levels. One explanation for this may be the heterogeneity in incubation habitat and the spatial distance between the dissolved oxygen probe and the egg basket location (Malcolm et al 2006).

From the above data, it can be asserted that high frequency logging techniques are a valuable tool in sensing small scale variations within the redd zone; especially during high precipitation events, where traditional methods of redd site sampling may be too coarse in resolution to pick up these fluctuations. Manual sampling methods are further exacerbated by problems in accessing sampling sites for manual measurements during high flows, which may result in further data gaps.

Bringing this into context, the phenomenon of GW-SW interactions - especially during higher flow events, is a key factor to be considered in assessing overall habitat quality, but additional and possibly inter-related factors have also shown links with survival and habitat quality and any comprehensive study on a catchment should encompass all potential contributory factors to the intragravel habitat quality.

It is with this in mind we carried out a number of water quality tests on interstitial water samples throughout the 2009 season. Details of the tests are described in section 6.5 below.

6.5 Water quality 2009

As described in chapter 3, nalgene™ tubes were inserted on redd-building and placed at the depth of the egg zone adjacent to the egg baskets, and samples periodically retrieved during site visits. Water quality tests were carried out for the main nitrogenous compounds which may have detrimental effects on aquatic life (Kincheloe 1979, Daniels 1987).

Tests for water chemistry were carried out to investigate the concentration of nitrogenous compounds within the incubation zone, due either to endogenous waste products which were not being readily evacuated or to inputs from outside the redd zone.

Figure 6.33 below illustrates the concentrations and temporal variation in nitrate, nitrite and ammonia as measured throughout the incubation period. Red lines on the graph indicate the limit of safe known concentrations above which, mortality can occur.

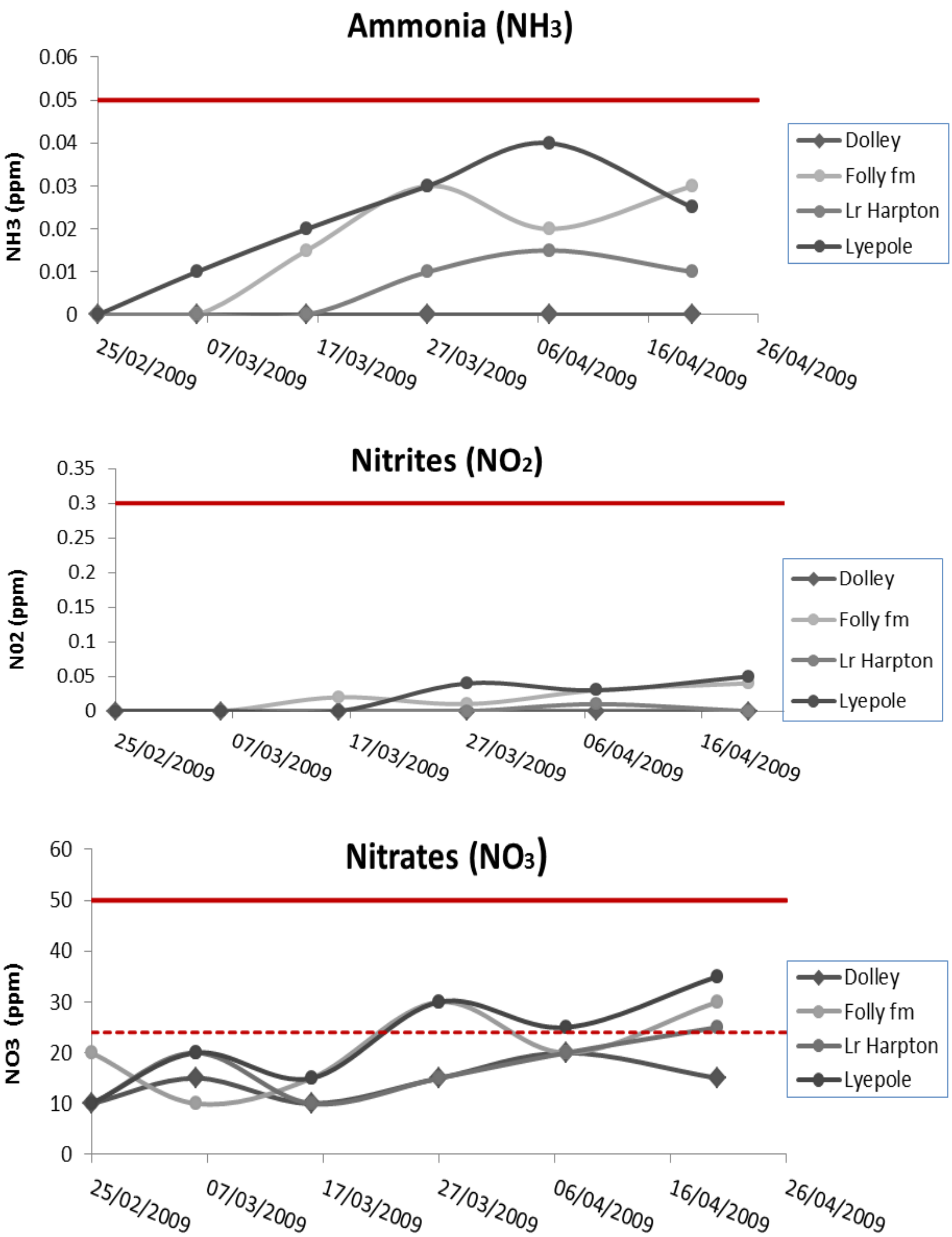


Figure 6.33 Egg zone concentrations of ammonia, nitrites and nitrates for each of the 2009 field sites. Solid red lines signify toxic levels to juvenile salmonids as reported in the wider literature. The dotted red line is the nitrate threshold level reported to be harmful in studies by Kincheloe (1979) and Mc Gurk et al (2006).

Test levels for ammonia remained low throughout the field season, reaching maximum levels of 0.03, 0.04 and 0.015 for the Folly farm, Lyepole Bridge and Lower Harpton sites respectively. No augmentation in ammonia levels was detected at the upstream site at Dolley Green over the period. Despite showing minor rises in ammonia over the incubation period, these levels are not thought to be detrimental to aquatic life and fish in particular (EPA 1984,1999, Randall 2002), so presented no cause for concern for the field season studied.

Nitrite levels were detected only at the Lyepole Bridge and Folly Farm sites where these was a minor increase over the test period. Levels however remained within safe known limits for stream biota and incubating fish eggs and larvae (Daniels et al 1987, Williams and Eddy 1989, EPA 2010). It has been shown that incubating salmonid larvae are more tolerant to nitrite concentrations than their adult counterparts (Bartlett and Neumann 1998, Kroupova et al 2005) and one study looking at brown trout alevin, showed their tolerance to nitrite levels of 3mg/l – a concentration considered lethal to adult trout.

Measures of nitrates for the same period generally showed a slight increase over the course of the incubation period, though levels remained within average values for a UK catchment, particularly one which drains an agricultural catchment area (Neal et al 2006).

However, previous studies regarding safe levels of nitrate in juvenile fish show variable results with differing tolerance levels reported by researchers. Some studies on closely related salmonids reported early-life stage salmonid embroyos and fry as among the most sensitive of species to elevated nitrate levels (McGurk et al 2006, Kincheloe 1979).

In a study by McGurk et al (2006) Lake whitefish fry (*Coregonus clupeaformis*) and Lake trout fry (*Salvelinus namaycush*) showed an initial negative response to a range of nitrate concentrations at levels of 111mg/l and 28mg/l respectively, but Kincheloe (1979) asserted that levels as low as 34mg/l for Cutthroat trout (*Oncorhynchus clarkii)* and 20mg/l for Chinook Salmon (*Oncorhynchus tshawytscha*) proved detrimental to developing fry.

If we consider the Lugg nitrate levels in the context of these studies, (indicated by dotted red line on the graph), it seems that levels detrimental to the health of developing alevins may have been reached. Survival levels do not however support this, remaining above 80% at all sites, but it may be reflected in sublethal effects that render the alevins less fit than they might otherwise have been under more optimal conditions.

A study on sublethal effects was carried out on the 2009 cohorts and results are presented and discussed in Chapter 7 Part II. The study looks at possible compromises that the alevins may have had to make in order to adapt to their environment and which then may be manifested in physcial, behavioural and physiological deviations from a healthy state.

However, the possibility that these levels may feasibly be much higher during high flow years should also be considered, due to a number of interrelated factors, Exogenous – such as the increased rate of overland nitrogenous contribution from agriculture (Jarvie 2000, Withers and Lord 2002, Green et al 2004, Lawler 2006), and endogenous- such as the build-up of nitrogenous waste products due to increased sediment infiltration and associated decreased intragravel flow velocities (Greig et al 2005, Hubner et al – in press).

So during higher flow years, as seen during 2008 where there were significantly higher levels of sediment deposition, a more significant impact on the water quality of the intragravel habitat may also be recorded. The deposited sediment may also be linked to increased DOC deposition and elevated BOD (Evans 2002, 2005, Morel et al 2009), or to sediment-bound phosphate or other contaminants.

All of these factors may come to play once a spate event is underway, and although evaluation of all of these factors were outside the scope of this study, quantification of the contributions and degree of impact that each may have on the incubation environment would be of future relevance for investigations. In the context of GW-SW interactions, no real relationship could be made with the data available from the 2009 season. The levels of nitrogenous compounds are seen to increase slightly as the season progresses, and this may be partly due to the decrease in discharge over the same period.

6.6 Summary

In summary, the result of investigations have shown that during higher flows, a combination of factors are at play which decrease the quality and viability of the incubation environment – These are: upwelling groundwater with lowered dissolved oxygen concentrations, increased sediment loads from agricultural sources (as evidenced by the fingerprinting study in Chapter 5) and increased sediment accumulation, resulting in decreased IGF and DO. Thus, evidence points to physically-based causes of poor quality incubation environment during higher flow years and improved habitat quality during low flow years. A generic conceptual model is provided below which highlights the factors which are seen to have an impact on incubation habitat quality in the Lugg catchment.

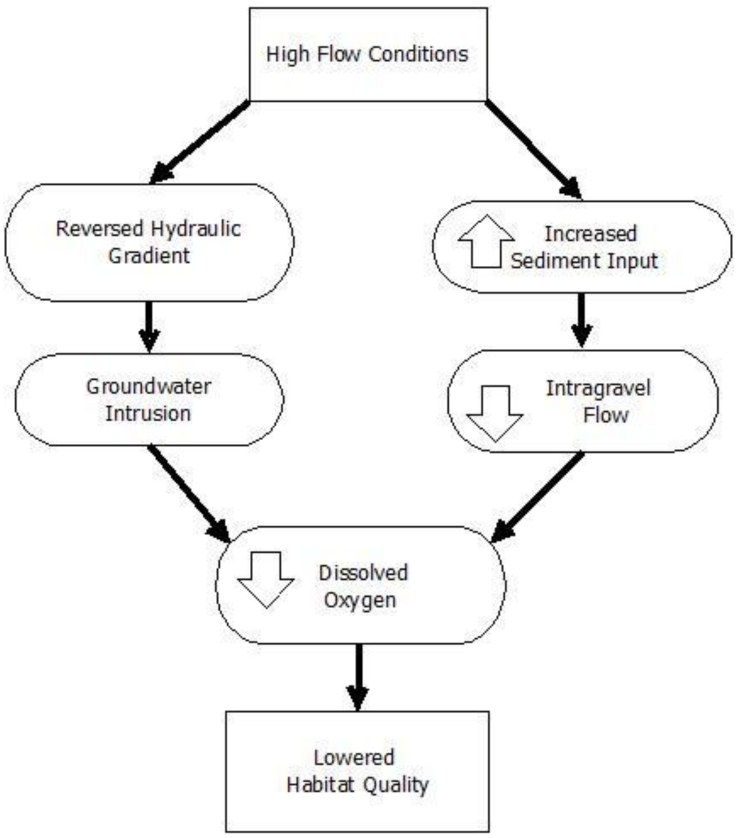


Figure 6.34. Generic conceptual model of the role of high flows on spawning habitat as evidenced by field investigations in the upper Lugg catchment

However, despite good survival to hatch/emergence, the incubation conditions may create sub-lethal effects that lead to poor survival in later life stages, and follow from the high flow year 2008 with moderate overall survival rates; this was considered a viable avenue to explore. Thus, tests for sublethal effects were carried out alongside the other field experiments and involved investigations into possible manifestations of sub-optimal habitat conditions which may be embodied by physical, behavioural and physiological deviations from those seen in alevins incubated in optimal environments. Chapter 7 outlines the experiment carried out on emergent alevins and details the results of each of a series of cohorts against a hatchery control.

6.7 Discussion

The field study involving the monitoring of artificial redds relative to survival, pointed towards the combined factors of dissolved oxygen and intragravel flow velocities – i.e. the oxygen 'flux' as the most important predictor of survival during the two field seasons 2008 and 2009. This is in agreement with a previous study by Grieg et al (2007) where oxygen flux was shown to be the best overall determinant of survival success in a study of 4 rivers. However, as discussed in Chapter 4 and as evidenced by Grieg (2005, 2007), sediment infiltration is highlighted as the main driver behind this causative factor. Additionally, in a study looking specifically at spate event interactions, Zimmerman and Lapointe (2005) reported fines infiltration correlated with reduced IGF after events of medium intensity. This is in agreement with the Lugg catchment findings where increased sediment infiltration and lower overall IGF velocities and lower dissolved oxygen levels were associated with lower survival during the 2008 high flow year, and opposing trend in DO, IGF sediment input and survival were found during the low flow 2009 season.

In the study looking at potential groundwater-surface water interactions at specific field sites, groundwater upwelling was found to be part of the main hydrological profile of the river, and the degree of streamward penetration of groundwater masses into the hyporheic zone depended on the magnitude of the event and of the pre-spate wetness of the catchment due to preceding events. This is in agreement with studies by Malcolm et al (2003; 2005) but further investigation into rest of the catchment should be undertaken to see if this low – dissolved oxygen phenomenon is an aquifer-related trend in areas where glacial drift is present or whether it could be occurring throughout the catchment.

The high resolution dissolved oxygen data from this part of the study highlights the degree of spatial and temporal variability within the egg zone. Apart from being of interest in itself, this has implications for how data collection for similar field studies might be improved upon given the availability of new technologies which allow in-situ long-term, high resolution sampling.

For example, the dynamic fluctuations detected by the continuous probe monitoring were not captured in the data collected through the periodic standpipe monitoring method. The failure to sample events lower down the catchment following prolonged high flows resulted in omission of important information on Redd zone DO dynamics which explain the poor survival at these sites

As such, the probes' detection of hypoxic periods during the 2008 and 2010 seasons would have resulted in more site points on Grieg et al's (2007) diagram being plotted nearer to or even inside the critical line, thus explaining the discrepancy between survival and apparent intragravel flow and dissolved oxygen levels during that season.

The implications of this are the possible effects of periods of hypoxia for incubating salmon and thus the relevance of sublethal effects on the emergent alevin (Silver et al 1963, Bjornn and Reiser 1991, Argent and Flebbe 1999, Shang and Wu 2004, Youngson et al 2004, Roussel 2007); where survival may be moderate to good, as found in the Lugg catchment, but where alevin may exhibit lowered fitness for later life stages due to stressful incubation conditions. This aspect is explored further in the following chapter.

Evidence collated from all parts of the field study; from assessments of sediment infiltration rates and associated DO and IGF studies to GW-SW interactions, and the probable water quality BOD /nitrate impacts, indicates that high flow events are key drivers affecting various mechanisms which in turn affect the intragravel environment. Identified mechanisms are described below.

1. Increased sediment infiltration rates associated with higher flow events, as described in chapter 5, influence dissolved oxygen concentrations and intragravel rates to reduce the overall habitat quality of the incubation environment.

2. Ground-water surface-water interactions have been shown to be more intense during and immediately after high flow events, with infiltration of groundwater of low oxygen content a feature of the falling limb of some spate events; particularly where catchment conditions are reaching saturation after periods of prolonged precipitation.

3. Increased turbidity is a common feature of high flow events, and turbidity is now seen as a key water pollutant in its own right and also now used as a surrogate variable for suspended solids concentration and as such is regarded as a primary indicator of pollution (Akan and Houghtalen 2003, Lawler et al 2006).

4. Water quality levels may decline in terms of increased N and P inputs due to entrained matter or sediment-bound compounds and delivery to the stream at times of peak flow (Jarvie 2000, Lawler 2006). Additionally, endogenous build-up of nitrogenous waste products due to increased sediment infiltration and associated decreased intragravel flow velocities (Greig et al 2005) may also play a part in reducing the overall quality of the interstitial pore water within the redd zone, although this was not evident within this study.

5. Scour, as mentioned in chapter 5 can prove deleterious to redds if discharges reach a point where scour exceeds the depth of the egg zone - thus excavating the embryos. At what point this occurs will depend not only on discharge, but also on the D50 and mobility of the substrate matrix.

From the above points and diagram 6.34, it is clear that discharge (Q) acts as a primary driver of many of the phenomena observed. However, from a catchment management point of view, an oversimplification of high Q as deleterious and low Q as beneficial to survival may mask much of the heterogeneity of response present in river systems. For example, low flows have been seen to be deleterious through other mechanism – e.g. & ref. While groundwater responses are likely to occur in susceptible catchments i.e. in those with higher baseflow indices. The magnitude of responses to higher Q will therefore be determined via catchment typology and underlying geology as well as land-use and connectivity. Consideration of catchment typology therefore is key to defining the magnitude and severity of impacts as driven by Q when establishing appropriate catchment management strategies.

Further evidence as to why an over-simplification of discharge as a driver of survival should be avoided is evidenced in table 6.8 below in which the potential responses to varying discharge conditions are listed. Low flow scenarios can also potentially create lower habitat conditions due to lowered water quality caused by the increased concentration of compounds (N P, synthetic chemicals) which may be harmful, increased river temperature (especially where salmonids are concerned) and accompanied by lowered stream oxygen content & Lowered IGF . Where the threshold of each of these phenomena are and where they compromise spawning habitat quality, will be catchment- specific and dependant on factors such as underlying geology, stream size, surrounding land-use and degree of cover.

Low Flows	**High Flows**
Increased nutrient concentrations	Increased sediment infiltration
Increased water temperatures	Decreased oxygen availability
Lowered water levels (drought) -Redd de-watering -inadequate spawning depths	Decreased water quality -entrained sed-bound contaminants
Decreased oxygen concentrations	Increased groundwater infiltration
Decreased intragravel flow velocities	Increased likelihood of scour

Table 6.8 Documented detrimental conditions which can occur during extremes of flow

For the Lugg, groundwater and sediment input responses rely on threshold values which are yet to be defined - requiring further monitoring of groundwater swell responses to catchment wetting and high flows events.

The effects of infiltrated sediment within the redd zone will depend also on the nature of that sediment, whether is it sediment with a high biochemical oxygen demand (BOD) signal, phosphate-bound or entraining other contaminants (Strmac et al 2002, Collins et al 2009).

There is evidence from the literature that sediment with a high dissolved organic carbon (leading to high BOD) can have important impacts on river systems and even go so far as to produce oxygen 'sags' during high flow events with high agricultural land derived sediment input (Kato et al 2009, Delpla et al 2011).

Having discussed the potential contributing factors to redd zone habitat quality, it would next be of most importance to differentiate the degree of influence of each of these, and define the relative contributions of BOD sediment (biogeochemical) and physical sediment-DO-flux effects from groundwater-surface water effects at each study site, and examine the variability of this within and between catchments. This would be a valid focus for future studies.

Of the factors exerting most influence during a given year on the Lugg catchment, it seems that there is some variability in habitat quality spatially and temporally, with an overall trend pointing to low flow years which reflect higher survival and higher flow years, lower survival.

6.8 Conclusion

Evidence from the field work undertaken indicates that the chief drivers of incubation habitat on the Lugg catchment affect oxygen supply to incubating eggs in two observed ways. Firstly, fine sediment impacts on intragravel flow velocities in turn negatively impact on oxygen supply within the incubation environment. Secondly, groundwater upwelling into the hyporheic zone sees lowered dissolved oxygen concentrations, sometimes for prolonged periods during the spawning season. Both of these mechanisms are exacerbated during higher flow years with increased incidences of sediment deposition and groundwater-surface water interaction.

IGV – DO 'flux' is the strongest determinant of survival in the catchment overall. The flux or supply of oxygen within the redd zone showed a stronger correlation with survival than either IGV, DO alone or any granulometric predictors. This supports the work of Grieg et al (2005) who found the oxygen flux parameter to be the best predictor of survival in 3 of the 4 catchments studied.

High frequency logging technologies are of key importance for future studies of this kind, as traditional lower resolution sampling methodologies risk oversight of the high frequency nature of redd dynamics, including redd sediment flushing, short-terms fluctuations in intragravel flow velocities and GW-SW exchanges.

In the study on possible groundwater interactions, which considered 3 specific sites on the catchment, 2 of the 3 exhibited multiple indications of groundwater influence. This is the first study of its kind to investigate this phenomenon acting in salmonid gravels outside a small highland burn, and highlights the possibility that these interactions may be more widespread than previously thought – acting both in low and higher order catchments.

There is a need for further investigation into the potential for upwelling and downwelling during higher flow years with associated spate events, using similar high resolution equipment at a variety of depths. Knowledge of the spatial variability in GW-SW interaction with in a catchment could help inform population rehabilitation efforts and restocking on this and other catchments.

In terms of sediment effects on spawning gravels, catchment management efforts can now be informed by fingerprinting studies which pinpoint sources and relative contributions of land-derived sediment as evidenced by the study described in chapter 5. Although not within the scope of this project, it would also be of interest to isolate the oxygen consuming substances in the infiltrated sediment, and define the BOD of the land derived sources as defined by the fingerprinting study.

Recalling results from the fingerprinting investigation of chapter 5, of the land use types looked at, agricultural inputs were implicated as the chief overall contributor - specifically during the higher flow year. Thus, with the potential of higher nutrient inputs during these years, catchment management efforts should prioritize mitigation of these effects during spate events. This is particularly pertinent now, in times of documented climate change impacts and the predicted likelihood of increased intensity events.

Chapter 7

7.1 Sublethal effects as indices of salmonid spawning habitat quality

7.1.1 introduction

Studies investigating the effects of sediment or other environmental factors which may negatively affect spawning gravels have with few exceptions used survival as an endpoint for demonstrating the quality of the habitat in question. However, there is growing evidence that emergent alevins may be stunted (Silver et al 1963, Argent and Flebbe 1999) or morphologically abnormal (Malcolm et al 2003, Youngson et al 2004), or that premature hatching or delayed emergence may be due to poor incubation environment (Rombough 1988, Kamler 2002, Roussel 2007).

Since salmonid juvenile stages are documented as being the life stage with highest associated mortality; a period during which critical adaptations to a new environment must be made, it follows that due attention should be given to assessing not only the developmental success in terms of growth indices, but also any other manifestations of chronic stress, which may diminish an organism's future fitness in its new environment. This is an aspect of salmonid spawning habitat investigations which has largely been overlooked.

Not only does stress have detrimental effects on growth, reproduction, immunological function and survival (Pickering 1992, Adams 1990, Ellis et al 2002) but the evidence of adaptive response to stressful environments can be detected first at the suborganismal level, and experiments targeted at key physiological stress pathways can report the earliest responses of an organism to a detrimental environment (Wedemeyer et al 1981, Adams 1990, Schreck 1990).

Physiologically-based studies have investigated some of the biological aspects of stress in fish – especially where application to aquaculture is applied. Chronic stress in some of these studies have been shown as being potentially manifest in juveniles on a number of levels which may ultimately have negative effects on later life fitness (Barton et al 2002, Portz et al 2006, Kondolf et al 2008).

Some approaches which have been used to quantify stress have involved measures of lipid content in Salmonids (Mc Farlane and Norton 2002), apoptotic (cell death) patterns in larval fish (Shang and Wu 2004) and lactate levels (Caruso et al 2005). Blood plasma glucose levels and the hormone cortisol are very commonly used indices of stress in fish (Pickering and Pottinger 1989, Barton and Iwama 1991, Caruso et al 2005, Davis et al 2010).

Additionally, research into the behavioural patterns of fish responding to a stressor has shown that behavioural response is reflective of several levels of biological compensation to stress and as such is an integrative measure of impairment and the ability to cope with life challenges (Schreck 1990, Barton et al 2002).

Figure 7.1 below highlights some of the potential avenues of investigation for chronic stress besides simple measures of growth, and some of the most documented in the field of physiological stress investigations are studies involving metabolic functioning using the biological indicator approach - a system which looked at measures of body fluids, cell tissues or other biotic indices that could indicate the presence and magnitude of stress responses.

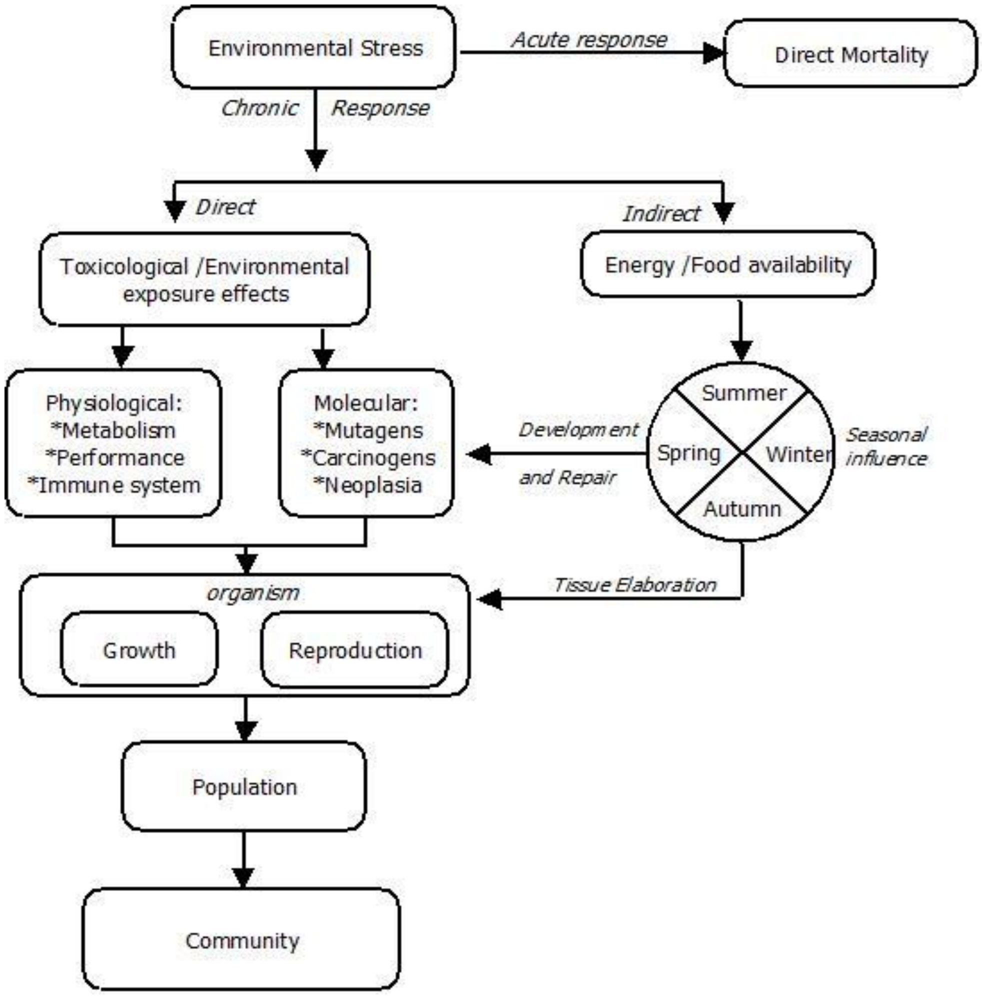


Figure 7.1. (adapted from Adams et al 1991) shows the potential response pathways of fish to exposure to environmental stress.

In terms of alevins likely response pathways to conditions in the Lugg spawning gravels, a chronic response to the egg zone environment would be expected in suboptimal conditions such as hypoxia or toxin exposure. The attended response to this exposure would be through metabolic stress reactions, possibly manifested in impaired performance or development.

The experiment for sublethal effects in this study consists of an integrated method - borrowing from physiological stress studies, behavioural analysis as well as a detailed gauge of developmental state. In this way a robust, multi-proxy test can be established for stress effects on several biological levels; and move away from measures of purely physical indices more commonly used in this field. Details on each of the three methods and rationale behind them are explained in section 7.2 below.

As expressed in section 1.9, Embryos can survive when dissolved oxygen is below saturation (above a critical level), but development can be affected such that the resultant hatchlings are abnormal (Silver et al 1963, Bjornn and Reiser, 1991). The working hypothesis of this study is that suboptimal oxygen levels act as a stressor which produce responses - expressed as changes in physiological condition, that deviate from the responses of larvae which developed in normoxic conditions. This then, may result in reduced overall health of the emergent alevins and with it, reduced chance of survival to adulthood (Barton et al. 2002, Fuiman 1994).

From an ecological perspective, fish of reduced performance – ie: growth, metabolism, immune response and predator evasion skills may affect overall population sustainability and ultimately, population size (Heintz et al 1999, Roussel 2007). Thus, it may be possible to establish a link between the effects of environmental conditions and population health and result in effective 'ecological death' – described in Murphy et al (2008) as;

> *'Ecological death is the phenomenon where animals are not overtly harmed by their environment, but exposure causes alterations in their behaviour or physiology such that the organism is unable to function ecologically as expected.'*

Three approaches were taken to test for sublethal effects on larvae during the 2009 field season. The rationale behind this was to account for effects on growth and developmental rate, on stress response to the incubation environment and on any subsequent deviant behaviour from the expected norms. The three approaches taken were developmental state, predator evasion response, and the stress hormone cortisol.

7.2 Methods

At the end of the field season, cohorts destined for behavioural tests were brought to a nearby hatchery at Cynrig and left to acclimatise to their new surroundings. Additionally, 10 Specimens of each field site sample were preserved in formalin for later inspection for developmental stage. Specimens were dispatched using a 0.40 ml^{-1} 2-phenoxyethanol solution, prior to formalin fixation.

For the hormonal tests, cohorts of 10 specimens from each site were retrieved at 10-day intervals throughout development to give detailed information on larval cortisol levels during development. The specimens were preserved via a 'flash-freezing' technique similar to that employed by Schreck (1990) to enable detection of in-situ levels of the hormone Cortisol. All larvae were derived from a single breeding pair in order to minimize natural variation in response.

7.2.1 Developmental state

As explained in section 1.9.1, the paper by Gorodilov (1996) on developmental stages with respect to temperature was used to gauge which stage the larvae at each site had reached.

For the three field sites a sample of 6 embryo/larvae were anaesthetised with 2-Phenoxyethanol and preserved in 4% formalin solution for later examination. In the laboratory, by means of a stereoscopic light microscope (Nikon SMZ1000), characteristics of key stages of development were observed for each of the cohorts from the three field sites.

The key characteristics observed were dependant on the stage of development according to the Gorodilov (1983, 1989, 1996) papers which describes the sequence of morphological changes from egg fertilization to yolk absorption in an optimal environment, with respect to temperature.

The time taken to form one somite pair (τ_s) – which is constant if all other factors remain stable, was used as the unit of relative age. These units are referred to as 'Tau units'.
Key morphological characters included the number of fin rays present in the caudal, anal, dorsal and pelvic fins. Additional markers of key states were the appearance of the adipose fin and the progressive appearance and deepening of melanophores in the skin.

Figure 7.2 Showing fin rays present in caudal and anal fins in a larval salmon. The newly developed adipose fin is present on the dorsal surface, and newly-formed melanophores are evident on the skin's surface (Magnification x20).

Descriptions of some of the key stages with their relative ages are described in table 7.1 below.

Key Characters of states	Main events and state characters	Relative age in 'T'	~ day at 5°C
10 Caudal fin rays	Posterior edges of gill arches are initially serrated; at the end of the state each serration develops into a short gill filament with 1 blood capillary growing into each~ 245. At ~250 blood begins to flow through them. Total length: 14.7 -15.2mm	245 - 250	80
13 caudal fin rays	Hatching begins at temps above 3°C. By time of hatching there is: 1: intensive pigmentation on dorsal surface of head (pigment cap); 2: vertical posterior margin of D; 3: initially spherical yolk-sac has become elongated; 4: head and snout part lengthening. Total Length: 16.5 -17.5mm	280 -285	91
Up to 20 Caudal fins	Peak hatching at temps of 1°C and below completed. Lepidotrichia appearing in D and A. Snout further lengthened. D becomes undercut posteriorly. Fanfold begins to widen in area of prosepective adipose fin. Weight of yolksac alone is 60 % of that of embryo & yolksac together. Total Length: 17.5 – 18.5 mm	310-320	101
Lepidotrichia in paired fins forming	Finfold in front of D greatly reduced. First row of segments appears on the caudal fins, dividing them into a proximal and distal part. Yolk sac weighs 35-40% of total weight. TL: 21 – 22mm	360	116
Formation of the fin outline in the post-anal fold	Posterior edges of the anal (A) and adipose fins appear. The number of melanophores increases on the whole body surface. Second row of segments form in caudal fin rays. Yolksac 35-40% of total weight . Total Length (TL) : 22.5 – 23.5mm	390	126
Absorption of the dorsal finfold	Finfold disappears anterior and posterior to D. The entire body is densely and evenly covered with melanophores. Three rows of segments in the caudal fin rays. Yolksac decreases to a great extent: its posterior end only reaches the pelvic fins, and weight is 25-30% of total wt. TL: 23-24mm	430	138
Parr marks begin to develop on anterior part of the body	Melanophores on sides of body concentrate in spots (parr marks). Finfold between anal and caudal fins has disappeared. Adipose fin complete. 4th row of segments appears in caudal fin rays -1st row of segments appears in D and A fin rays (470 ts) then 485 ts in pectoral fin rays	450	145
Appearance of parr marks also in posterior region	Parr marks appear on the caudal part of the body. Preanal finfold still remains. The fifth row of segments in caudal fin rays, the 2nd row in D and A fin rays, and 1st in pelvic fin rays. Yolksac 7-10% TL = 27-28mm	520	167
State of 'Button-up'	Preanal fanfold disappeared. Yolksac has been absorbed – only button-up scar remains. Pyloric Caeca begin to form on stomach. Segment per fin ray as follows: Caudal – 5; Dorsal & Anal - 3 each; Pelvic – 2 TL: 31 – 32mm	570-600	188

Table 7.1 Key characters of developmental states in Atlantic salmon embryos from the late eyed stage to complete yolk sac absorption, based on the system of interval identification of the early ontogeny of Salmo Salar as described by Gorodilov, 1996.

Using this system as a gauge of developmental state, an initial gauge of 'expected' developmental state was calculated according to the daily temperature fluctuations within each of the redd sites. This was based on the daily developmental increments (in Tau units) relative to the average daily temperature at each of the sites. For example, an average daily temperature of 11.3°C corresponds to a daily developmental increment of 7.717 Tau units. The sum of these developmental increments calculated over the entire incubation period will result in the expected value in Tau units.

Individual alevin specimens retrieved from the gravels were analysed according to the Gorodilov methodology and developmental states defined, with their accompanying Tau unit allocation. A comparison between expected and actual developmental states for each site was thus made possible, and any retardation in development due to sub-optimal environmental condition was evaluated.

7.2.2 Stress Hormone levels

Teleost fish exhibit primary, secondary, and in some cases tertiary stress responses (Wedemeyer et al 1990, Barton and Iwama 1991, Mommsen et al 1999, Barton et al 2002, Lankford et al 2003, Portz 2006). The responses specific to each stage are outlined in table 11 below. The primary stress response involves the release of corticosteroids (e.g., cortisol) from the interrenal tissue due to stimulation of the hypothalamic-pituitary interrenal (HPI) axis (Barton et al 2002). The release of other stress-related compounds; catecholamines (e.g.: epinephrine, norepinephrine) into the circulatory system also occurs as first response to a perceived stressor.

Primary Response	*Secondary Response*	*Tertiary Response*
Corticosteroids ⇧	**Glucose** ⇧	**Swimming capacity** ⇩
Catacholamines ⇧	**Lactate** ⇧	**Feeding & avoidance behaviour** ⇩
	Gill permeability ⇧	**Growth** ⇩
	Hydromineral balance ⇩	**Disease resistance** ⇩

Table 7.2. Stages of stress response observed in teleost fish.

The release of catecholamines into the bloodstream is rapid (Randall and Perry 1992), while cortisol synthesis has a temperature-related delay of minutes (Wedemeyer et al. 1990, Lankford et al. 2003). Sampling of individuals for stress responses requires a delay in that response so that the sampling procedure does not form part of the measured stress-response. Thus, measurements of plasma catecholamine are more difficult than corticosteroid measurement, which has an inherent delay of between 60 seconds and 3 minutes in larval salmonids (Schreck 2009 – personal communication).

Primary biological stress responses (in this case production and release of cortisol) can trigger secondary responses, such as increases in plasma glucose and lactate concentrations, heart rate, gill blood flow, metabolic rate, and decreases in plasma chloride, sodium, potassium, liver glycogen, and muscle protein in teleosts (Barton et al. 2002). Immune function can also be suppressed as a result of increased cortisol levels in the blood (Yin et al 1995; Ortuño et al. 2001).

With chronic stress (stress that persists over a long period of time), secondary responses may eventually result in tertiary responses, which include decreased growth rate, metabolic activity, disease resistance, and reproductive capacity, as well as altered behaviour and reduced chances of survival (Wedemeyer et al. 1990, Barton and Iwama

1991). The extent of the tertiary responses is thought to be related to the severity and duration of the stressor (Lankford et al. 2005).

In this study, whole body cortisol levels using a method developed by Sink et al (2007) were used as a gauge of chronic stress of the alevins while in the incubation environment. Four separate cohorts of 10 individuals were extracted from the gravels over the course of the incubation period, and cortisol levels measured by means of an enzyme immunoassay test (ELISA) (Barton et al 2002, Schreck 1990, Sink 2007).

7.2.2.1 Sampling

Over the course of the incubation period, four separate baskets were retrieved from the gravels at approximately 10-day intervals. A sample of 10 specimens from each retrieved basket was flash-frozen in liquid nitrogen and sample of that cohort were taken via flash-freeze from hatchery as a control. It was ensured that the retrieval time for either of these scenarios was <60secs, to obtain a valid cortisol measurement. If not, a subsequent sample was taken. Surplus egg baskets had been planted for this purpose.

During the season, samples of stressed specimens were taken as a positive, or stressed control from the hatchery in Cynrig, Wales. It is known that anoxia causes a positive stress response in fish, and this was achieved through a 30 second period of exposure to air. Sampling was then undertaken by the flash freezing technique at intervals of 10, 20, 30 and 40 minutes after the stress stimulus, in order to create a positive curve and enable peak cortisol response to be found. The positive controls enabled a perspective on the field-based specimens' cortisol levels and a context from which they could be assessed.
Samples of 10 hatchery-incubated alevins per basket retrieval were taken as a negative or 'unstressed' control.

7.2.2.2 Cortisol Extraction procedure

In the laboratory, extraction of cortisol was carried out by adaptation of the method by Sink et al. (2007) for whole–body cortisol extraction on golden shiners. The method involved an addition of vegetable oil to improve volume and results in better cortisol extraction efficiency. The flash frozen larvae were removed from storage at –20°C. Each fish was weighed, sliced into small sections, and placed into 3ml aliquots. 2 ml of phosphate buffered saline was added and the sample placed in a lab mixer for 60 seconds to achieve a homogenate. The contents were transferred to a 50-ml beaker, and 1 ml of PBS was used to rinse the remaining contents of the aliquot into the beaker. 5 ml of laboratory grade ethyl ether were added to the contents of the beaker. The contents of the beaker were then transferred to a 10-ml test tube. Two millilitres of ethyl ether was used to rinse the remaining contents of the beaker into the tube and the tube was capped. The tube was vortexed for 1 min to ensure mixing of the tissue with the ethyl ether for cortisol extraction. The test tube was centrifuged for 10 min at 3000 rpm to condense the tissue at the bottom of the tubes. The tube was then immediately frozen at –20°C to remove the aqueous phase and the unfrozen portion (ethyl ether containing cortisol) was then decanted into a 10-ml test tube. The ethyl ether was evaporated under a gentle stream of nitrogen for 2 hours, yielding a lipid extract containing the cortisol.
An ELISA test (Enzyme linked immunosorbent assay) for cortisol (Cortisol EIA Kit by Assay Designs #900-071) was carried out on individual samples from each of the cohorts to test for cortisol whole body cortisol concentration. Tests were run in duplicate to minimise error associated with test kit use. The test is a competitive immunoassay which involves binding of the fish extract on contact with an antibody specific to cortisol present at the base of each of 96 wells within a microtiter plate.

Individual fish extracts are inserted into each of the wells and allowed to react with the antibody present. Immediate addition of a conjugate after the samples incites a competitive binding, where the conjugate will fill any antibody site spaces available which were not already taken by the cortisol in the sample. The blue-coloured conjugate will give a chromogenic response via chromatographic readings, which is inversely proportional to the amount of cortisol present; ie: the higher the sample antigen (cortisol) concentration, the lighter the blue signal. The analysis data were evaluated with Dynex Revelation 3.2 software.

7.2.3 Behaviour

Behaviour is often used as an endpoint in environmental and toxicological studies because an animal's behaviour represents an integrated expression of its physiological response to its environment (Fuiman 2006; Murphy et al 2007). Predation challenges can represent an integration of behavioural and physiological processes, and provide insight to the effects of molecular and cellular changes at the ecological level. It has been found that fish that experience stresses may increase their susceptibility to predators (Cada 2003). More specifically, in a study by Portz (2007) juvenile Chinook salmon from treatment groups that demonstrated significant plasma constituent (cortisol) stress responses also showed a decreased maximum swimming and startle response performances.

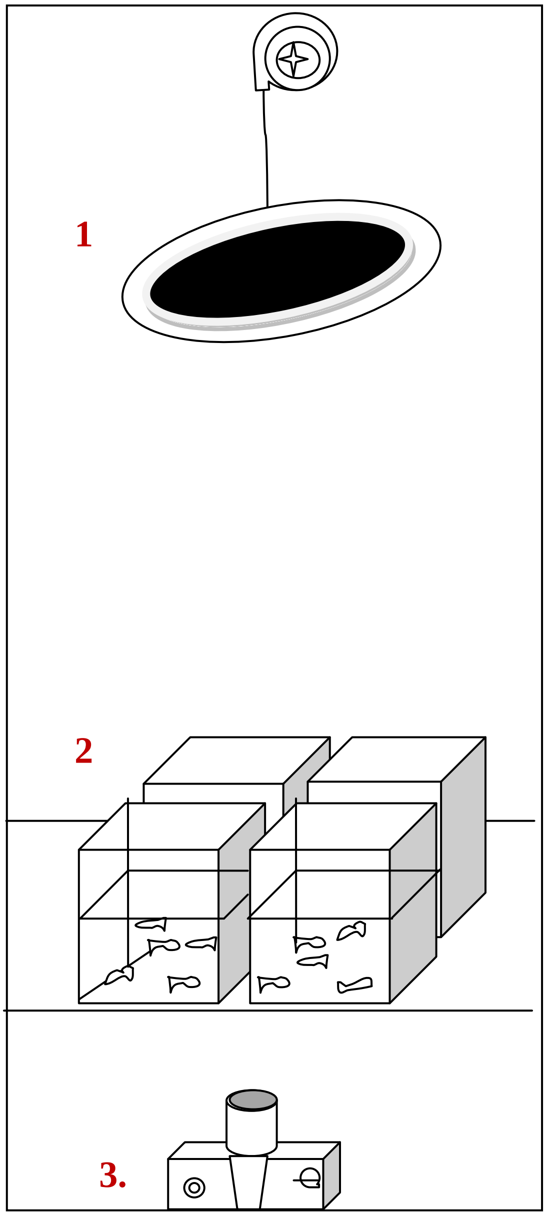


Figure 7.3. Diagram of the set-up for startle response tests performed on each of the sample groups.
1. Retracted 'startle device' on a free-falling pulley
2. 4 perspex tanks of 10cm³ with 1cm grid on base
3. High-speed video camera (300fps)

Fish utilize high speeds and burst swimming (eg: startle responses) to capture food and evade predation (Fuiman 1986, Hale 1996). Burst or fast-start swimming movements involves a rapid spurt of high-acceleration muscle activity from either a stationary or from a steady swimming state (Wakeling 2006).

The three kinematic stages in burst swimming behavior in fishes are. 1. The preparatory stage, where the fish bends into a 'C shape', induced by the simultaneous activity of muscle down one side of the body. 2. A propulsion stage, where there is a rapid undulation of the body and caudal fin to a position opposing that of the preparation stage. 3. A 'gliding stage' where the fish is propelled forward with a straight body position.

A strong 'C-shape' will ensure the fish has a higher velocity as it is propelled during stage 3 than a fish that only flexes a small amount before swimming. A fish suffering sublethal stress may exhibit a reduced C-shape response, resulting in a lower propulsion velocity and so, reduced chances of predator escape. (Wakeling 2006, Portz 2007).

For fish larvae, escape success also depends upon the ontogenetic state of the larva, since well-developed larvae are more likely to survive than poorly developed ones (Fuiman & Magurran 1994, Fuiman 2006).

Figures 7.3 and 7.4 detail the setup used to simulate fast start responses in the alevins is shown in fig 7.3 above, and involved four separate Perspex chambers situated above a slow-motion video camera. A high-contrast pulley device was suspended at a height of

1m above the tanks which, on release free-fell to a halt at 5cm above the tanks, creating the stimulus required to incite a fast-start response in the fish. Water in the tanks was kept to a depth of 3cm to minimize vertical swimming.

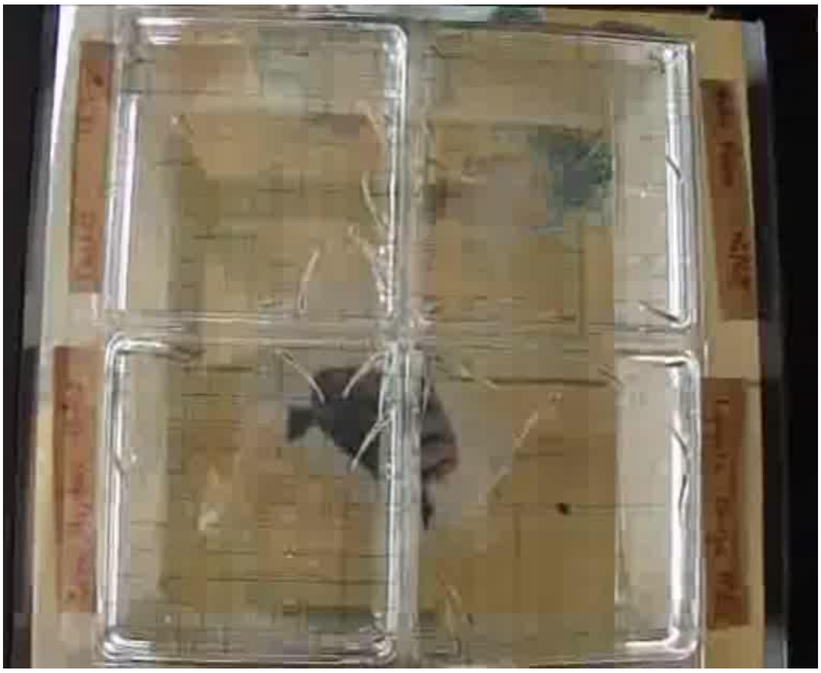


Fig 7.4. Digital image of startle test setup as viewed from below: A 1cm grid on the base of the Perspex chambers aids calculation of distances travelled by the fish – also in view. The 'startle device' is visible in its retracted state above the tanks.

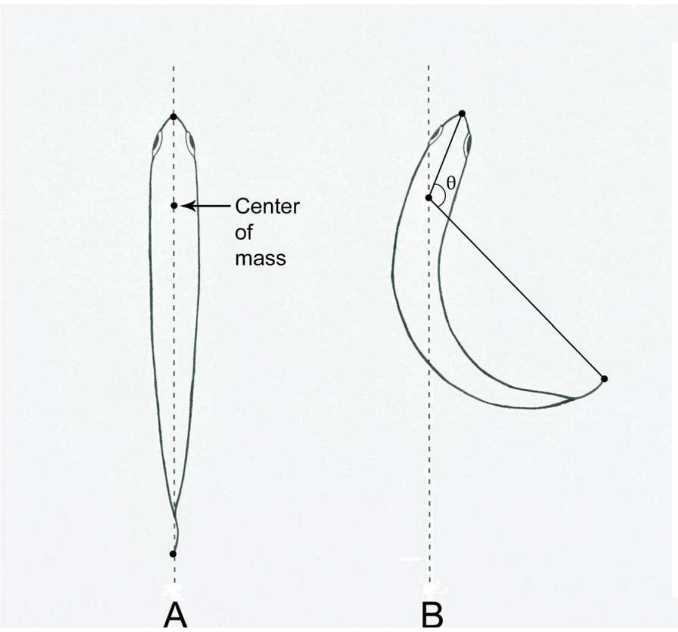


Figure 7.5. Diagram of the startle response of a juvenile Chinook salmon. (A) at rest and (B) at the preparation stage where the fish bends into a "C" shape. Angle ϑ is at the centre of mass and is measured as angle between a: the line from nose tip to centre of mass and b: Centre of mass to tip of tail. Angle ϑ is smaller when salmon are bent in a tighter "C" shape. (from Portz, 2007).

The frames from the slow motion footage (300 fps) were analysed with the Tracker© video analysis and modelling software (Brown 2008). Figure 7.28 below shows the analysis of trajectories taken by some fish specimens as response to a startle stimulus. The centre of mass was the point from which all measurements were made, and velocity was calculated according to distance travelled per frame.

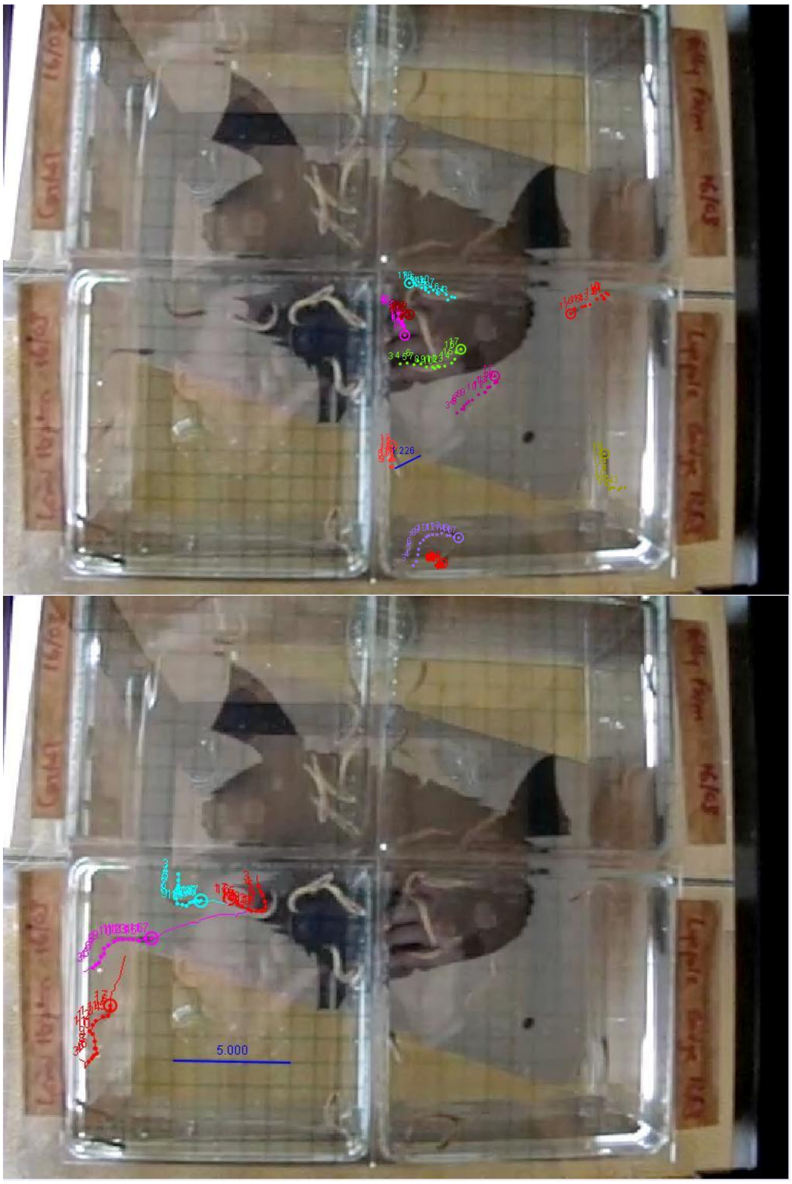


Figure 7.6. Example of video frame analysis using the tracker software. The centre of mass of each specimen was tracked through it trajectory following a startle stimulus, and measurements of response criteria were made, including C-shape curvature, mean velocity, max velocity and total distance travelled.

Two key measures of C-start performance; distance travelled by the centre of mass during the response period (cm) and maximum head velocity (cm/sec) were taken as the representative indicators for the tests.

For each of the 4 cohorts – i.e.: the three field sites and the control, five consecutive startle tests were carried out at intervals of 5 minutes. The performance measures were calculated on the basis of response over the 5 tests. Non-response was also recorded as percentage response per cohort.

Analyses of variance were carried out to examine the difference in response between the cohorts and ascertain significant differences between groups.

7.3 Results

7.3.1 Developmental state

The key developmental states defined during analysis of expected against observed specimens are displayed in figs 7.7 to 7.8 below.

The time taken to form one somite pair (τ_s) ; 'Tau units' are the standard measure of developmental state as calculated from average daily temperatures. Expected developmental state is plotted against observed state in figure 7.7 below and some differences are apparent.

The Lower Harpton site plotted closest to its expected developmental state of 532 Tau units with the Folly farm site plotting second at 514 to its expected 519 Tau units.

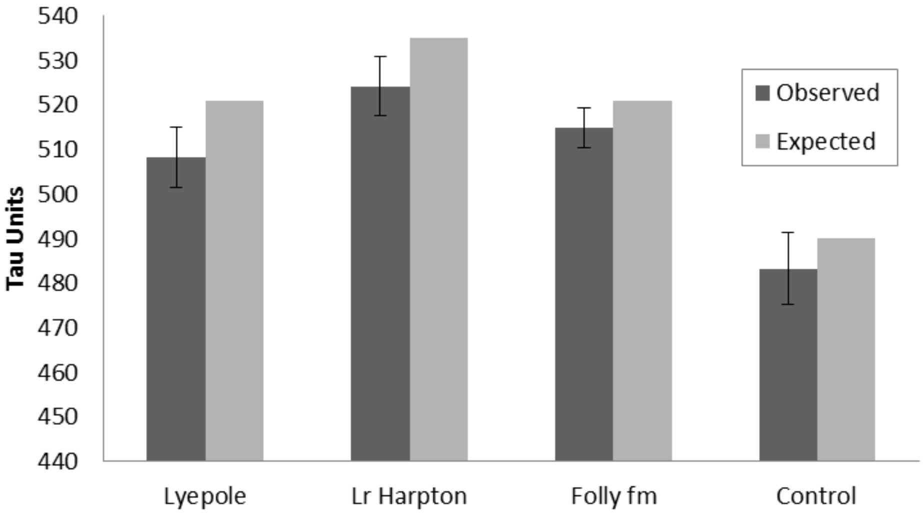


Figure 7.7 Developmental state of specimens from the 2009 sites and hatchery controls as expressed in Tau units, against the corresponding expected state as calculated from high resolution temperature history. Error bars indicate the standard deviations.

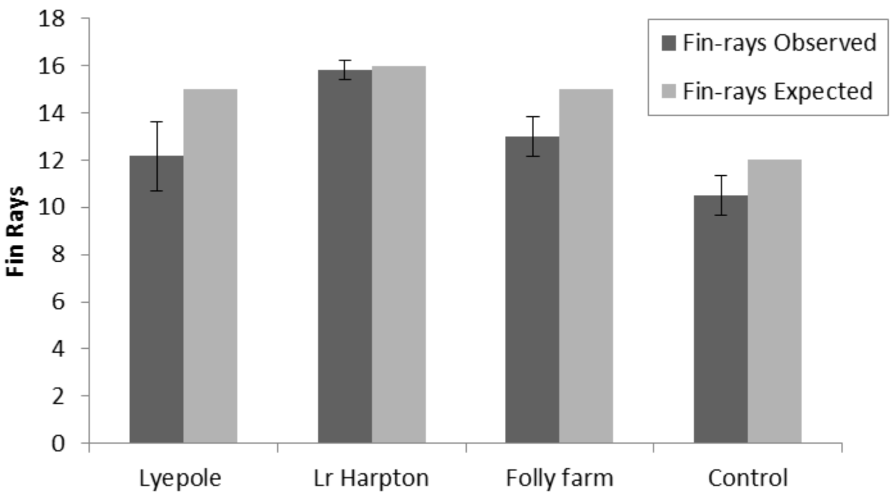


Figure 7.8 Developmental state of specimens from the 2009 sites and hatchery controls as expressed in fin rays present, against the corresponding expected state as calculated from high resolution temperature history. Error bars indicate the standard deviations.

Figure 7.8 shows observed versus expected fin-rays present in the alevins from all sites. Again, Lower Harpton site shows almost optimal conditions when compared with the expected state for that temperature history. There is a slight difference between the Folly farm and Lyepole sites, showing Folly farm to be slightly ahead and thus a more optimal incubation environment than Lyepole bridge.

It should be noted that there were some issues with the control, since its situation on another tributary meant that overall temperatures were lower than for the main Lugg and Arrow channels, and thus developmental states reached were not comparable to the field sites states. It should also be mentioned that on comparison of observed against expected states, the control specimens deviated considerably from expected values at the given temperatures, thus indicating a largely sub-optimal environment within the hatchery set-up.

Despite the lack of a reliable control, it was considered that comparison of specimens between each of the field sites might still reveal interesting results. Overall, on comparison of the three field sites, the upstream site at lower Harpton was shown to be the most optimal environment according to developmental state, with Folly farm second and Lyepole indicated as the most sub-optimal environment for these tests. Temperature history at Lyepole Bridge was similar to the Folly Farm site. The site Lower Harpton had a temperature history which was slightly elevated as compared to the other 2 field sites, and the control. Corroboration of these results was sought from the response of the other two sublethal proxies; behavioural and hormonal.

7.3.1.1. Retrospective study

Specimens which had been retrieved from the 2008 Lugg Meanders site an preserved in formalin were newly analysed in the context of this study; allowing an inter-annual comparison of developmental sites.

Since Lugg Meanders was the designated 'supersite' with high-resolution monitoring installed. The high resolution temperature data available here enabled analysis of developmental state against the Gorodilov scale as with the 2009 specimens.

10 specimens were examined by the above method and the results of this analysis is displayed against expected states for that temperature history in terms of Tau units (1) and bodyweight percentage relative to yolksac remaining (2) in figures 7.31 and 7.32 below.

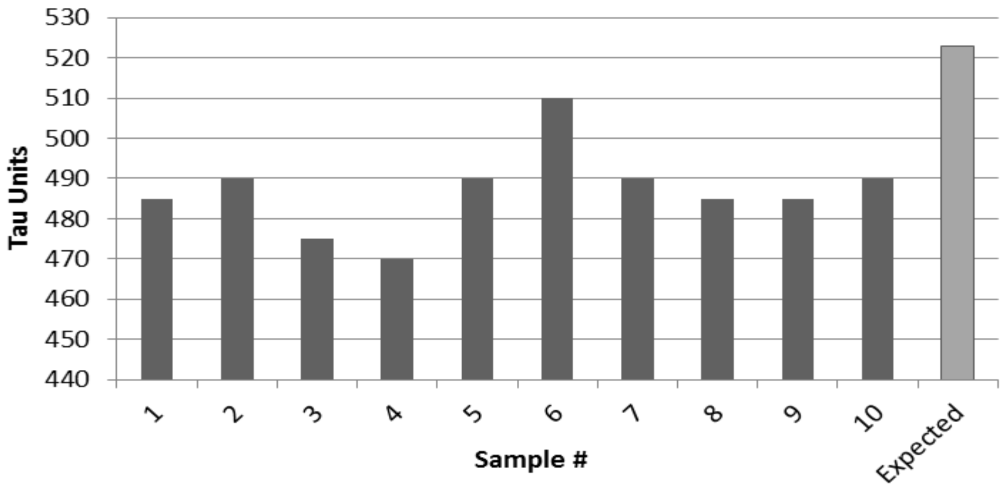


Figure 7.9. Developmental state of 10 specimens retrieved from the 2008 Lugg Meanders site , as expressed in Tau units, against the expected state as calculated from high resolution temperature history.

There is some variation in Tau units amassed between specimens for the 2008 Lugg meanders site. However all fall short of the calculated developmental state expected for the given temperature history. Average Tau unit of the Lugg meanders specimens is 492 as compared to 523 units for the calculated expected state.

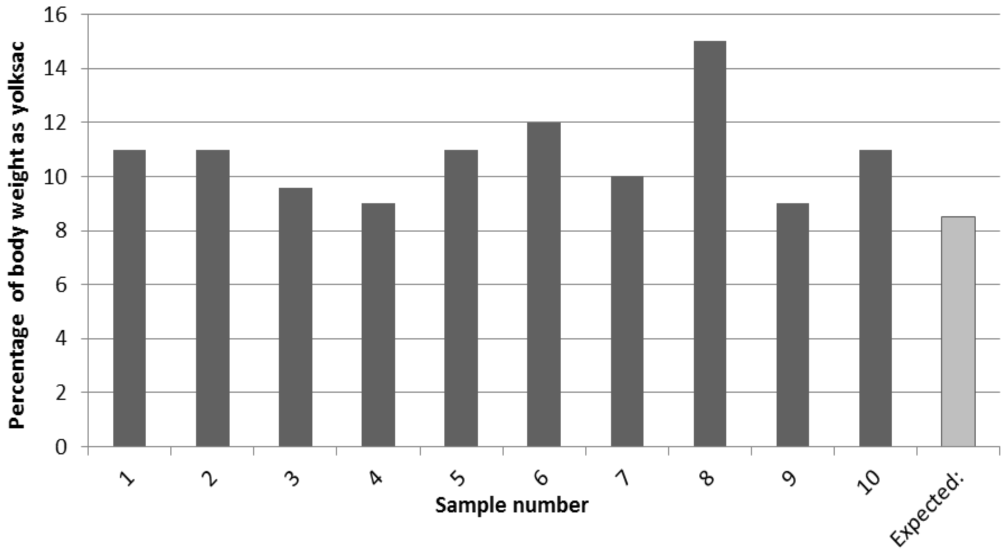


Figure 7.10. Developmental state of 10 specimens retrieved from the 2008 Lugg Meanders 2008 site, as expressed by percentage of body weight remaining as yolksac mass. This is plotted against the expected state for the site's given redd temperature history.

In larval salmonids, the yolksac mass to bodyweight ratio generally declines over the course of development as the yolksac's reserves are used up during the incubation period. This is used within the Gorodilov system as a means by which to estimate developmental state in an optimal environment, with respect to temperature.
The expected yolksac mass for the calculated Lugg meanders temperature history was 7.5% bodyweight. This compared with an average specimen value of 11.2 % indicates a lag between the Lugg site specimens and the expected yolksac absorption state for that temperature history.

Thus, both parameters indicate that the 2008 site did not reach expected levels of development using the Gorodilov method of state characteristics as defined by the temperature history, indicating the possibility of sub-optimal incubation conditions.

It is interesting to note how the degree of deviation from the expected state exceeds the deviations seen for the 2009 sites (1.8% compared to 7.1%), which may be related to the hydrological conditions experienced during the 2008 spate year. These results reflect survival indices for the two field seasons with the 2008 season showing poorer survival than the successful 2009 season.

7.3.2 Plasma Cortisol concentration

While there have been many studies looking at cortisol stress responses in adult fish of a variety of species, there are very few studies in the literature which look at typical cortisol concentrations during larval salmon development. Some recent studies in larval salmonids have shown cortisol levels to rise from hatching up to a peak at emergence time (Barry et al 1995, Nechaev et al 2005) however actual 'at rest' cortisol concentrations of larvae and alevins in these studies vary significantly.

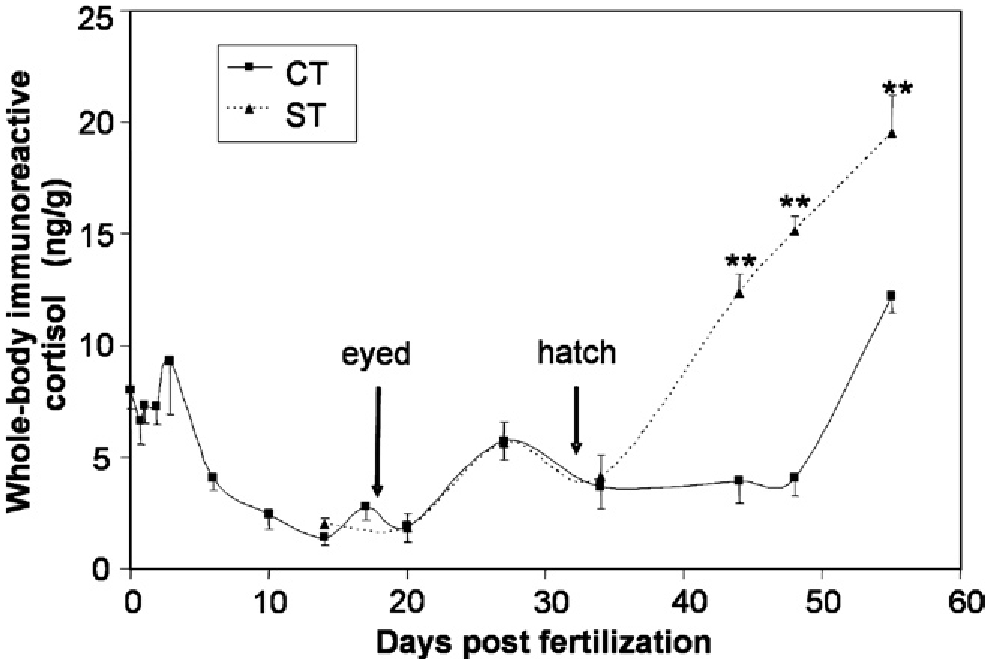


Figure 7.11. From Auperin and Geslin (2008) control (CT) and stressed (ST) cortisol levels in rainbow trout.

A study by Auperin and Geslin 2008 found the above responses in unstressed and stressed rainbow trout. In this study, resting (unstressed) cortisol levels are high at fertilization, and decline towards the eyed stage with a slight increased just before hatching. It is only at approximately 50 days post hatch that resting cortisol levels rise significantly. Stressed specimens however, showed a cortisol response as from hatching.

The Lugg study was carried out on 4 different cohorts at stages of approximately 5, 15, 25 and 35 days after hatching and overall, the corresponding cortisol response was within the range of those in previous papers mentioned above.

However, the Elisa tests showed no detectable quantities of cortisol in the first two cohorts – those first samples collected on the 16th and 27th of March 2009 levels being lower that the detectable limits of the test. Only the final two cohorts showed a detectable response.

Nonetheless, the final two cohorts did show an increasing overall cortisol concentration between the penultimate and ultimate samples (retrieved on 7th and 20th of April respectively). Figure 7.12 below demonstrated the concentrations found.

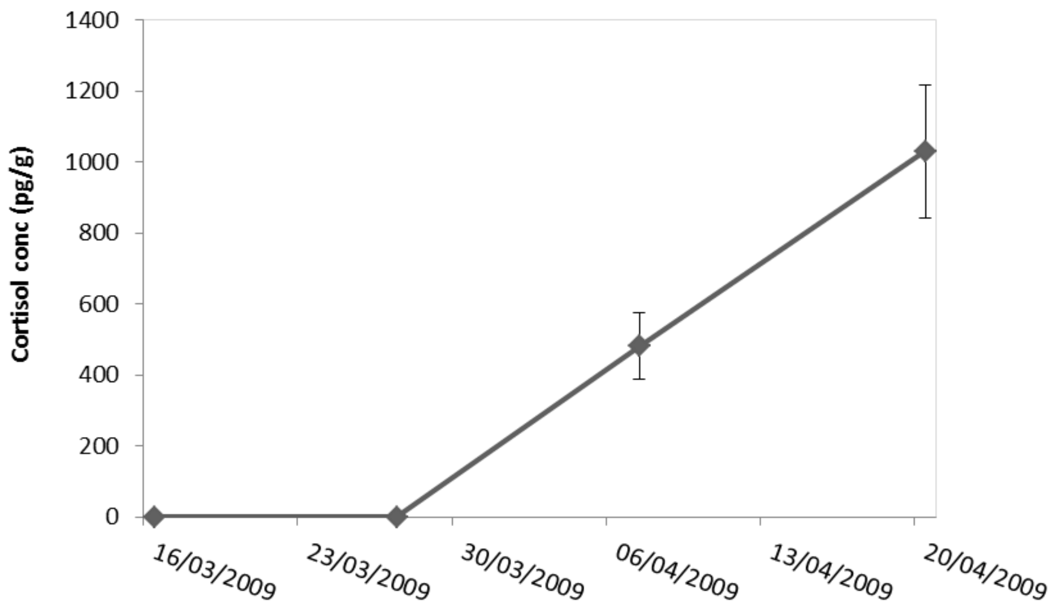


Figure 7.12 Average grouped cortisol concentrations based on samples retrieved from Lugg gravels. Error bars indicate the standard deviations.

In general, data suggests that the cortisol levels evident from the test cohorts were not very different from those of the control. Indeed the control registers in Figure 7.35 on the grouped cortisol concentrations as the highest overall concentration, with the Lyepole bridge site a close second. In order to put these results into context, it was thought that creation of a positive or 'stressed' control was the best way of providing a benchmark on high or low cortisol levels –especially given the wide variation of larval / juvenile cortisol stress levels reported in the literature.

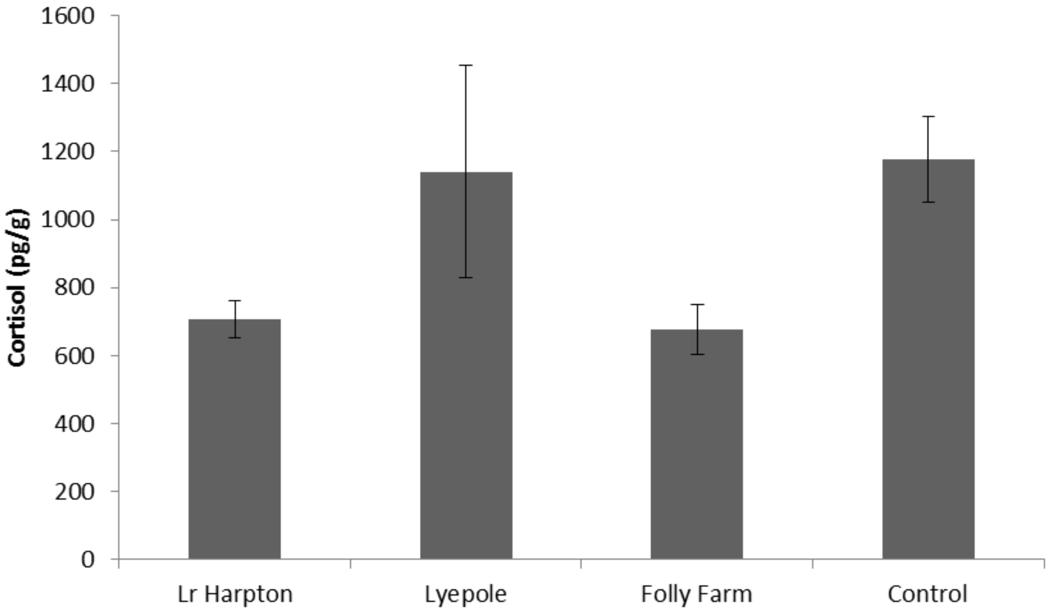


Figure 7.13 Average cortisol concentrations at each of the field sites against a hatchery control. Error bars indicate the standard deviations.

As explained in section 7.3.2 above, positive controls were created by means of exposure of specimens to air. Sampling of three specimens was then undertaken by the flash freezing technique at intervals of 10, 20, 30 and 40, 50 and 60 minutes after the stress stimulus. The tests were done in triplicate so that response curve could be constructed and enable peak cortisol response to be located.

Once this had been achieved, and a peak cortisol response after around 50 minutes predicted, a further, test using 10 individuals was undertaken using the same technique but testing only at 50 minutes after the stress stimulus. This enabled a fuller range of cortisol responses to be established for comparison with the field specimens.

Figure 7.14 below outlines the results of both the initial curve-defining trials and the later tests performed at the 50-minute post-stress window.

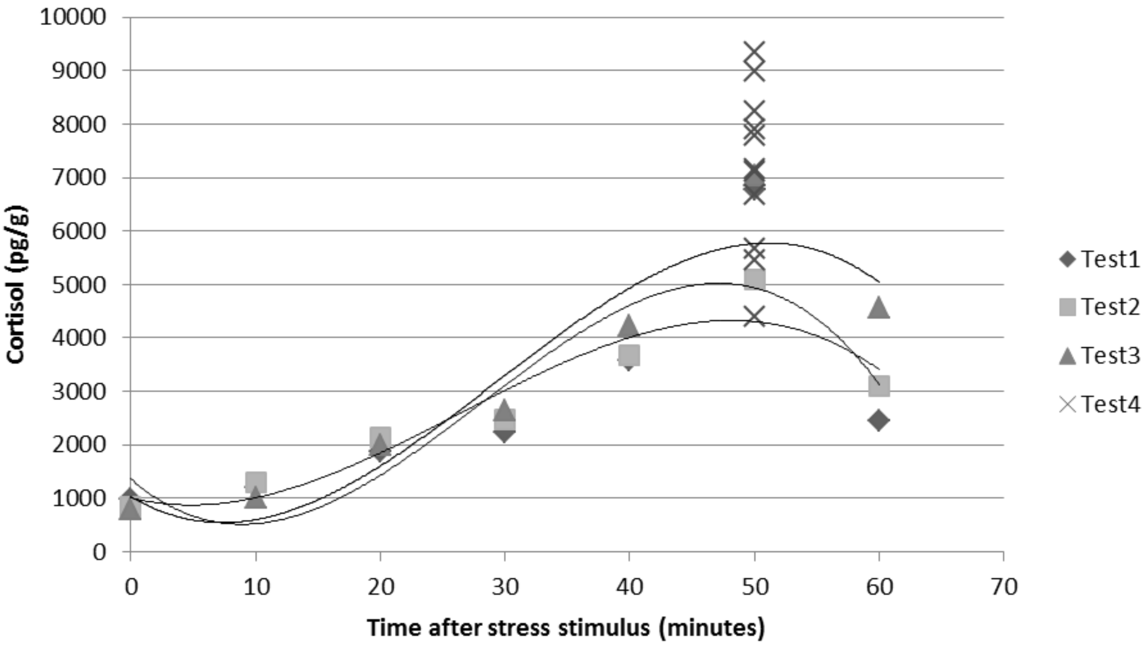


Figure 7.14 Positive controls showing the stress response at a variety of time intervals post stress stimulus. Test 4 shows the range of cortisol concentrations in 10 specimens sampled uniquely at the 50 minute post-stress time.

Figures 7.15 and 7.16 below show the results of the individual tests done on the cohorts for 7th April. All Error bars indicate the standard deviations.

Results for the earlier cohort - which studied larvae which would have been 4-5 weeks post hatch, show all field sites exhibiting lower cortisol levels than the corresponding hatchery control. Statisically, Anova testing showed all groups to be significantly different for the 7th April Cohort (F = 19.94, P = 0.001). For the cohort of 20th April however, only the Lyepole bridge site was significantly different from the other groups, which themselves could not be classed as significantly different

(F = 1.96 P = 0.152).

When compared to the positive control however, all groups demonstrate comparatively low cortisol concentrations; none of which reach the concentrations seen during the 50-minute positive control trials.

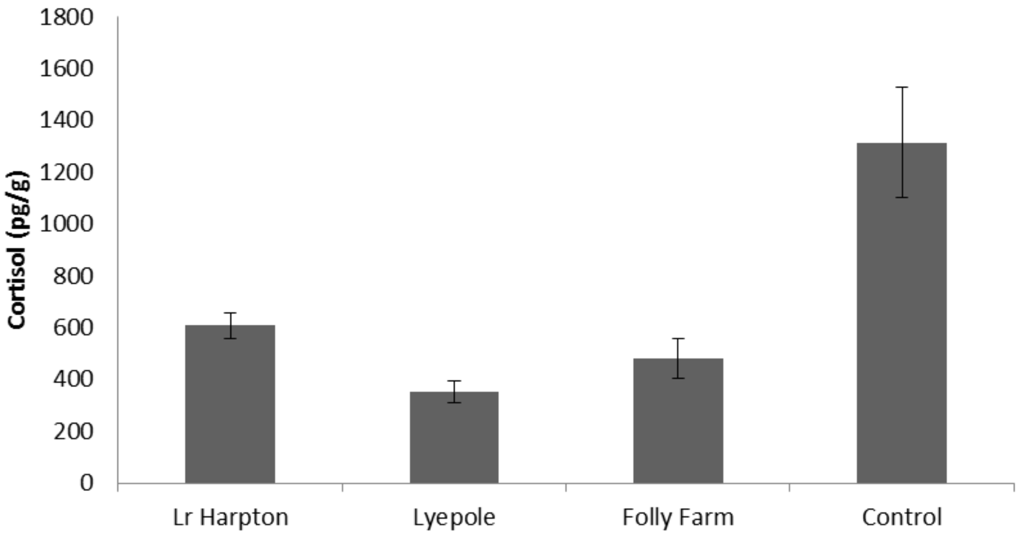


Figure 7.15 Average cortisol concentrations for the cohort of 7th April 2009

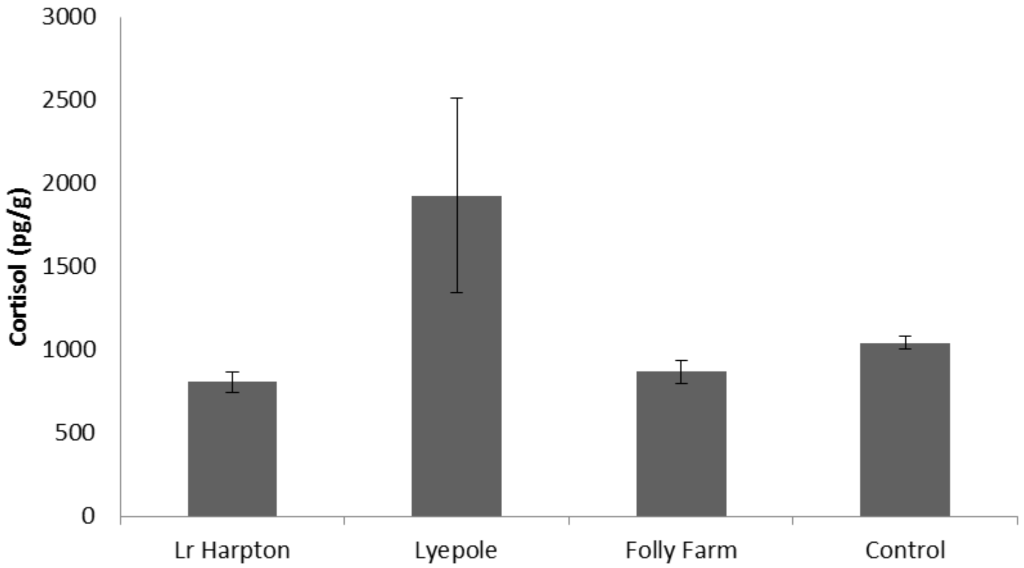


Figure 7.16 Average cortisol concentrations for final cohort of 20th April 2009

Cortisol tests on the final cohort- approx. 6-7 weeks post hatch shows a different pattern – this time with the Lyepole bridge site showing elevated cortisol levels in comparison to the other field sites and the control. Once again, however, these levels remain relatively low as compared to the positive control values.

The hatchery control concentrations represent the ‘at rest’ or unstressed conditions one might expect. With this in mind, the field site cohorts did not deviate significantly from the *at rest* state – with the minor exception of Lyepole site on the last retrieval which had slightly elevated cortisol levels.

Thus, the evidence for stress hormones suggests that the alevins were not stressed while within the incubation environment, with only minor indication that levels may have been slightly elevated at the Lyepole bridge site.

With this in mind, it is perhaps to be expected that in the 2009 dry year, low flow context, redd conditions might not be detrimental or stress-inducing. Indeed, survival during the 2009 suggests that conditions were excellent, with high survival rates overall. It is of interest however, that there were differences in cortisol response detected between both the cohorts and the sites, and this should be considered in the context of sublethal responses in higher flow or spate years, when conditions might not be so favourable. For example, during the 2008 or other spate years - which give rise to hypoxic events or other compromises in water quality, the cortisol response effects may be more severe.

7.3.3 Behavioural Test : Predator–evasion response

Through analysis of the slow motion video footage of the startle stimulus, two key measures of performance were taken as the representative indicators for the tests.
These were distance travelled by the centre of mass during the response period (cm) and maximum head velocity (cm/sec).

Average values of specimens from each field site over five separate startle stimuli are displayed in figure 7.17 below. Highest velocities were seen in the Lower Harpton cohort, with folly farm specimens reaching second fastest velocities overall.

The Lyepole bridge cohort had slightly slower maximum velocities, with the hatchery specimens scoring lowest on this performance criterion.

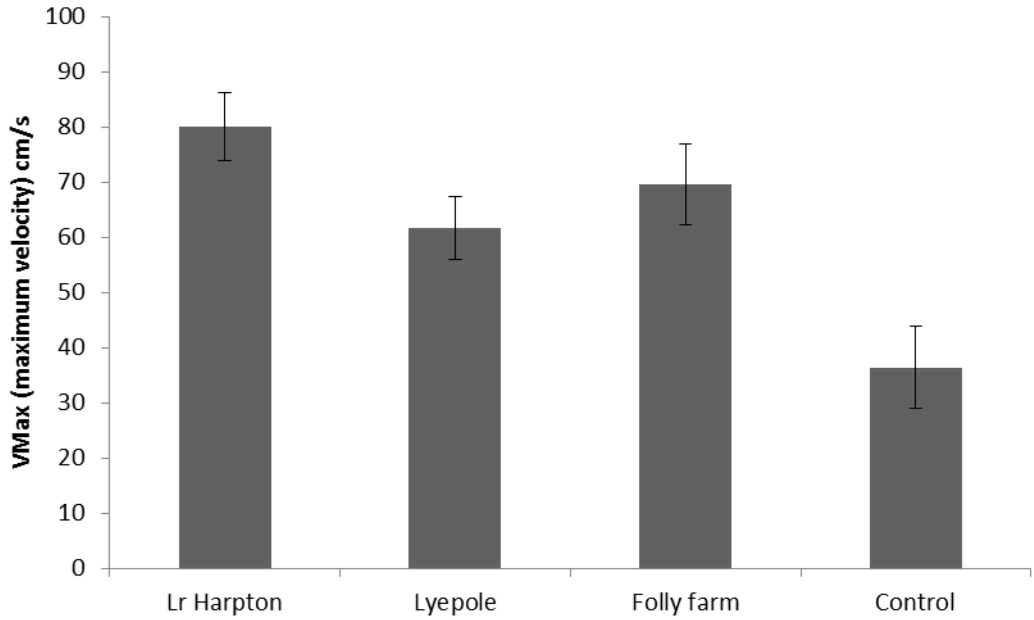


Figure 7.17 V-Max (maximum velocity) of alevins in response to startle stimulus for each of the 3 field sites and the hatchery cohort

On analysis with one-way Anova, response group mean values were found to be significantly different at the 1% level, with a p-value of 0.001.

	N	Mean	St Dev	
Lye	60	61.67	18.21	
LH	60	80.01	12.55	
FF	54	70.19	19.68	
Con	35	51.96	14.82	P =0.001

Table 7.3. Max Velocity values for each of the cohorts with corresponding standard deviations

Calculated values for distance travelled during the startle response are displayed in figure 7.18 Below. Again, Anova–based analysis of variance between response groups was shown to be significant at the 1% level.

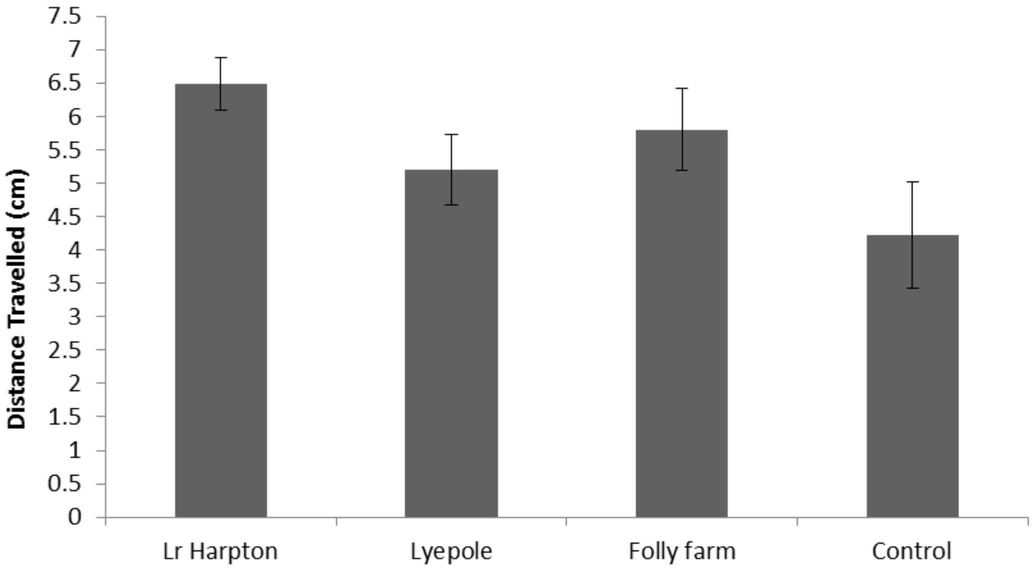


Figure 7.18 Distance Travelled by alevins in response to startle stimulus for each of the 3 field sites and the hatchery cohort

	N	Mean	St Dev	
Lye	60	5.206	1.058	
LH	60	6.488	0.778	
FF	54	5.802	1.236	
Con	35	4.226	1.106	P= 0.0009

Table 7.4 mean distance values for each of the cohorts with corresponding standard deviations

The values calculated in the two response variables were also dependant on whether an actual response was registered, which was not always the case. The number of non-responses increased with increasing number of startle stimuli interactions, and the number of individual responses per tests is displayed in tables 7.5 and 7.6 below.

This may be in part to habituation to the stimulus, which has been documented in previous studies (Cada et al 2003) where in the absence of any overt 'punishment' individuals learn not react to, or to reduce the intensity of their response to a particular stimulus.

Table 7.5 below summarizes the percentage response of cohorts over course of tests :

Tests	Lyepole	Lr Harpton	Folly Farm	Control
1	100	100	100	80
2	90	100	90	70
3	80	90	80	80
4	90	90	80	80
5	80	90	70	70
Average %	**88**	**94**	**84**	**76**

Table 7.5 Percentage response of cohorts over course of five tests

Additionally, because the tests were carried in small groups, there was the possibility that some individuals may react not directly to the intended 'startle stimulus, but to other fish. In order to eliminate this potential confounding factor, slow motion frames were examined for bi-modal distribution of response latencies. This enabled determination of threshold values where only those individuals reacting with in a set 'window' or number of initial frames (usually 4-8 frames) within a test, were included in the calculated response for that test (Alvarez 2010, Fuiman 2010 -personal communication).

Tests	Lyepole	Lr Harpton	Folly Farm	Control
1	70	80	70	60
2	70	70	60	60
3	80	90	80	70
4	60	70	60	50
5	80	80	70	70
Average %	**72**	**78**	**68**	**62**

Table 7.6 Percentage response of cohorts accounting for first responses and bimodal distribution

Results show that Lower Harpton performance values highest for both criteria and perhaps not surprisingly control values lowest given the differences in temperature history as explained in section 7.8.1 on developmental state above.

Behavioural responses were affected in terms of temperature history – as with developmental state, so that more highly developed individuals which had experience an overall higher temperature history could be expected to exhibit better overall performance values, which in the case of Lower Harpton, is true. This also comes to play when considering the lower performance and temperature history of the hatchery control specimens, which cannot really be relied upon in this case as a viable control for comparison with field specimens.

Due to time and resource constraints of the project, there was no further opportunity to carry out tests at a point when the developmental state was due to match that of the field site specimens. However, this approach could be utilized in future studies as a potential way around this confounding factor.

What is evident from this test is despite identical temperature histories for both Lyepole and Folly farms sites, significant differences between the sites for both performance criteria was shown. This is further supported by the other sublethal proxies - where developmental state in the Lyepole Bridge site lags slightly behind that of Folly farm. Additionally, the cortisol response in the later Lyepole bridge cohort is elevated with respect to all other sites – including Folly farm, which also agrees with the proposed hypothesis of Lyepole Bridge being the most suboptimal of spawning gravels during the 2009 field season. Figure 7.7 below summarizes this evidence.

Site	**Development**		**Behaviour**		**Cortisol**
	Tau units	Fin rays	Distance	Vmax	Combined
Lower Harpton	524 *(6.64)*	15.8 *(0.41)*	6.42 *(0.77)*	80.01 *(12.5)*	707 *(108.9)*
Folly Farm	515 *(4.47)*	12.5 *(0.83)*	5.80 *(1.23)*	70.19 *(19.68)*	675 (*146.9)*
Lyepole Bridge	508 *(6.8)**	12.2 *(1.47)**	5.20 *(1.06)**	61.67 *(18.21)**	1140.3 *(674.8)**

Table 7.7 Summary of sublethal tests results showing mean and standard deviations for each of the parameters tested. The poorest performance result for each criterion is indicated by an asterisk.

7.4 Conclusions

Putting the 2009 season in context, where dry conditions prevailed and survival as a whole was excellent, the combined results indicate that even in a good spawning year, sub-lethal stresses are detectable using this combination of methods. Furthermore, the results are supported by the physical measurements recorded at the study sites. Although high resolution oxygen data was not available for the three study sites, the amount of infiltrated fine sediment was highest at the Lyepole bridge site which is the site all sublethal tests indicated as the most suboptimal incubation environment.

This, compounded with the developmental evidence of more deleterious effects during the 2008 spate year, suggests that the use of tests for sublethal effects may prove to be a valid tool for assessing spawning habitat quality, particularly in rivers where there is a high variability in hydrology and other associated factors which may impact on the quality of the intragravel environment and subsequent health of incubating larvae.

Thus these approaches may have multiple applications in fisheries and conservation science. In terms of future research, the usefulness of defining sublethal effects at key points of development in refining predictive models of survival and future stage success should be considered. Some such models which may benefit from more detailed information of ontogenic physiology and development could be the SIDO model (Alonso et al 1996), Individual based models (Murphy et al 2007) and vitality models (Beer and Anderson 1997, Anderson et al 2000, 2008).

In their recent study on the physiological effects of Methyl mercury on fish using an IBM model, Murphy et al. (2007) showed that the results of their analysis of sublethal behavioural effects lead to parameterization of their matrix projection models which are commonly used to model fish populations, thus refining the link between toxicological effects and population modelling. This aspect of sublethal study applications is discussed further in chapter 8.

These approaches may also directly serve fisheries managers with accurate information on the viability of the fry produced within their catchment spawning gravels, and may also be of use to hatcheries involved in restocking and where optimum health of released fry is of importance in sustaining future populations.

Chapter 8 Conclusions

8.1 Factors affecting spawning habitat on the Lugg catchment

Factors affecting the incubation of salmon progeny were assessed in the context of government agency concern for declining salmon spawning habitat on the Lugg catchment. Initial catchment-wide investigations into sedimentation impacts on spawning redds served as a framework to evaluate spawning habitat quality on both spatial and temporal scales, and enabled assessment of whether other significant contributory or interlinked factors were also at work.

As demonstrated in Chapter 4, physical granular parameters were weak to moderate indicators of habitat quality on the catchment. Traditional gravelometric indices such as D_{50} and D_g did not predict survival for the Lugg sites. However, total amount of fine sediment of both <2mm & <63µm showed a moderate correlation with survival, while <63 µm portions on its own was a weaker indicator of survival overall. This indicates that while the clay & silt-sized portions likely have some effects on survival success as identified by Grieg et al (2005) and Zimmerman and Lapointe (2005), the cumulative effects of all fine sediment - particularly within the 2mm -63µm category, should be considered when investigating sediment – survival associations.

As seen from figure 8.1 showing compiled sediment-survival data from several UK studies, there is a predictive relationship evident, with sites of > 25% fines showing < 15% survival. A higher range of survival (between 0% and 90%) is evident in redds with low levels (<10%) of fines, suggesting that there may be other factors at play which contribute to the probability of survival.

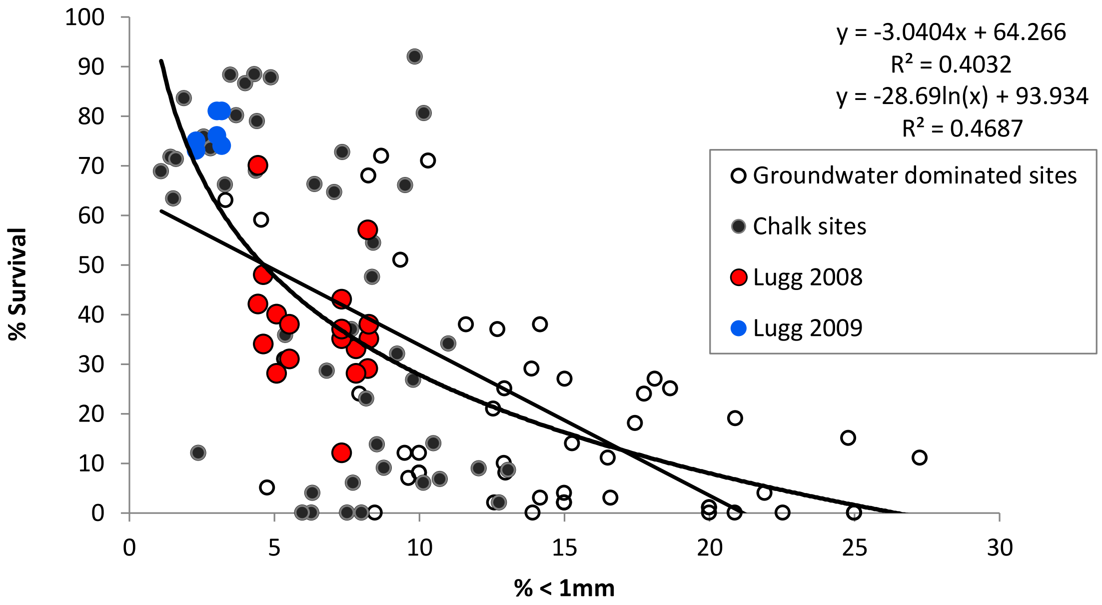


Figure 8.1. Linear and logarithmic relationships between fine sediment and survival from the Lugg catchment in the context of UK-wide studies. Data is compiled from Greig et al.(2007)—artificial redds; O'Connor, and Andrew (1998)—instream incubators; Julian and Bergeron (2006)—artificial redds; Heywood and Walling (2007)—artificial redds. The linear relationship shows an R^2 value of 0.4032 for all combined sites, while the log model shows a prediction of 0.4687

Spatial variability in sediment deposition between the study reaches was higher during the 2008 season with a range of between 12.3% and 24.9% in fine sediment deposition during the incubation period. For 2009 the inter-site variability ranged between 5.2% and 7.5%. Thus, both temporal and spatial variation is a feature of sediment dynamics on this catchment, and highlights the need for full coverage of a catchment when undertaking studies of this kind in order to obtain representative data.

Additionally, the possibility of scour & fill action is likely for certain sites – especially at Lugg Meanders where scour chains detected a significant lowering of gravel bed levels as the season progressed. Bedload impact sensors detected some bed mobility even during the low flow year in which they were deployed - 2009. This phenomenon should be explored further with respect to this catchment which experiences spate events and bed mobility, since studies have shown that survival may be jeopardized if gravels are scoured to or mobilized to depths equal to egg burial depth (Kondolf 1991, de Vries 2008). Although scour did not reach egg-burial depth during the 2008 season, more powerful spate events may cause more severe bedload scour and mobilization and the possibility of egg excavation. Other studies have found that scour increases the depth to which sediment intrusion can occur, thus exposing the incubation habitat to further sedimentary hazards (Sear et al 2008).

Although periodic sampling for redd sediment content allowed quantification of sedimentary trends throughout the incubation periods of 2008 and 2009, higher resolution sampling would provide insight into finer-scale sediment dynamics such as scour & fill action during high flow events. Such mechanisms may be at work during high flow times but remain undetected due to sampling limitations during high-flow events and the resolution of the sampling strategy. Automated bedload sediment–samplers may surmount this issue and allow detection of temporal variability of sediment intrusion over the entire period (Habersack et al 2001, 2010). Due to budgetary constraints this was not possible, but is something to consider for similar future studies in catchments of this type.

In terms of geomorphic indices, it is recognized that fine sediment is deleterious and remains a significant contributing factor to incubation success. Additionally, the potential for scour and bedload movement should be addressed and considered, and the possibility of bedload impacts (even in the absence of scour) should be looked considered for potential detrimental effects during the early and shock-sensitive embryonic stages of development (Crisp 1990, Jensen and Alderdice 1989).

8.1.1 Sediment sourcing

Land-use practices are intrinsically tied into the supply and nature of sediment delivered to a river system. From a catchment management perspective, sediment control strategies have been proposed as a means to effectively reduce the amount of fine sediment reaching water courses. However, the planning of such sediment control strategies has been hindered by the lack of reliable information on the source of the fine sediment reaching catchment spawning gravels (Walling et al 2003, Collins and Walling 2007).

Mitigation efforts informed by knowledge of the provenance of that sediment may facilitate catchment management efforts to minimise land-derived input due to anthropogenic activities. Minella et al 2008 demonstrated the effectiveness of land use management informed by source fingerprinting techniques where source contributions from field surfaces and unpaved roads decreased significantly post-treatment after management initiatives involving minimum-till cultivation and the maintenance of good crop cover were implemented.

Apart from the amount of fine sediment reaching spawning gravels, and the physically-based effects this may have on spawning gravels, the *type* of sediment, sediment-bound contaminants and the proportion of organics (Fertilizers, agricultural waste, animal faeces) can also potentially affect the quality of the incubation environment (Theurer 1998). Sediment-bound contaminants such as fertilizers, pesticides or other anthropogenic chemicals can act as toxins to developing embryos, and organics can alter the BOD of the sediment intruded into the redd system; an important consideration when looking at intensively managed agricultural catchments (Greig et al 2005, Haygarth 2005).

Sediment samples from each of the redd sites were examined to quantify the proportion of of organic sediment within the redds. Tests showed an average value of 2% which was considered low, and thus associated impacts on SOD/BOD likely not significant. Thus quantification of sedimentary oxygen demands was deemed unnecessary for this catchment. Some tests for nitrogenous compounds were carried out through redd water sampling during 2009, but in-depth chemical analyses of sediment-bound toxins were beyond the scope of this study.

The most important aspect from a catchment management perspective was to define the main contributing sediment sources in a spatial and temporal context.

The fingerprinting approach allowed determination of sediment source proportion for each of the field sites during 2008 and 2009 season, thus discrimination of which sites were most vulnerable to land-derived sediment input.

The results of the Lugg study showed that contribution of agricultural and channel bank sources were most important (32%-94% and 4%-65% respectively) and that agricultural sediment became by far the most dominant source during wet periods such as the 2008 field season. Since 2008 also produced the highest sediment yield within the redds, consideration of catchment management efforts toward mitigation of sediment mobility during wet weather periods would prove the most expedient way to reduce redd sedimentation during these times.

Estimates of land derived sediment from this study amounted to an average value of 70% (combined agricultural and woodland sources), with a maximum input of up to 94%.

Mitigation efforts informed by knowledge of agricultural sources susceptible during high flow events would help control input. Possible mitigation options such as riparian buffer strips, increased land cover during winter months, and decreased tillage, may help reduce yield in susceptible zones. Recent research efforts on mitigation options within a small subcatchment of the lower Lugg, has shown that the incorporation of post-harvest cereal straw residues may have a similar effect to using a cover crop – significantly reducing sediment runoff (Deasy et al 2009, 2010). Other research studies have found that reduction or interruption of tramline wheelings in fields reduces the connectivity to water courses Deasy et al 2010, Siligram et al 2010), and the use of riparian buffer strips or 'beetle banks' have proved useful intercepting sediment delivery (Withers et al 2006, Deasy et al 2010). However, it has been recognised that buffer zones are least effective during the winter season (Kay et al 2009), which is the maximum delivery period of sediment and nutrients (Uusi-Kämppä et al 2000) due to combinations of high local water tables, reduced infiltration capacities, and poor plant growth/cover. This then coincides with salmonid spawning time, so accurate appraisal of their use for mitigation with a view to improving spawning grounds, is necessary. That said, the importance of discharge effects in sediment delivery to water courses in certain catchments may always frustrate land-use treatments/ remedies through extremes of overland flow during spate events which can result in sediment delivery regardless of land-use or mitigation efforts in place. The natural dynamics of a system are dependant not only on landuse and strategies but on features such as catchment geology and soils and riparian slope.

Mitigation options will also depend on soil properties and physico-chemical characteristics, so locating the main contributing source areas; in a catchment specific context can be a useful means of defining which methods should be implemented.

8.1.2 Sedimentary controls on incubation

The effects of fine sediment on spawning gravels was the initial thrust of the investigation as commissioned by the funding body, and field investigations did indicate some correlation of increased fine sediment with decreased survival in the Lugg catchment. Additionally, analysis of the relationship of intruded sediment with intragravel flow and dissolved oxygen revealed the more complex interplay of sediment on IGF (intragravel flow) and dissolved oxygen held a stronger predictive relationship than simple sediment-survival indices. This support previous work carried out by Grieg et al (2007) who found that DO (dissolved oxygen) flux (the product of DO and IGF) through the redd zone was a better predictor of survival than any single variable – sediment, DO, or IGF alone (with R^2 values of 0.53, 0.38 and 0.48 respectively). Figure 8.2 below illustrates the oxygen flux – survival relationship for the Lugg sites with those of Grieg et al (2005) showing a linear R^2 value of 0.51 and a Pearson correlation value of 0.72 for the combined datasets.

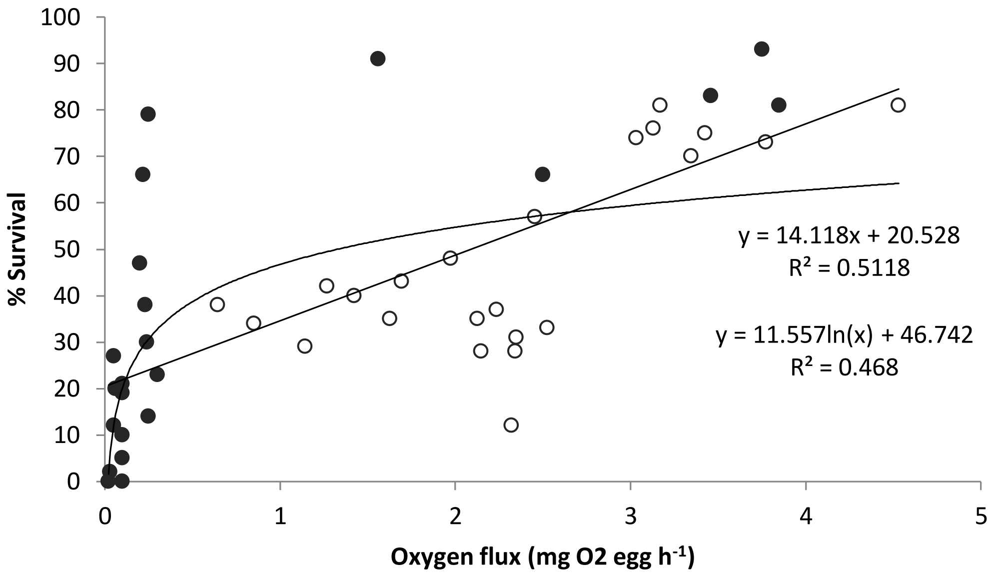


Figure 8.2. Oxygen flux – survival relationship for the Lugg sites (white points) plotted with those of Grieg et al. 2005 (black points).

A recent paper by Malcolm et al (2011) reported dissolved oxygen concentrations as the most important control on survival and that intragravel flow velocity had no relationship with survival on the catchment studied.

The study was undertaken on sites previously known to exhibit groundwater upwelling of low oxygen content, which would naturally act as a confounding factor for the relationship attributed to sedimentary controls on the rate of oxygen supply due to decreased intragravel flow velocities. Malcolm et al also reported that the application of their 'dissolved oxygen-(log) velocity' model to the data of other field studies improved the predictive capability for survival. This study was undertaken on one small highland burn catchment, and very little is known of the possible transferability of these findings to other geographical areas. As such, we lack crucial evidence from the wider literature from which the more numerous sedimentary controls studies have gained recognition.

In this study, the Impact of fine sediment accumulation on intragravel flow was highlighted by a moderate negative correlation, and results pointed to the interlinkage of controls on survival such as the IGF-Oxygen–Sediment interaction effects as highlighted by Greig et al (2005, 2007). However, the moderate nature of these correlations indicates that other factors may play a part in the fate and viability of incubating embryos. Also, high-resolution data from both the 2008 and 2010 supersites revealed low dissolved oxygen troughs which remained unexplained by sediment infiltration data, and required further investigation.

8.1.3 Groundwater- Surface water interactions

Rationale for looking at GW-SW interactions stems from the above observation of only moderate correlation of the sediment- survival mechanism. Other studies have found that their investigations into sediment relations with dissolved oxygen concentration were uncorrelated (Peterson and Quinn 1996, Ingendahl 2001, Malcolm et al 2004). In their study on survival to emergence of natural redds, Peterson and Quinn (1996) did not find a significant correlation between dissolved oxygen in egg pockets of chum salmon and the quantity of fines in freeze cores. Similarly, Ingendahl (2001) found a significant correlation between a series of sediment parameters investigated (Dg, D50, Fredle index) but no relation of these to dissolved oxygen levels within the redds.

One new avenue of research has explored the possibility that some of the variation in dissolved oxygen levels encountered and not explainable by sediment parameters may be influenced by groundwater-surface water interactions within the hyporheic zone, and at a depth that may affect incubating salmonid eggs. The investigations stemmed from hyporheic zone research where the groundwater bodies were found to have differing characteristics, with groundwater often defined by low dissolved oxygen levels (Fowler and Death 2001 , Boulton et al 1998). Further investigation into this phenomenon has revealed that in the interaction between these two water bodes is seasonal, dependent on discharge patterns and regulated by the upward force of baseflow and the downward force of advecting surface water (Fraser and Williams, Soulsby et al, Malcolm et al).

Studies on these boundary layer interactions relative to salmonid spawning gravels (Soulsby et al 2001, Malcolm et al 2003, 2004, 2009 Youngson et al 2004) have highlighted the detrimental effects of groundwater of depleted oxygen content on developing salmonid embryos.

Built on these findings and GW-SW theory from studies undertaken over the past 20 years generally, the Lugg study investigated the possibility of low-DO groundwater intrusion into the egg zone as another possible cause of decreased incubation habitat quality.

Results indicate that groundwater upwelling is part of the main hydrological profile of the river, and the degree of streamward penetration of groundwater masses into the hyporheic zone depended on the magnitude of the event and of the pre-spate wetness of the catchment due to preceding events. These findings broadly concur with studies by others (Soulsby et al 2001, Malcolm et al 2003, 2005, 2009) and lend support to the few studies currently available on this topic, thus broadening the knowledge base for catchment GW-SW interactions and their effects on incubation habitat.

Site	Girnock burn	Lugg M	Lyepole	Lr Harpton
Stream order	3rd order	4th order	4th order	3rd order
Catchment area	$30.3 km^2$	$257.7\ km^2$	$231.4\ km^2$	$56.9\ km^2$
Gradient	$28.9m\ km^{-1}$	$8m\ km^{-1}$	$6m\ km^{-1}$	$20m\ km^{-1}$
Altitude	400m	81m	122m	174m
Mean discharge	$0.52\ m^3\ s^{-1}$	$4.64\ m^3\ s^{-1}$	$4.47\ m^3\ s^{-1}$	$1.11\ m^3\ s^{-1}$
Stream width	1 – 3m	17m	12m	6m
Groundwater detected	✓	✓	✓	✗

Table 8.1 Summary of field site locations which have been the subject of GW-SW investigations.

Previous studies of this kind in relation to salmonid spawning habitat have been carried out of small upland streams. This study extends the evidence for groundwater-surface water interactions into larger rivers, and at spawning sites further downstream than previously observed.

8.1.4 Sublethal effects

Despite moderate to good survival indices on the Lugg catchment, there are data to suggest that sublethal effects can still jeopardize the chances of survival into the later life stages, via reductions in fitness and thus on successful recruitment within the catchment (Silver et al 1963, Chapman 1988, Youngson et al 2005).

The higher resolution nature of the 2009 study enabled assessment of influences which may not overtly kill embryos but cause sublethal effects. However, in context, this was a year when survival was excellent and no major high flow events occurred. Nonetheless, the combined laboratory test results indicated that even during a good spawning year, sub-lethal stresses are detectable using this combination of methods. Furthermore, the results are supported by the physical measurements recorded at the study sites: expressed as differences in, sediment infiltration and egg zone water quality results.

The study showed that even small differences in habitat quality may be reflected in physiological differences in alevin cohorts from different environments. The study has also shown that a multi–proxy approach to sublethal investigations provide a robust measure of alevin health and demonstrated some possible experimental avenues for further tests.

The 2009 results, compounded with the evidence of more deleterious effects during the 2008 spate year – as seen from the retrospective developmental state comparisons, suggests that the use of tests for sublethal effects would be a valuable tool in assessing spawning habitat quality, particularly in rivers where there is a high temporal variability in hydrology and other associated factors which may impact on the quality of the intragravel environment on a and subsequent health of incubating larvae.

Approaches such as demonstrated in this study may thus have useful applications in fisheries and conservation science, since – as stated by Barton (2002) 'an appreciation of the factors that affect the magnitude of physiological changes caused by stress in fish is important design of effective biological monitoring programs'. This usefulness can then extend from biological monitoring to catchment management objectives.

The usefulness of defining sublethal effects at key points of development in refining predictive models of survival and future stage success should be considered. Some such models which may benefit from more detailed information of ontogenic physiology and development could be the SIDO model (Alonso et al 1996) Individual based models (Murphy et al 2007) and vitality models (Beer and Anderson 1997, Anderson et al 2000, 2008). This is discussed further in section 8.1.5.

In their recent study on the physiological effects of Methyl mercury on fish using an IBM model, Murphy et al (2007) showed that the results of their analysis of sublethal behavioural effects lead to parameterization of their matrix projection models which are commonly used to model fish populations, thus refining the link between toxicological effects and population modelling.

These approaches may also directly serve fisheries managers with accurate information on the viability of the fry produced within their catchment spawning gravels, and may also be of use to hatcheries involved in restocking and where optimum health of released fry is of importance in sustaining future populations.

8.2 Implications of study results for modelling spawning habitat

The new evidence from the Lugg study regarding the multiple causes of degraded habitat quality means that current modelling capabilities for spawning gravel processes are inadequate due to omission of a number of controlling factors – and whose degree of influence can also be catchment specific. Figure 8.3 below highlights the chief factors known to have an effect on hyporheic habitat and how in the context of salmonid habitat quality some of the drivers and feedback loops have been incorporated into habitat models; however many gaps remain, and even in the context of Lugg catchment alone, gaps in modelling stressor-response relationships are clear.

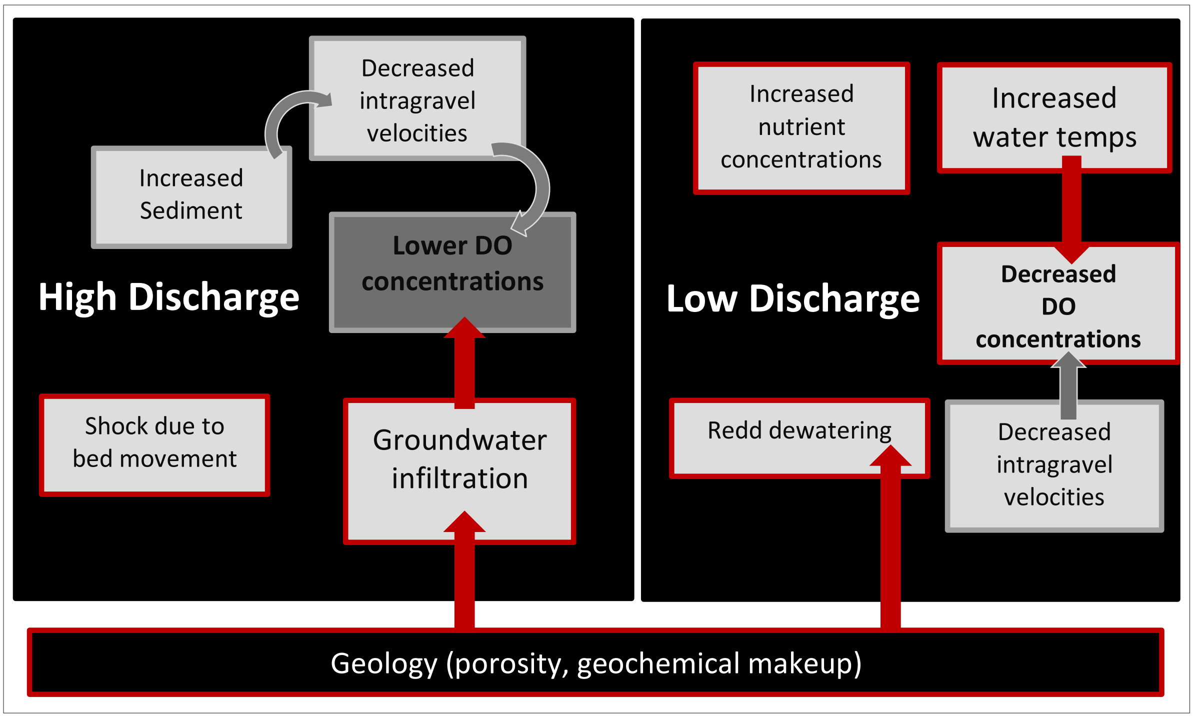


Figure 8.3 Conceptual model of the chief factors and processes negatively affecting survival during contrasting discharge conditions. Those highlighted in red are not encompassed by current models. Black boxes and grey boxes signify primary and secondary drivers of incubation habitat respectively.

Two current models which attempt to simulate spawning habitat have been proposed as offering the potential to predict spawning habitat quality under a range of hydrological conditions. These are the SIDO (Sediment Intrusion and Dissolved Oxygen) model (1996) and the Wu model (2000).

The SIDO-UK model (Carling et al 2003) which is based on the original model by Alonso et al (1996) which was designed for use on North American streams is currently being developed for use with UK-based catchment data. SIDO-UK is a process based model which incorporates physically-based processes affecting fine sediment intrusion and dissolved oxygen transport in spawning habitat.

The aim of the model is to quantify the relationship between the survival of native salmonid species and the quality of their environment within gravel-bed rivers by simulating the movement of water, sediment and dissolved-oxygen through the stream-redd system.

The principle parameters are: (i) bed particle size and composition; (ii) sedimentary material available for deposition; (iii) interstitial dissolved-oxygen concentration; (iv) interstitial flow rate, and (v) the water temperature. Figure 8.4 below highlights the basic input and output parameters produced by the model.

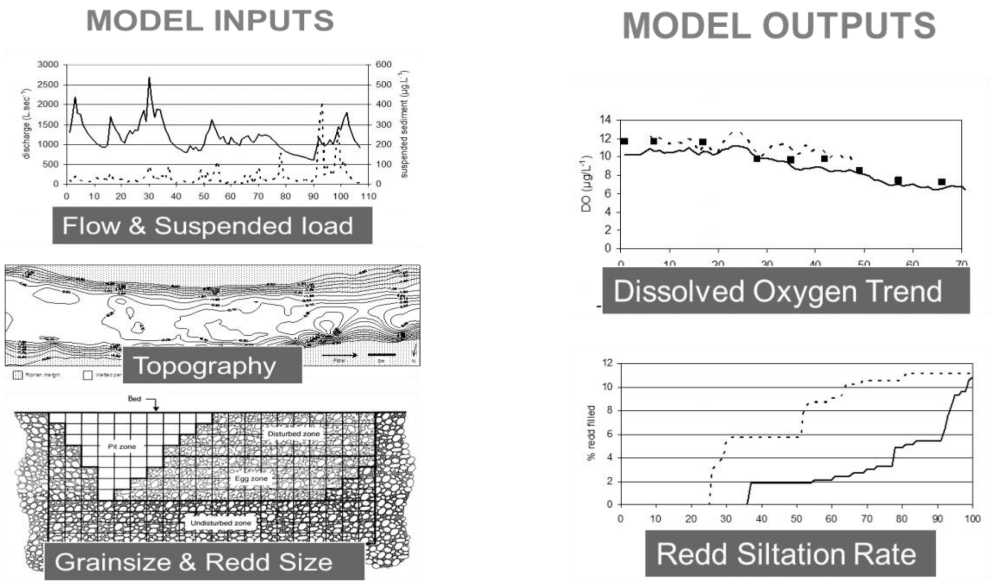


Figure 8.4 An example of SIDO-UK input and output parameters

The relationship between suspended sediment load and the infiltrated amount of sediment in the spawning gravels is established based on the accumulation of fine sediment within the riverbed and the flux of near-bed suspended sediment from empirical field sampling. From this, the intragravel flow rate and related dissolved oxygen concentration is derived and applied to indices for survival at these oxygen concentrations.

The Wu model (2000) is based on premise that seepage velocity is the main controlling factor on oxygen supply rate within the redd zone, and calculates the impact on embryo survival based on factors that control the seepage velocity – namely stream discharge, geometry and sediment deposition.

However, these kinds of model, which may be fit to derive an accurate suspended sediment – fine sediment infiltration relationship, cannot fully model the complexity of interactions occurring in a stream-redd system as illustrated in figure b. ? above for the following reasons:

The model does not account for GW-SW surface: subsurface water exchange and vertical migration of low quality groundwater into the hyporheic zone. The evidence of GW-SW interactions revealed in this study and in studies by Malcolm et al (2003, 2004, 2009) necessitates that this vital aspect of flow dynamics within the redd be considered. The ability to model these processes would enable a link to be established with longer-term flow records. Hence an assessment of changes in hydrology resulting from climate or catchment changes might be linked directly to conditions within the gravels.

Measures of scour layer dynamics need to be included within assessments of spawning habitat quality. As discussed above, as well as the negative impacts, positive effects may also arise from shallow scour. There is a need to understand the relationship between scour layer dynamics and the penetration of oxygen rich surface water into the hyporheic egg zone. Incorporation of this parameter based on field observation would refine the model and improve its predictive accuracy during higher flow events.

Additionally, the models work from the assumption that there is minimal flushing of fines from the gravels once material has accumulated, which in a spate-prone river such as the Lugg is probably unrealistic.

The models do not account for consideration of the type or provenance of that sediment which may have variable influence on alevin health & survival even if similar weights but of differing provenance or land-use type. Related to this is consideration of the proportion of organic compounds, which can have significant SOD (sediment oxygen demand) and interfere with the available oxygen supply with the redd. The model does not account for sediment-bound chemicals of anthropogenic origin which may have deleterious effects on health and survival of alevins. Knowledge from studies of the SOD of various sediments for different sources could be applied to the model, again improving its predictive capabilities.

Lastly, integration of sublethal effects in reaction to various habitat conditions as informed by field and laboratory studies would enable further refinement of the model. There is a paucity of knowledge of these effects and reactions to differing habitat conditions, but this aspect has great potential for modelling the health and recruitment of alevins on a finer scale than survival, which the current output parameter is provided by the models.

The Vitality model developed by Anderson (2000) is a mechanistic model which describes organism survival in terms of age-dependent and age-independent mortality.

The underlying concept is that the survival capacity of organisms, quantified by vitality (Anderson 1998), is an abstract hidden process representing the combined effects of metabolic degradation on ageing, senescence and damage accumulation at the cellular level. External stressors affect the rate of damage accumulation over a treatment stage, which in turn lowers the level of vitality. The model's applicability to dose–response studies has been tested with case studies of natural stressors (temperature, feeding interval, and population density) and xenobiotic stressors (organic and inorganic toxicants). The vitality model could also potentially be applied to the effects of hypoxia stress on egg development using data from sublethal effects tests against healthy controls, and extrapolate the impact of stressors to develop a quantitative relationship between hypoxia and vitality of alevin and emerging fry. Additionally, predictions on how these effects may alter the adult survival capacity could be made using the model.

In terms of the projected usefulness of models which can simulate redd processes and resultant alevin survival and fitness, of particular concern is the predicted increases in flood frequency and magnitude under climate change.

Thus by refining such models as SIDO-UK to include newly discovered controls on redd habitat (GW-SW influences) and the possibility of linking this to a biological model for development and growth, we could attempt to define likely hazards and potential remediation measures to protect spawning habitat under future projected climactic conditions and land uses.

This would require a catchment-specific tailored approach given that the factors mentioned vary depending on catchment type, land use and aquifer interaction. e.g: More GW-SW interactions, less sediment, more sediment–bound substances and organics or water quality concerns. If we were to consider new evidence for groundwater impacts along with sediment input, this would require defining threshold values via groundwater-discharge curves to refine the timings of when groundwater interactions came into play during high flow conditions. Also, interactions between sediment input and groundwater would need further in depth empirical validation. For example, if the hyporheic zone is only partially effected, or how GW influx affects the dynamics of sediment when flow directionality changes - could this displace fines?

Specific considerations for Lugg river might be GW-SW in gorges and where likely underlying geology would promote groundwater aquifers. Also, increased agricultural sedimentary input, especially during spate years and the possibility of scour in the more downstream sites could be factored into model runs for the catchment.

8.3 Conceptual model of Lugg study contribution

A generic conceptual model as seen from the perspective of sedimentary controls on spawning habitat is described below. This is the dominant current theory in catchment management practice. The model as is stands is described below with the main controls and causative links (as proposed by Grieg et al) such as the interplay between oxygen concentration which produce an oxygen 'flux' value which ultimately determines incubation habitat quality.

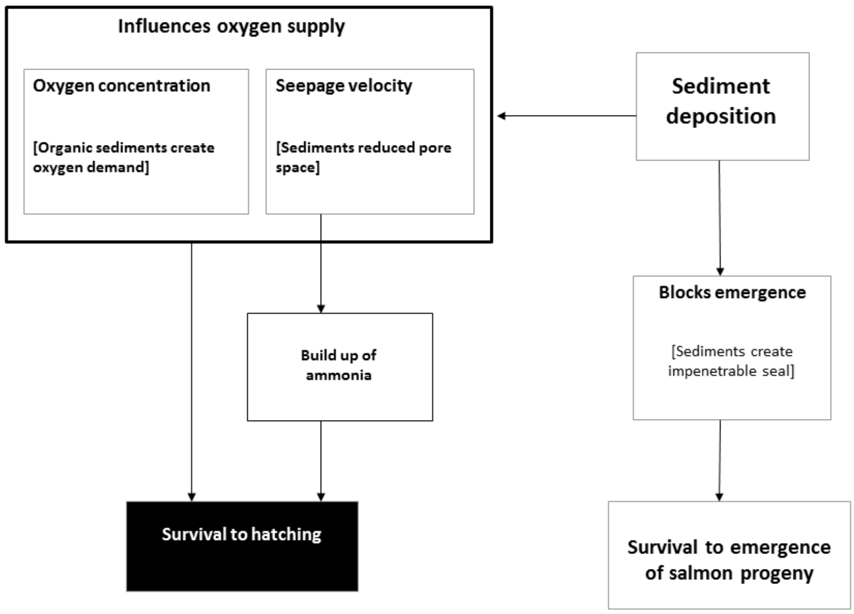


Figure 8.5 Generic conceptual diagram (From Greig et al) illustrating the fine sediment impacts on embryonic survival in Atlantic salmon

With results from the Lugg study in mind, the factors that can broadly be seen as measures of spawning habitat quality may be classed as: Geomorphic, Hydrologic, and catchment (land-use) based, and these influences may act together during events to reduce survival.

Hydrology is an important contributing factor and aside from the traditionally observed indices of flow throughout the hyporheic zone, the source of this water – whether from low-oxygen groundwater needs to be addressed. Additionally, hydrological controls in reactions to increased spate occurrence and intensity or other climate-related effects (drought) should be factored into appraisals of habitat quality.

Integration of the concepts of groundwater upwelling, and the application of the fingerprinting technique in the thesis has arrived a new perspective which is related to discharge and catchment wetness and links the system together. Catchment connectivity to river is key - for land use, and groundwater influences alike.

From a land-use perspective, the nature of the land use, soil type and management controls delivery of sediment, which then can sediment infiltrate salmonid redds. Delivery is controlled chiefly by precipitation and catchment wetness and riparian connectivity and influenced by land management decisions.

Groundwater upwelling is largely controlled by underlying geology, wet weather events and overall catchment wetness.

Sublethal effects investigated in the study have highlighted new methods of appraisal of spawning habitat health on a very fine scale, which may be of use in catchment remediation initiatives.

A generic conceptual model is displayed below which highlights the concomitant causes of lowered survival within the incubation zone, and the major controls that act on the spawning habitat as revealed through Lugg catchment investigations. The conceptual model is based on the traditional model of sedimentary impact on spawning gravels, with modified controls - as seen from evidence arising from the Lugg catchment study.

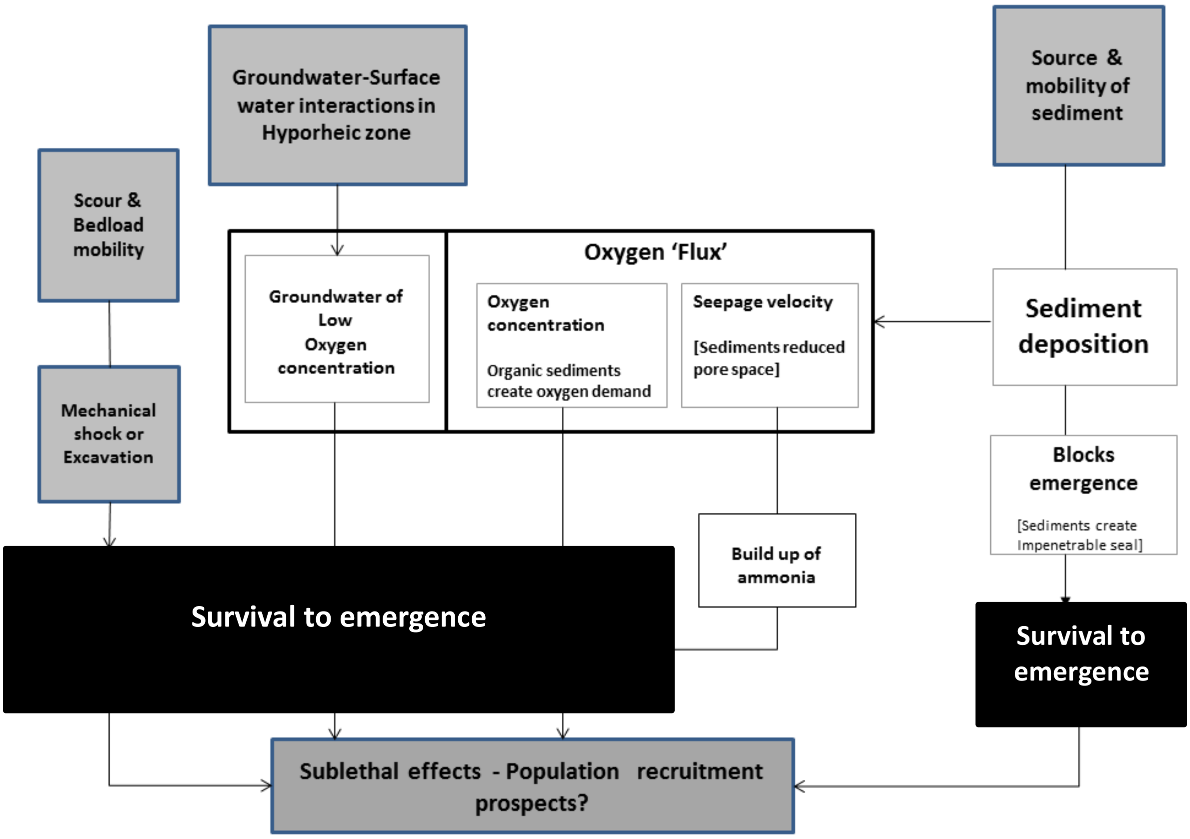


Figure 8.6 Updated generic conceptual model of the main controls on spawning habitat as based on the findings from the Lugg catchment study. Grey boxes signify newly integrated elements.

As highlighted in chapter 6, both sedimentary pressures and groundwater factors exert an influence on survival during a given year on the Lugg catchment. Habitat quality is seen to vary spatially and temporally, with an overall trend pointing to low flow years reflecting higher survival indices and higher flow years, lower survival. Discharge has been shown to act as the primary controlling factor on survival due to a number of mechanisms.

Additionally, discharge has been found to be strongly correlated with many of the critical physicochemical characteristics of rivers, such as water temperature, channel geomorphology, and habitat diversity and is considered a 'master variable' that limits the distribution and abundance of riverine species (Power et al 1995, Resh et al 1988, Poff and Ward 1997). From studies monitoring discharge-ecosystem relationships on a wide variety of stream types, Poff and Ward (1989) and Poff et al (1997) derived the now widely used core environmental flows references, which list the component parts of discharge that contribute to freshwater ecosystem health.

According to the model, the five major aspects of flow which were shown to have direct or indirect impact upon ecosystem health were: flow magnitude, flow frequency, flow duration, flow timing and rate of change influence integrity both directly and indirectly, through their effects on other primary regulators of integrity. Modification of flow thus has cascading effects on the ecological integrity of rivers.

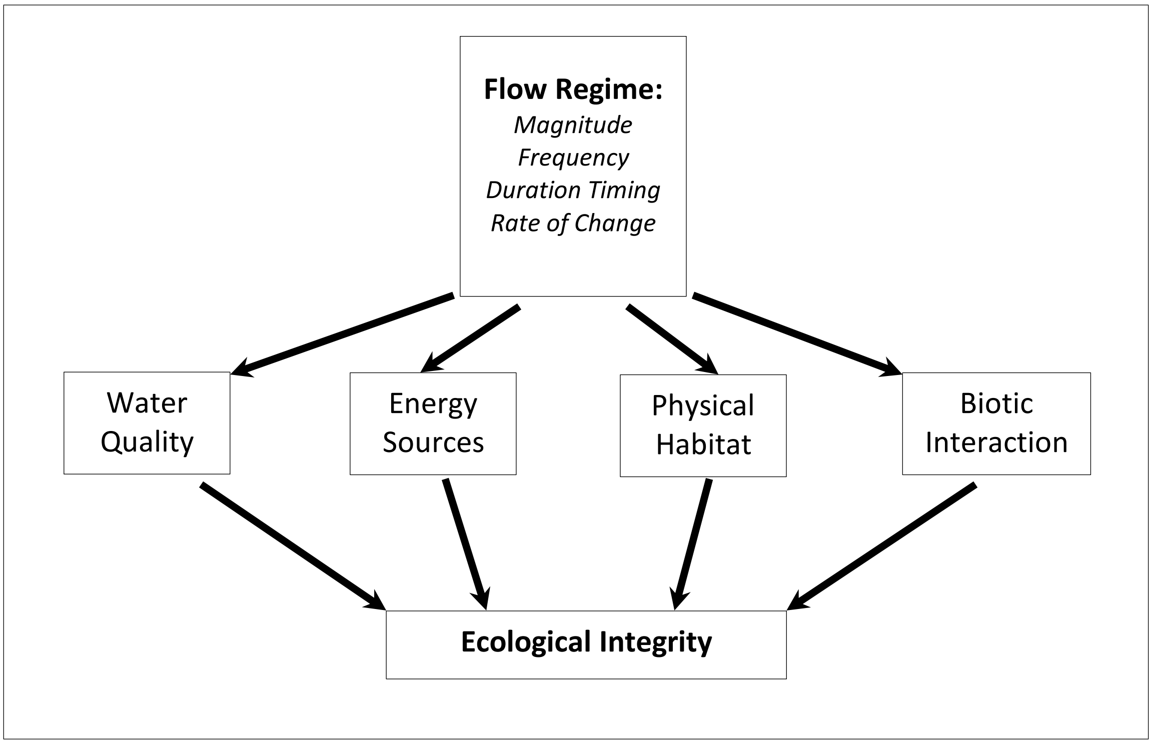


Figure 8.7 Mechanisms by which flow regime affects ecological integrity (from Poff and Ward 1989)

Flow Component	Specific alteration	Ecological response	Reference
Magnitude and Frequency	Increased variation	Wash-out and/or stranding Loss of sensitive species	Cushman 1985, Petts 1984 Gehrke et al. 1995, Kingsolving and Bain 1993, Travnichek et al. 1995
		Increased algal scour and wash-out of organic matter	Petts 1984
		Life cycle disruption	Scheidegger and Bain 1995
	Increased GW-SW occurrence in hyporheic zone	***Salmonid egg incubation failure***	***This study (2011)***
	Flow stabilization	Altered energy flow Invasion or establishment of exotic species	Valentin et al. 1995 Kupferberg 1996, Meffe 1984 Stanford et al. 1996
		Reduced water and nutrients to floodplain plant species.	Duncan 1993, Nilsson 1982 Fenner et al. 1985, Rood et al. 1995, Scott et al. 1997
Timing	Loss of seasonal flow peaks	Disrupt cues for fish: Spawning Egg hatching Migration Loss of fish access to wetlands	Fausch and Bestgen 1997, Montgomery et al. 1993, Nesler et al. 1988 Nzsje et al. 1995 Williams 1996 Junk et al. 1989, Sparks 1995 Power 1992, Wootton et al. 1996 Fenner et al. 1985
Duration	Prolonged low flows	Concentration of aquatic organisms	Cushman 1985, Petts 1984
		Diminished plant diversity	Tavlor 1982
	Prolonged baseflow 'spikes'	Downstream loss of floating eggs	Robertson 1997
	Altered inundation duration	Altered plant cover types	Auble et al. 1994
	Prolonged inundation	Loss of riffle habitat for aquatic species	Bogan 1993
	Rise in groundwater levels	***Salmonid egg mortality***	***This study (2011)***
Rate of change	Rapid changes in river stage	Wash-out and stranding of aquatic species	Cushman 1985, Petts 1984
	Accelerated flood recession	Failure of seedling establishment	Rood et al 1995

Table 8.2 The five major components of flow regime as derived by Poff et al (1997) with corresponding ecological responses. Additional hyporrheic responses as evident from this study are highlighted in red.

In diagram 8.7, the components of flow regime are treated individually for the sake of clarity. In reality they will interact to regulate both geomorphic and ecological processes. In describing the impacts of flow regime on the ecology of a system, the effects of extremes of high or low flow are often highlighted, as they serve as ecological ‘bottlenecks’ which provide either critical stresses or opportunities for riverine species. However, the complexity of flow regime dynamics in terms of duration, timing and rate of change of flows is also of importance. Table 8.2 above lists some of the ecological responses to changes in each of the five ‘components’ of flow as derived by Poff et al (1997); but incudes the responses to hyporheic zone stresses as reported in this study, which should also be considered as part of this system, and heretofore was not highlighted.

This is pertinent to current practices of abstraction and ecosystem conservation efforts under these pressures, where the groundwater component should also be considered. Compensation flows are currently seen as mitigation options for licenced abstraction at facilities such as STW / WTW. However, flow rates of these additional discharges on groundwater impact element should be considered in depth also if conservation of hyporheic zone habitat is to be respected.

8.4 Summary of findings and research contribution

1. Increased fine sediment infiltration rates are associated with higher flow years, as described in chapters 4 and 5, which in turn can influence dissolved oxygen concentrations and intragravel rates to reduce the overall habitat quality of the incubation environment.

2. The main source of sediment during high flow years are from agricultural land use. During low flow years, there is less sediment overall but proportionally; the channel bank contribution is dominant. This highlights the high degree of connectivity of adjacent agricultural land to the river during wetter periods.

3. Groundwater is implicated as a control on embryonic survival two of the three sites investigated on the catchment. Hypoxic conditions falling below critical concentrations and lasting for period of up to 10 days have been detected in association with GW-SW

interactions. This is sufficient to cause mortality of developing embryos even in the absence of sedimentary pressures. Ground-water surface-water interactions have been shown to be more intense during and immediately after high flow events, with infiltration of groundwater of low oxygen content a feature of the falling limb of some spate events; particularly where catchment conditions have already reached saturation after periods of prolonged precipitation.

5. Tests for sublethal effects were shown to offer a valid method of assessing the quality of incubation habitat. The combination of proxies provided a robust test which could act as a sensitive indicator of alevin health. This approach could be taken forward by management initiatives and used as a high resolution gauge of spawning habitat quality.

6. Evidence collated from all parts of the field study indicates that high flow events are key drivers of the quality on incubation environment with sediment infiltration and groundwater effects as the main drivers on this catchment. Evidence of groundwater interactions and ecological responses in the hyporheic zone in this study has augmented the Poff et al discharge components which contribute to freshwater ecosystem health.

By including groundwater variables for the hyporheic zone into ecological driver-response models, a more holistic view of fluvial systems is achieved which includes more variables, thus improving both our model of ecosystems responses to flow regime and our chances of success in catchment management efforts where abstraction pressures and compensation flow considerations are key.

As detailed in points 1 to 6 above, this research has expanded on the standard design and scope of previous studies on factors affecting salmonid spawning gravels. This has been achieved in several ways. Firstly, by investigating a total of 9 sites on a particular catchment - (where most field studies focus on one or two sites), an understanding of the spatial and temporal variability in redd conditions on the catchment was achieved. By implementing multi-parameter investigations observing sedimentary, groundwater and other environmental pressures, new insights on potential controlling factors were made, which have previously not been achieved studies of this kind.

At the catchment scale, the fingerprinting study shed light on the source of the sediment reaching spawning gravels and at the micro-scale, sublethal effects investigations highlighted the potential for use of alevin and fry as indices of incubation habitat quality. It is hoped that these aspects of the study will prove both informative and useful to future catchment management efforts.

8.6 Limitations of the study

High resolution sampling shows dissolved oxygen sags to be a feature common to spawning sites on the catchment – a phenomenon which lower resolution sampling strategies do not reveal.

Although not possible to explore fully within the remit of the study, high resolution dissolved oxygen data and testing for other groundwater parameters on a wider spatial array of sites than possible in this study would help determine whether the depleted oxygen phenomenon is an aquifer-related trend in areas where confined geology and/or glacial drift is present or whether it could be a catchment-wide occurrence.

Application of the sublethal tests during a high flow year when survival might be less than ideal would likely yield more definitive sublethal effects and consolidate the evidence found during the 'good' year. Time limitations and the mortality of eggs during the 2010 experiment did not allow this within the scope of the study.

New high resolution monitoring devices emerging due to advances in technology are promising new tools in assessment of spawning habitat, but remain an expensive option. So, where this may be not possible, another means of assessing spawning habitat quality is through testing for fitness and sublethal effects. These provide a sensitive gauge of habitat quality although does not enable interpretation of cause and effect.

Chapter 9

9.1 Future research recommendations

With a view to differentiating the degree of influence of groundwater-influenced habitat and physical sediment influences, simultaneous GW-SW detection and sediment infiltration monitoring with continuous monitoring at higher resolutions than heretofore undertaken, would help elucidate the degree of impact of each of these phenomena. Consideration of this should be carried out in a catchment–specific context.

Controlled laboratory experiments looking at the effects of varying types of sediment on embryonic development could help determine the geochemical aspect of sedimentary impacts. Laboratory controlled tests on the effects of sediments derived from varying land use types and /or containing a variety of sediment-bound commonly used anthropogenic substances applied routinely to the land or used in animal management could prove useful.

The use of sublethal performance biological indices as proxies for healthier emergent alevins could be brought to new levels of investigation and applied more widely to a variety of catchment types. Application of these indices to a vitality model such as that developed by Anderson (2000) would provide further insight into population viability.

The development of a model for simulating spawning habitat coupled with parameters for groundwater infiltration and water quality considerations would enable more realistic representation of the redd-zone processes involved. Additionally, coupling of an instream model as just described with a sediment delivery model which accounted for landscape processes such as catchment slope, land use and underlying geology would help determine the amount of sediment delivered and the ground-water upwelling potential. Relevant to the fingerprinting study, the inclusion of BOD / SOD into this model depending on sediment source information would also help its refinement. A model with capabilities such as these would hold much interest for future predictions under climate change scenarios and for catchment management initiatives generally.

Having expressed some goals for integration of new data from further empirical studies to refine models, it is worth expressing the increasing concern in catchment science over new knowledge of the complexity of connections between hydrological regimes and ecological impacts in rivers, which involve multiple interacting parameters operating at different spatial and temporal scales, and the ability to model these interaction to a reasonable degree of certainty. This spatial and temporal dynamism of rivers must be taken into consideration before relationships among stated parameters have any ecological meaning or relevance in deriving environmental standards or river management tools. This is an area of concern among many river scientists regarding the applicability of hydraulic-habitat models to ecologically-based river management.

Tetzlaff et al (2008), Soulsby et al (2008) and Dunn et al (2008) expressed their thoughts on the outcome of workshop 'From Catchment Scale Process Conceptualisation to Predictive Capability' which looked at the integration of newly emerging concepts of stream hydrology function based on improved data collection, into catchment models. On the basis of hydrological processes, concerns were that inclusion of new and different types of data in a model is accompanied by the need for added parameters to represent the new variables being simulated. Also the spatial heterogeneity of processes was seen as particularly challenging to parameterize. For example, heterogeneity in processes may across a catchment, but appropriate spatial data to quantify this variability are limited, and the inclusion of spatially varying parameters in the model exacerbates parameter identifiability issues.

These are issues that are relevant to this study but here even more complex; with multi-disciplinary data from several fields requiring integration as new model parameters. Creation of a model which reflected real catchment processes would require conceptualization of those processes which this study has contributed to, followed by wider-scale data collection to aid identification of inter-catchment variability of those parameters. As advocated by Tetzlaff, Soulsby and others (Dunn 2008, Beven 2007) the way forward is use of an iterative integrated modelling and fieldwork approach to help identify heterogeneity in responses and across spatial scales through the model experiments, and then subsequent investigation through targeted monitoring in the field, either in specific locations or at specific times. The value of closer collaboration between field experimentalists and modellers is beginning to be recognized and the integration of stakeholders has been central to several recent projects funded by the European Union.

References

Acornley RM, Sear DA. 1999. Sediment transport and siltation of brown trout (Salmo trutta) spawning gravels in chalk streams. Journal of Hydrology 13: 447–458.

Adams, S.M. (1990). Status and use of bioindicators for evaluating effects of chronic stress on fish. American Fisheries Society Symposium 8:1-8.

Adams, S.M. (1990). Biological indicators of stress in fish. American Fisheries Society Symposium 8.

Allan A, Frostick LE. 1999. Framework dilation, winnowing, and matrix particle size: the behaviour of some sand-gravel mixtures in a laboratory flume. Journal of Sedimentary Research **69**(1): 21–26.

Alonso CV, Theurer FD, Zachmann DW (1996) Sediment intrusion and dissolved oxygen transport model-SIDO. U.S. Department of Agriculture, Agricultural Research Service, National Sedimentation Laboratory, Technical Report 5, Oxford, Mississippi

Alderdice, D.W., Wickett, W.P., Brett, J.R., 1958. Some effects of exposure to low dissolved oxygen levels on Pacific salmon eggs. J. Fish. Res. Board Can. 15, 229-250.

Anderson, J.J., (2000). A vitality-based model relating stressors and environmental properties to organism survival. Ecol. Monograph 70, 445_470.

Anderson, J.J., Gildea, M.C., Williams, D.W., Li, T. (2008) Linking growth, survival and heterogeneity through stochastic vitality. Amer. Nat. 171 (1)

Argent,G. and Flebbe,P. (1999) Fine sediment effects on brook trout eggs in laboratory streams Fisheries Research 39: 253-262

Armour, C.L., Duff, D.A., and Elmore, W. 1991. The effects of livestock grazing on riparian and stream ecosystems. Journal of Fisheries, 16(1): 7–11.

Armstrong JD, Kemp PS, Kennedy ML, Milner NJ. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62: 143–170.

Arnell, N. W. 1998, ‘Climate Change and Water Resources in Britain’, Clim. Change **39**, 83–110.

Auble GT, Friedman JM, Scott ML. 1994. Relating riparian vegetation to present and future streamflows. Ecological Applications 4: 544-554.

Auperin and M. Geslin, (2008) Plasma cortisol response to stress in juvenile rainbow trout is influenced by their life history during early development and by egg cortisol content, Gen. Comp. Endocrinol. 158, pp. 234–239

Bača P. 2002 Conference Paper. ERB and Northern European FRIEND Project 5 Conference, Demänovská dolina, Slovakia.

Bardonnet, A. and Baglinière, J.L. (2000) Freshwater habitat of Atlantic salmon(Salmo salar) Can. J. Fish. Aquat. Sci. 57: 497–506 (2000)

Barry, T.P., Malison, J.A., Held, J.A., Parrish, J.J., (1995). Ontogeny of the cortisol stress response in larval rainbow trout. Gen. Comp. Endocrinol. 97, 57–65.

Battin, T.J. and Sengschmitt, D. (1999): Linking sediment biofilms, hydrodynamics and river bottom clogging: Evidence from a large river. *Microbial Ecology*, 3: 185-196

Battin, T.J., Kaplan, L.A., Newbold, J.D., Cheng, X. and Hansen, C. (2003): Effects of current velocity on the nascent architecture of stream microbial biofilms. *Applied and Environmental Microbiology* 69: 5443-5452

Barlaup, B.T., H. Lura, H. Saegrov & R.C. Sundt. 1994. Inter and intraspecific variability in female salmonid spawning behaviour. Can. J. Zool. 72: 636–642.

Barton, B.A., Morgan, J.D. and Vijayan, M.M. (2002). Physiological and condition-related indicators of environmental stress in fish. In Adams, S.M. (ed), Biological Indicators of Aquatic Ecosystem Stress (pp. 111-148). Bethesda, MD: American Fisheries Society.

Barton, B.A.,(2002). Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integr. Comp. Biol. 42, 517–525.

Barton, B.A., Iwama, G.K., (1991). Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Annu. Rev. Fish Dis. 1, 3–26.

Baxter, C. V., and F. R. Hauer. 2000. Geomorphology, hyporheic exchange and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1470–1481

Bartlett F., Neumann D. (1998): Sensitivity of brown trout alevins (Salmo trutta L.) to nitrite at different chloride concentrations. Bulletin of Environmental Contamination and Toxicology, 60, 340–346.

Beer, W. N. and Anderson, J. J. (1997). Modeling the growth of salmonid embryos. J. theor. Biol. 189:297-306.

Beschta RL, Jackson WL. 1979. The intrusion of fine sediments into a gravel bed. Canadian Journal of Fisheries and Aquatic Sciences. 36.

Beven K. 2007. Towards integrated environmental models of everywhere: uncertainty, data and modelling as a learning process. Hydrology and Earth System Sciences 11: 460– 467.

Bilotta, G.S., and Brazier, R.E. 2008. Understanding the influence of suspended solids on water quality and aquatic biota. Water Research, 42(12): 2849–2861

Binkley D & Brown TC (1993). Forest practices as non-point sources of pollution in North America.Water Resources Bulletin 29, 5, 729–740.

Bjorn TC, Reiser DW. 1991. Habitat requirements of salmonids instreams. In Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats, Meehan WR (ed.). American Fisheries Society, Special Publication Number 19. American Fisheries Society: Bethesda, MD; 83–138.

Bjornn TC, Reiser DW. 1991. Habitat requirements of salmonids in streams. In Influence of Forest and Rangeland Management on Salmonid Fishes and their Habitats, Meehan WR (ed.). American Fisheries Society Special Publication No. 19. American Fisheries Society: Bethesda, MD; 83–128.

Blott S.J. and Pye, K. (2001) GRADISTAT: A grainsize distribution and statistics package for the analysis of unconsolidated sediments Earth Surf. Process. Landforms 26, 1237–1248

Bogan AE. 1993. Freshwater bivalve extinctions (Mollusca: Unionida): a search for causes. American Zoologist 33: 599-609.

Boulton AJ, Findlay S, Marmonier P, Stanley EH, Valett HM. 1998. The functional significance of the hyporheic zone in streams and rivers. Annual Review of Ecology and Systematics **29**: 59–81.
Brown D. (2008) Tracker© Video analysis software (open source) Cabrillo Edu. (http://www.cabrillo.edu/~dbrown/tracker)

Brown, A. G. 1985. “The potential use of pollen in the identification of suspended sediment sources.” Earth Surf. Processes Landforms, 10, 27–32.

Brown, D. 2009. Tracker™ video analysis and modelling tool. Open source physics website: http://www.cabrillo.edu/~dbrown/tracker/

Bull, L. J. 1997, Magnitude and variation in the contribution of bank erosion to the suspended sediment load of the River Severn, UK. Earth Surface Processes and Landforms, 22: 1109–1123.

Burt, T. P. 1996. `Hydrology of headwater catchments', in Petts, G. E. and Calow, P. (Eds) River Flows and Channel Forms, Blackwell Scientific, Oxford. 19-36.

Cada, G.F., M.G. Ryon, D.A Wolf, and B.T. Smith. (2003) Development of a new technique to assess susceptibility to predation resulting from sublethal stresses (indirect mortality). ORNL/TM-2003/195, Oak Ridge National Laboratory, Oak Ridge, TN.

Caldwell, J. M. and M.C. Doyle. 1995. Sediment Oxygen Demand in the Lower Willamette River, Oregon, 1994. United States Geological Survey Water- Resources Investigations Report 95-4196.

Calvache M. L.; Duque, C.; Gomez Fontalva, J. M.; Crespo, F., (2011). Processes affecting groundwater temperature patterns in a coastal aquifer. Int. J. Environ. Sci. Tech., 8 (2), 223-236.

Carling, P. A., Boole, P. (1986) "An improved conductiometric standpipe technique for measuring interstitial seepage velocities" Hydrobiologia 135: 3-8

Carling PA, McCahon CP. 1987. Natural siltation of brown trout (Salmo trutta) spawning gravels during low flow conditions. In Regulated Streams: Advances in Ecology, Craig JF, Kemper BJ (eds). Plenum Press: New York; 229–224.

Carling PA, Taylor P, Hankin B, Benson I. 1999. Fluid exchange and oxygen flux through salmon redds. Environment Agency R&D Report W985.

Carling PA. 1984. Deposition of fine and coarse sand in an open-work gravel bed. Canadian Journal of Fisheries and Aquatic Sciences 41: 263–270

Carling, P.A. and N.A. Reader, 1981. A freeze-sampling technique suitable for coarse river bed material. *Sedimentary Geology* 29: 233-239.

Carling, P.A. and N.A. Reader, 1982. Structure, composition and bulk properties of upland stream gravels. *Earth Surface Processes and Landforms* 7: 349-365.

Caruso G, Genovese L, Maricchiolo G, Modica A, (2005) Haematological, biochemical and immunological parameters as stress indicators in Dicentrarchus labrax and Sparus aurata farmed in off-shore cages. Aquaculture International 13, 67-73

Chadwick , E. M. P. Stock-Recruitment Relationship for Atlantic Salmon (Salmo salar) in Newfoundland Rivers. Canadian Journal of Fisheries and Aquatic Sciences, 1982, 39:(11) 1496-1501, 10.1139/f82-201

Chambers, B. J., Davies, D. B. and Holmes, S. (1992). Monitoring of water erosion on arable farms in England and Wales, 1989-90. Soil Use and Management 8, 163–170.

Chambers, B.J., Garwood, T.W.D., Unwin, R.J., 2000. Controlling soil water erosion losses from arable land in England and Wales. J. Environ. Qual. 29, 145–150

Chambers, J. S. R. T. Pressey, J. R. Donaldson. and W. R. McKinley. 1954. Research relating to study of spawning grounds in natural areas. Annual report to US Army Corps of Engineers, Contract DA-35026-Eng-20572. (Available from State of Washington. Department of Fisheries. Olympia.)

Chapman DW. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117: 1–21.

Chen B, Li Y. 1999. Numerical modelling of biofilm growth at the pore scale. In Proceedings of the 1999 Conference on Hazardous Waste Research.

Chevalier B.E. Carson, C. (1985) 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, 99p.

Chevalier BE, Carson C, Miller WJ. 1984. Report of engineering and biological literature pertaining to the aquatic environment with special emphasis on dissolved oxygen and sediment effect on salmonid habitat . Colorado State University, Department of Agriculture and Chemical Engineering ARS Report No. 5602 20813-008A.

Chevalier, B.E. and V.G. Murphy. 1985. Intragravel Dissolved Oxygen Model. Colorado State Univ., Dept. Ag. Chew. Eng., ARS CWV No. 5402-20810-004-015. 68 p

Claret, C. Marmonier, P. Bravard , J.P. (1998) Seasonal dynamics of nutrient and biofilm in interstitial habitats of two contrasting riffles in a regulated large river. Aquat.sci.60 (1998) 33–55

Clarke, D., W. K. Purvis & D. Mee, 1991. Use of telemetric tracking to examine environmental influence on catch effort indices. A case study of Atlantic salmon (Salmo salar L.) in the River Tywi, South Wales. In I. G. Cowx (ed.), Catch Effort Sampling Strategies: their Application in Freshwater Fisheries Management. Blackwell, London: 33–48.

Clarke, S. J. and Wharton, G. 2001: Sediment nutrient characteristics and aquatic macrophytes in lowland English rivers. Science of the Total Environment 266, 103-112

Clews, E., Durance, I., Vaughan I.P., and Ormerod, S.J. (2010). Juvenile salmon populations in a temperate river system track synoptic trends in climate. Global Change Biology 16: 3271-3283.

Collins, A.L., Walling, D.E., Leeks, G.J.L., 1997a. Source type ascription for fluvial suspended sediment based on a quantitative composite fingerprinting technique. Catena 29, 1–27.

Collins, A.L., Walling, D.E., Leeks, G.J.L., 1997b. Fingerprinting the origin of fluvial suspended sediment in larger river basins: combining assessment of spatial provenance and source type. Geografiska Annaler 79A, 239–254.

Collins, A.L., Walling, D.E., Leeks, G.J.L., 1997c. Sediment sources in the upper Severn catchment: a fingerprinting approach. Hydrology and Earth System Sciences 1, 509–521.

Collins, A.L., Walling, D.E., Leeks, G.J.L., 1998. Use of composite fingerprints to determine the provenance of the contemporary suspended sediment load transported by rivers. Earth Surface Processes and Landforms 23, 31–52.

Collins, A.L., Walling, D.E., 2002. Selecting fingerprint properties for discriminating potential suspended sediment sources in river basins. Journal of Hydrology 261, 218–244.

Collins, A.L., Walling, D.E., 2004. Documenting catchment suspended sediment sources: Problems, approaches and prospects. Progress in Physical Geography 28 (2), 159–196.

Collins, A.L.,Walling, D.E., 2007a. Sources of fine sediment recovered from the channel bed of lowland groundwater-fed catchments in the UK. Geomorphology 88, 120–138.

Collins, A.L., Walling, D.E., 2007b. The storage and provenance of fine sediment on the channel bed of two contrasting lowland permeable catchments, UK. River Research and Applications 23, 429–450.

Collins, A.L., Stromqvist, J., Davison, P.S. and Lord, E.I. (2007). Appraisal of phosphorus and sediment transfer in three pilot areas identified for the Catchment Sensitive Farming initiative in England: application of the prototype PSYCHIC model. Soil Use and Management 23, 117-132.

Collins AL, Anthony SG, Hawley J, Turner T. 2009a. The potential impact of projected change in farming by 2015 on the importance of the agricultural sector as a sediment source in England and Wales. Catena 79: 243–250

Collins, A.L. , Walling , D.E. , Webb, L., King, P. 2010 Apportioning catchment scale sediment sources using a modified composite fingerprinting technique incorporating property weightings and prior information Geoderma 155 (2010) 249–261

Collins, A.L. and Walling, D.E. (2004). Documenting catchment suspended sediment sources: problems, approaches and prospects. *Progress in Physical Geography* **28**:159-196.

Collins AL, Walling DE, 2006. The storage and provenance of fine sediment on the channelbed of two contrasting lowland permeable catchments, UK. River. Res. Applic. 23: 429–450

Collins AL, Walling DE, Leeks GJL. 2005. Storage of fine-grained sediment and associated contaminants within the channels of lowland permeable catchments in the UK. In Sediment Budgets 1,Walling DE, Horowitz AJ (eds). IAHS Publ. No. 291, IAHS Press:Wallingford, UK; 259–268.

Collins AL,Walling DE. 2002. Selecting fingerprint properties for discriminating potential suspended sediment sources in river basins. Journal of Hydrology 261: 218–244.

Cooper, A. C. 1965. The effect of transported stream sediments on the survival of sockeye and pink salmon eggs and alevins. International Pacific Salmon Fisheries Commission Bulletin, 18.

Crisp DT, Carling PA. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34: 119–134

Crisp D.T. 1990 Some effects of application of mechanical shock at varying stages of development upon the survival and hatching time of British salmonid eggs. Hydrobiologia , Volume 194, Number 1, 57-65

Crisp, D.T. 1993. The ability of U.K. salmonid alevins to emerge through a sand layer. Journal of Fish Biology, 43(4): 656–658.

Crisp D.T. 1981. A desk study of the relationship between temperature and hatching for the eggs of five species of salmonid fishes. Freshwater Biology 11: 361–368.

Crisp DT. 1996. Environmental requirements of common riverine European salmonid fish species in fresh water with particular relevance to physical and chemical aspects. Hydrobiologia 323: 201–221.

Crisp DT. 2000. Trout and Salmon. Ecology, Conservation and Rehabilitation. Blackwell Science: Oxford; 212.

Cross, P. (1966) The glacial geomorphology of the Wigmore and Presteigne basins and some adjacent areas. MSc thesis. Univ. London

Cushman RM. 1985. Review of ecological effectsof rapidly varying flows downstream from hydroelectric facilities. North American Journal of Fisheries Management 5: 330-339.

Danner, G. R. 2008. Salmonid embryo development and pathology. In Salmonid Spawning Habitat in Rivers: Physical Controls, Biological Responses, and Approaches to Remediation. *American Fisheries Society Symposium* 65:37–58.

Davis, M. W. (2010), Fish stress and mortality can be predicted using reflex impairment. Fish and Fisheries, 11: 1–11

Daniels, H.V. Boyd, C.E. Minton R.V. (1987) Acute Toxicity of Ammonia and Nitrite to Spotted Seatrout The Progressive Fish-Culturist, 1548-8640, Volume 49, Issue 4, 1987, Pages 260 – 263

Dey, D.B., Damkaer, D.M., 1990. Effects of spectral irradiance on the early development of chinook salmon. Prog. Fish-Cult. 52, 141–154.

Davis JC. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species, a review. Canadian Journal of Fisheries and Aquatic Sciences 32: 2295–2332.

Davis RJ, Gregory KJ. 1994. A new distinct mechanism of river bank erosion in a forested catchment. Journal of Hydrology 157: 1–11

Davison, P.S., Withers, P.J.A., Lord, E.I., Betson, M.J., Stromqvist, 2006 J., PSYCHIC – a process-based model of phosphorus and sediment transfers within agricultural catchments. Part 1. Model description and parameterisation.

Daykin, P. (1965) Application of the mass transport theory to the problem of respiration of fish eggs. Journal of the Fisheries Research Board of Canada, 22: 159-170.

De Boer and Crosby, 1995 D. De Boer and G. Crosby, Evaluating the potential of SEM/EDS analysis for fingerprinting suspended sediment derived from two contrasting topsoils, Catena 24 (1995), pp. 243–258

De Vries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54:1685-1698.

Dearing, J.A., Mahar, B.A., and Oldfield, F. 1985. Geomorphological linkages between soils and sediments: the role of magnetic measurements. In Geomorphology and soils. Edited by K. Richards, R. Arnett, and S. Ellis. Allen and Unwin, London. pp. 245–266.

Dearing, J.A. Alström, K. Bergman,A. Regnell, J. and P. Sandgren, P. 1990 Past and present erosion in southern Sweden. In: Boardman, Foster and Dearing, Editors, Soil Erosion on Agricultural Land, Wiley, Chichester p. 687

Deasy, C., Brazier, R. E., Heathwaite, A. L. and Hodgkinson, R. (2009), Pathways of runoff and sediment transfer in small agricultural catchments. Hydrological Processes, 23: 1349–1358

Deasy, C., Quinton, J.N., Silgram, M., Jackson, R., Bailey, A.P., Stevens, C.J., 2008. Field Testing of Mitigation Options. Final Report to Defra Under Contract PE0206.

Deasy, C. Quinton, J.N. Silgram, M. Bailey, A.P. Jackson, B. Stevens, C.J. 2009a Mitigation options for sediment and phosphorus loss from winter-sown arable crops. Journal of Environmental Quality, 38 (2009), pp. 2121–2130.

DEFRA report. Project PE0202 (2006) - Paul Davison and Eunice Lord. ADAS Environment Systems Modelling, ADAS Wolverhampton.

Dickson, R.R., T.J. Osborn, J.W. Hurrell, J. Meincke, J. Blindheim, B. Adlandsvik, T. Vinje, G. Alekseev, and W. Maslowski. 2000. The Atlantic Ocean response to the North Atlantic oscillation. J. Clim. 13(15):2671–2696.

Duke, J. R., et al. (2007). Riparian influence on hyporheic-zone formation downstream of a small dam in the Blackland Prairie region of Texas. Hydrological Processes 21, pp. 141–150.

Duncan RP. 1993. Flood disturbance and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand. Journal of Ecology 81: 403-416.

Dunn SM, Freer J, Weiler M, Kirkby MJ, Seibert J, Quinn PF, Lischeid G, Tetzlaff D, Soulsby C. 2008. Conceptualization in catchment modelling: simply learning? Hydrological Processes 22 (13) 2389–2393 (2008)

Dunne, T. and Leopold, L. B. 1978. Water in Environmental Planning, Freeman, San Francisco, 818 pp.

Einstein, H.A. (1968) Deposition of suspended sediment particles in a gravel. Journal of Hydraulic Engineering. 94: 1197-1205.

Einum, S., and Fleming, I.A. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). Evolution, 54: 628–639.

Eiserman, F. Dern, G. Doyle, J. (1975). Coldwater stream handbook for Wyoming USDA Soil Conservation service.

Environment Agency. River Wye Salmon Action Plan (2003 – 2008). Environment Agency; 2003. p. 1-29.

Environment Agency (2009). Water for life and livelihoods. River Basin Management Plan, Severn River Basin District. December 2009.

Environment Agency (2011) River Wye Salmon Action Plan: Building the case for further exploitation control measures – requirements and options.

EPA Method 3051A (2007) Microwave-Assisted Acid Digestion of Sediment, Sludges, Soils and Oils.

Ellis, T., James, J.D., Stewart, C. and Scott, A.P. (2004) A non-invasive stress assay based upon measurement of free cortisol released into the water by rainbow trout. *Journal of Fish Biology*, 65,1233-1252.

Elliot J.M. et al 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, Salmo salar. Freshwater Biology, 25: 61-70.

Elliott, A., and Brooks, N. H. (1997). Transfer of nonsorbing solutes to a streambed with bed forms: laboratory experiments. Water Resources Research 33, pp. 137–151

Environment Agency (1999). Fisheries Statistics 1999. Environment Agency, Cardiff.

Environment Agency Fisheries Technical Manual, 1997.

Ellis, T. James, J.D. Stewart, C. Scott, A.P. A non-invasive stress assay based upon measurement of free cortisol released into the water by rainbow trout (2004) Journal of Fish Biology 65, 1233–1252

Ellis, T., North, B., Scott, A.P., Bromage, N.R., Porter, M., Gadd, D.,(2002). The relationship between stocking density and welfare in farmed rainbow trout. J. Fish Biol. 61, 493–531.

Evans, R. Extent, frequency and rates of rilling of arable land in localities in England and Wales. In: S. Wicherek, Editor, Farm Land Erosion in Temperate Plains Environment and Hills, Elsevier, Amsterdam (1993), pp. 177–190.

Evans, R., 1997. Soil erosion in the UK initiated by grazing animals. Applied Geography 17, 127–141

Evans, L. (2009) Effects of sediment-derived pesticides on Atlantic salmon embryos. (Unpublished PhD thesis).

Evans CD, Freeman C, Montieth DT, Reynolds B, Fenner N. 2002. Terrestrial export of organic carbon. Nature 415: 861–862. DOI: 10.1038/415862a.

Evans EC, Greenwood MT, Petts GE. 1995. Thermal profiles within river beds. Hydrological Processes 9: 19–25.

Evans CD, Montieth DT, Cooper DM. 2005. Long-term increases in surface water dissolved organic carbon: observations, possible causes and environmental impacts. Environmental Pollution 137: 55–71.

Fast, D.E., Q.J. Stober, S.C. Crumley, and E.S. Lillebrew. 1981. Survival and movement of chinook and coho salmon alevins in hypoxic environments. Pages 51-60 .in E. L. Brannon and E.O. Salo, eds. Salmon and trout migratory behavior symposium. University of Washington Seattle.

Fausch KD, Bestgen KR. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131-166 in Knopf FL, Samson FB, eds. Ecology and conservation of Great Plains vertebrates. New York: Springer-Verlag.

Feist, G. Schreck, C.B. (2002). Ontogeny of the stress response in chinook salmon, Oncorhynchus tshawytscha Fish Physiology and Biochemistry 25: 31–40, 2002.

Fenner P, Brady WW, Patten DR. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. Journal of Range Management 38: 135-138

Findlay SEG, Sinsabaugh RL, Sobczak WV, Hoostal M. 2003. Metabolic and structural response of hyporheic microbial communities to variations in supply of dissolved organic matter. *Limnology and Oceanography* 48: 1608–1617.

Finn, R.N. (2007) Review: The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria. Aquatic Toxicology 81 (2007) 337–354

Fleming and Reynolds 2004 from Salmon breeding systems- Salmon illuminated: Salmon and their relatives. Oxford uni press. Editors – A.P.Handry and S.C.Stearns

Fowler, R.T. and Death, R.G. (2001).The effect of environmental stability on hyporheic community structure. Hydrobiologia, 445, 85–95

Fraser BG, Williams DD. 1998. Seasonal boundary dynamics of a groundwater/surface-water ecotone. Ecology 79: 2019–2031.

Friedland, K.D., 1998. Ocean climate influences on critical Atlantic salmon (Salmo salar) life history events. Can J Fish Aquat Sci **55** Suppl 1, pp. 119–130.

Frostick, 1.,. E., P. M. Lucas, and 1. Reid, The infiltration of fine matrices into coarse-grained alluvial sediments and its implications
for stratigraphical interpretation, *J. Geol. Soc. London*, *141*(6), 955-965, 1984.

Fuiman, L.A., Cowan Jr., J.H., Smith, M.E., O'Neal, J.P., 2005. Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect. Can. J. Fish. Aquat. Sci. 62, 1337–1349.

Fuiman, L.A., Rose, K.A., Cowan Jr., J.H., Smith, E.P., 2006. Survival skills required for predator evasion by fish larvae and their relation to laboratory measures of performance. Anim. Behav. 71, 1389–1399.

Gehrke PC, Brown P, Schiller CB, Moffatt DB, Bruce AM. 1995. River regulation and fish communities in the Murray-Darling river system, Australia. Regulated Rivers: Research & Management 11: 363-375

Gorodilov, Y. N. (1983). Stadii emfriona Inogo razvitiya Atlanticheskogo lososyce Salmo salar L. II. Opisaniye i khronologiya. [Stages of the embryonic development in the Atlantic salmon Salmo salar L. 2. Description and chronology.] Trudy GosNIORKh 200, 107–126 (in Russian).

Gorodilov, Y. N. (1989). Comparative analysis of the dynamics of early ontogeny of species of the genus Salmo. Journal of Ichthyology 29, 19–31

Gorodilov YN (1996) Description of the early ontogeny of the Atlantic salmon, Salmo salar, with a novel system of interval (state) identification. Environ Biol Fish 47:109–127

Green, P.A., Vorosmarty, C.J., Meybeck, M., Galloway, J.N., Peterson, B.J., Boyer, E.W., 2004. Pre-industrial and contemporary fluxes of nitrogen through rivers: a global assessment based on typology. Biogeochemistry 68, 71–105.

Greenhalgh, M. (2005) The Atlantic Salmon: An Illustrated Natural History. Pub: Merlin Unwin Books.

Greig S. M., Sear, D.A., Smallman, D. and Carling, P.A.(2005b) Impact of clay particles on cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs. Journal of Fish Biology. 66, 1681-1691.

Greig SM, Sear DA, Carling PA. 2007. A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. Hydrological Processes 21: 323–334.

Greig, S.M., Sear, D.A., & Carling, P.A. (2005a) Fine sediment accumulation in salmon spawning gravels and the survival of incubating salmon progeny: implications for spawning habitat management, Science of the Total Environment, 344, 241-258.

Gruszowski, K.E. Foster, I.D., Lees, J.A. Charlesworth, S.M. (2003) Sediment sources and transport pathways in a rural catchment, Hereford, UK. Hydrol. Process. 17, 2665–2681

Gruszowski, K.E., Foster, I.D.L., Lees, J.A., Charlesworth, S.M., 2003. Sediment sources and transport pathways in a rural catchment, Herefordshire, UK. Hydrological Processes 17, 2665–2681.

Grimshaw, D.L., and Lewin, J. 1980. Source identification for suspended sediments. Journal of Hydrology (Amsterdam), 47(1–2): 151–162.

Gunnes, (1979).Survival and development of Atlantic salmon eggs and fry at three different temperatures, Aquaculture 16 (1979), pp. 211–218.

Harvey and Bencala (1993) the effect of stream bed topography on surface-sub-surface water exchange in mountain catchments. Water Resources research Vol 29 (1) 89-98.

Hale M (1996) The Development of Fast-Start Performance in Fishes: Escape Kinematics of the Chinook Salmon (Oncorhynchus tshawytscha) AMER. ZOOL., 36:695-709

Harrison C.W. (1923) Planting eyed salmon and trout eggs. Transactions of the American fisheries society. 52: 191-200.

Hassell KL, Coutin PC, Nugegoda D. 2008. Hypoxia impairs embryo development and survival in black bream (Acanthopagrus butcheri). Marine Pollution Bulletin 57:302-306

Harshbarger, T. J., and P. E. Porter. 1982. Embryo survival and fry emergence from two methods of planting brown trout eggs. North American Journal of Fisheries Management 2:84–89.

Hatcher, K.J. 1950. Sediment Oxygen Demand. Institute of Natural Resources, University of Georgia. Athens, Georgia.

Heintz R.A, Short J.W, Rice SD (1999) Sensitivity of fish embryos to weathered crude oil. Part II. Increased mortality of pink salmon (*Oncorhynchus gorbuscha*) embryos incubating downstream from weathered Exxon Valdez crude oil. Environ Toxic Chem 18(3):494–503

Haggerty, M.J., Ritchie, A.C., Shellberg, J.G., Crewson, M.J., and Jalonen, J. 2009. Lake Ozette Sockeye Limiting Factors Analysis. Prepared for the Makah Indian Tribe and NOAA Fisheries in Cooperation with the Lake Ozette Sockeye Steering Committee, Port Angeles,

Hamor T. and Garside E. T. (1979). Hourly and total oxygen consumption by ova of Atalntic salmon, salmo salar L., during embryogenesis at two temperatures and three levels of dissolved oxygen. Canadian Journal of Zoology. 57: 1196-1200.

Hannah, D.M., Webb, B.W., Nobilis, F. 2008. River and stream temperature: dynamics, processes, models and implications. Hydrological processes 22: 899-901.

Hayes F.R. Wilmot, I.R. Livingston, D.A. (1951) The oxygen consumption of the salmon egg in relation to development and activity. The Journal of Experimental Zoology. 116(3): 377-395.

Hendry K & Cragg-Hine D (2003). *Ecology of the Atlantic Salmon*. Conserving Natura 2000 Rivers Ecology Series No. 7. English Nature, Peterborough

Heywood M. J. T. , Walling D.E. 2007, The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen content of intragravel water and embryo survival Hydrological. Processes. 21, 770–788

Hinton, M. J., S. L. Schiff, and M. C. English. (1993) Physical-properties governing groundwater-flow in a glacial till catchment, J. Hydrol., 142, 229–249.

Hooke, J. M. and Redmond, C. E. (1989), River-Channel Changes in England and Wales. Water and Environment Journal, 3: 328–335.

Howden N.J.K. Wheater, H.S. Peach, D.W. Butler A.P. 2004 Hydrogeological controls on surface-groundwater interactions in lowland permeable catchments. Hydrology: Science and practice for the 21st Century, Vol 2. 2004 British Hydrological Society.

Hoyal, D.C.J.D., Bursik, M.L., Atkinson, J. & Depinto, J.V. (1997) Filtration enhances suspended sediment deposition from surface water to granular permeable beds. Water, Air & Soil Pollution. 99. 157-171.

Hobbs D.F. (1937) Natural reproduction of salmon, brown and rainbow trout in certain New Zealand waters. N.Z. Marine department of fisheries Bulletin No 6.

Hübner,D. Borchardt, D. Fischer,J. 2011 Cascading effects of eutrophication on intragravel life stages of European Grayling (Thymallus thymallus L.) – in Press -Arch. Hydrobiol. (Advances in Limnology): The hyporheic zone of running waters: ecological patterns, processes and bottleneck functions.

Ingendahl D. 2001. Dissolved oxygen concentration and emergence of sea trout fry from natural redds in tributaries of the River Rhine. Journal of Fish Biology 58: 325–341.

Jackson, S.J., 1986. Soil erosion survey and soil erosion risk in mid-Bedfordshire. Seesoil 3, 95–104.

Jarvie, H.P., Withers, P.J.A., Neal, C., 2002d. Review of robust measurement of phosphorus in river water: sampling, storage, fractionation and sensitivity. Hydrol. Earth Syst. Sci. 6, 113–132.

Jarvie, H.P., Neal, C., Withers, P.J.A., Robinson, A., Salter, N., 2004a. Nutrient water quality of the Wye catchment, UK: exploring patterns and fluxes using the Environment Agency data archives. Hydrol. Earth Syst. Sci. 7, 722–743.

Jensen, E. Steel, A. Fullerton, A.H. Pess, G.R. (2009) Impact of Fine Sediment on Egg-To-Fry Survival of Pacific Salmon: A Meta-Analysis of Published Reviews in Fisheries Science, 17(3):348–359, 2009

Jensen, J. Alderdice, D. 1989. Comparison of mechanical shock sensitivity of eggs of five species of Pacific salmon (Oncorhynchus) species and steelhead trout (Salmo gairdneri). Aquaculture 78: 163-181.

Jones, J. W. & Ball, J. N. (1954). The spawning behaviour of brown trout and salmon. British Journal of Animal Behaviour 2, 103-114.

Jonsson, B. & I.A. Fleming. 1993. Enhancement of wild salmon populations. pp. 209–242. In: G. Sundnes (ed.) Human Impact on Self-recruiting Populations, Tapir Press, Trondheim.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66:20–65.

Jordan W. C. Verspoor, E. Youngson, A. F. (1997) the effect of natural selection on estimates of genetic divergence among populations of the Atlantic salmon (Salmo salar L.). Journal of Fiish Biology, 51: 546-560

Jordan, W. C., Cross, T. F., Crozier, W. W., Ferguson, A., Galvin, P., Hurrell, R. H., McGinnity, P., Martin, S. A. M., Moffett, I. J. J., Price, D. J., Youngson, A. F. and Verspoor, E. (2005), Allozyme variation in Atlantic salmon from the British Isles: associations with geography and the environment. Journal of Fish Biology, 67: 146–168.

Julien and Bergeron (2006) Julien HP, Bergeron NE. 2006. Effects of fine sediment infiltration on Atlantic salmon (Salmo salar) embryo survival. Hydrobiologia 53: 61–71.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Jurajda, P. (1999), Comparative nursery habitat use by 0+ fish in a modified lowland river. Regulated Rivers: Research & Management, 15: 113–124

Kalbus, C. Schmidt, J.W. Molson, F. Reinstorf and M. Schirmer, Influence of aquifer and streambed heterogeneity on the distribution of groundwater discharge. Hydrol Earth Syst Sci, 130 1 (2009), pp. 69–77

Kamler E. (2002) Ontogeny of yolk-feeding fish: an ecological perspective Reviews in Fish Biology and Fisheries Volume: 12, Issue: 1, Publisher: Springer, Pages: 79-103

Kincheloe JW, Wedemeyer GA, Koch DL., 1979. Tolerance of developing salmonid eggs and fry to nitrate exposure. Bull Environ Contam Toxicol 23: 574–578

Kingsolving AD, Bain MB. 1993. Fish assemblage recovery along a riverine disturbance gradient. Ecological Applications 3: 531-540.

Kondolf and Wolman, 1993 Kondolf G. M., Sale M. J. and Wolman M. G. (1993). Modification of fluvial gravel size by spawning salmonids. Water Resources Research. 29, 7: 2265-2274.

Kondolf G. M., Lisle, T.E. & Wolman, G.M. (2003) Bed sediment measurement, in Kondolf G. M., & Piegay, H. (Eds) tools in fluvial geomorphology, J.Wiley 7 Sons, Chcihester, UK, 347-395.

Kondolf GM, Wolman MG. 1993. The sizes of salmonid spawning gravels. Water Resources Research 297: 2275–2285.

Kondolf GM. 2000. Assessing salmonid spawning gravel quality. Transactions of the American Fisheries Society 129: 262–281.

Koski K.V. (1975) The survival and fitness of two stocks of chum salmon (Oncorhynchus keta) from egg deposition to emergence in a controlled stream environment at Big Beef Creek. Doctoral dissertation. University of Seattle.

Koski, K. V. 1966. The survival of coho salmon (Oncorhynchus kisutch) from egg deposition to emergence in three Oregon coastal streams. Master's thesis, Oregon State University, Corvallis, Oregon, USA.

Koutný, J., and M. Rulík (2007), Hyporheic biofilm particulate organic carbon in a small lowland stream (Sitka, Czech Republic): Structure and distribution, Int. Rev. Hydrobiol., 92, 402–412.

Krause, S. Heathwaite, L Binley, A. Keenan, P. (2009) Nitrate concentration changes at the groundwater-surface water interface of a small Cumbrian river Hydrol. Process. 23, 2195–2211 (2009)

Krishnappan, B.G. 2009. Effect of pulp mill effluent on the transport of suspended sediment in the Athabasca River near Hinton, Alberta, Canada. Canadian Journal of Civil Engineering 36(10):1598-1604.

Krough A. (1941) The comparative physiology of respiratory mechanisms. University of Pennsylvania Press, Philadelphia. 172 pp.

Kroupova, H; Machova, J. Svobodova, Z. Nitrite influence on fish: a review Vet. Med. – Czech, 50, 2005 (11): 461–471

Kruskal, W. H., and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47:583–621.

Kuhnle, R.A.Fluvial transport of sand and gravel mixtures with bimodal size distributions (1993) Sedimentary Geology. Volume 85, Issues 1-4, May 1993, Pages 17-24

Kupferberg SK. 1996. Hydrologicand geomorphic factors affecting conservation of a riverbreeding frog (Rana boylii). Ecological Applications 6: 1332-1344.

Lankford SE, Adams TE, Cech JJ Jr (2003) Time of day and water temperature modify the physiological stress response in green sturgeon, Acipenser medirostris. Comp Biochem Physiol A 135:291–302

Lankford, S.E., Adams, T.E., Miller, R.A., and Cech, J.J., Jr. (2005). The cost of chronic stress: Impacts of a nonhabituating stress response on metabolic variables and swimming performance in sturgeon. Physiol Biochem. Zool. 78, 599-609.

Lapointe, M. Eaton, B. Driscoll, S. Latulippe, C. (2000). Modelling the probability of salmonid egg pocket cosur due to floods. Canadian Journal of Fisheries and Aquatic Sciences. 57: 1120-1130.

Lawlor, P.A., M.J. Helmers, J.L. Baker, S.W. Melvin, and D.W. Lemke. 2005. Nitrogen application rate effects on corn yield and nitrate-nitrogen concentration and loss in sub-surface drainage. ASAE Paper no. 052025. St. Joseph, MI, ASAE.

Lazar, A., Butterfield, D., Futter, M.N., Rankinen, K., Thouvenot-Korppoo, M., Jarritt, N., Lawrence, D.S.L., Wade A.J. and Whitehead, P.G. (2010) An assessment of the fine sediment dynamics in an upland river system: INCA-Sed modifications and implications for fisheries. Science of the Total Environment. 408 (2010) 2555–2566

Levasseur, M., Bérubé, F. & Bergeron, N.E. (2006) A field method for the concurrent measurement of fine sediment content and embryo survival in artificial salmon redds, Earth Surface Processes and Landforms, 31, 526-530.

Lisle, T.E. (1989) Sediment transport and resulting depostion in spawning gravels, North Coastal California. Water Resources Research. 25 (6): 1303 – 1319.

Lord E.I. and Anthony, S.G. 2000. MAGPIE. A modeling framework for evaluating nitrate losses at national and catchment scales. Soil Use Management 16, 167-174.

Lotspeich F.B., Everest F.H. (1981) A new method for reporting and interpreting textural composition of spawning gravel. US Department of Agriculture Research Note PNW-369.

Louhi, P. Maki-Petays, A. Erkinaro, J. Spawning habitat of Atlantic salmon and brown trout: General criteria and intragravel factors. River. Res. Applic. 24: 330–339 (2008)

Lucas M, Baras E (2001) Migration of freshwater fishes. Blackwell Science, Oxford

Luckman B.B. (1970) In: The glaciation of Wales and adjoining regions (edited by C.A. Lewis) pg 175 -196.

Lura, H., B.T. Barlaup & H. Saegrov. 1993. Spawning behaviour of a farmed escaped female Atlantic salmon (Salmo salar). J. Fish Biol. 42: 311–313.

MacFarlane, R.B. and E.C. Norton (2002) Physiological ecology of juvenile chinook salmon (Oncorhynchus tshawytscha) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fish. Bull. 100:244-257.

MacKenzie, C. &Moring, J. R. (1988). Estimating survival of Atlantic salmon during the intra-gravel period. North American Journal of Fisheries Management 8, 45–49.

Macklin MG, Lewin J. 2008. Alluvial responses to the changing Earth System**.** Earth Surface Processes and Landforms, 33: 1374-1395

Malcolm I.A., Soulsby C., Youngson A. and Petry J. (2003). Heterogeneity in ground water surface water interactions in the hyporheic zone of a salmonid spawning stream: towards integrating hydrometric and tracer approaches. Hydrological Processes. 17: 601-617

Malcolm IA, Soulsby C. Youngson A, Hannah, D.M. 2004b. Spatial and temporal variability of groundwater – surface water interactions in salmon spawning streams: implications for eggs survival and development. Hydrology: Science and Practice for the 21st Century, Proceedings for the British Hydrological International Symposium, London, Vol. 2, 130–138

Malcolm IA, Soulsby C. Youngson A, Hannah, D.M. Mclaren, I.Thorne, S. 2004a. Hydrological influences on hyporheic water quality: implications for salmon egg survival. Hydrological Processes, 18, 1521–1542.

Malcolm IA, Youngson A, Soulsby C. (2003). Survival of salmonid eggs in gravel bed streams: effects of groundwater-surface water interactions. River Research and Applications 19: 303–316.

Malcolm, I.A., Middlemiss, C.A., Soulsby, C., Middlemiss, S., and Youngson, A.F. (2010) Hyporheic processes in a small agricultural stream: implications for salmon embryo survival. *Fundamental and Applied Limnology*

Malcolm, I.A., Soulsby, C. Youngson, A.F., Tetzlaff, D. (2009) Fine scale spatial and temporal variability of hyporheic hydrochemistry in salmon spawning gravels with contrasting groundwater-surface water interactions. *Hydrogeology Journal,* 17, 161-174

Malcolm, I.A., Soulsby, C., Youngson, A.F., 2006. High frequency logging technologies reveal state dependence of hyporheic

Malcolm, I.A., Soulsby, C., Youngson, A.F., Hannah, D.M., 2005. Catchment scale controls on groundwater - surface interactions in salmon spawning gravels. Rivers Research and Applications 21,977–989.

Malcolm, I.A., Youngson, A.F., Soulsby, C. and Imholt, C. (2011) Is interstitial velocity a consistent predictor of salmonid embryo survival? *Transactions of the American Fisheries Society.*

Marsh and Lees 2003 (eds) Hydrological Data United Kingdom, Hydrometric Register and Statistic 1996-2000. Centre for Ecology and Hydrology, Wallingford, UK 208p.

Marsh, T.J. and Lees, M.L (2003). Hydrological Data, United Kingdom, Hydrometric Register and Statistics 1996-2000. CEH Wallingford, UK

Mason JC. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26: 63–91.

Matschak, T.W., Stickland, N.C., Crook, A.R., Hopcroft, T., 1995. Is physiological hypoxia the driving force behind temperature effects on muscle development in embryonic Atlantic salmon (Salmo salar L.)? Differentiation 59, 71–77.

Mc Cormick et al, 1998. Movement, migration, and smolting of Atlantic salmon (Salmo salar) Can. J. Fish. Aquat. Sci. 55(Suppl. 1): 77–92 (1998).

McCormick, S.D., Saunders, R.L., 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. American Fisheries Society Symposium 1, 211–229.

McDowell-Boyer, L.M., Hunt, J.R. & Sitar, N. 1986. Particle transport through porous media. Water Resources Research. 22 (13). 1901-1921.

McGinnity P., Prodöhl P., Ferguson A., Hynes R., Maoiléidigh N., Baker N., Cotter D., O'Hea B., Cooke D., Rogan G., Taggart J. & Cross T. (2003). Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar,* as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society: Biological Sciences*, 270, 2443-2450.

McGurk, M.D.; Landry, F.; Tang, A.; Hanks, C.C. (2006). Acute and chronic toxicity of nitrate to early life stages of Lake Trout (Salvelinus namaycush) and Lake Whitefish (Coregonus clupeaformis). Environmental Toxicology and Chemistry 25(8): 2187–2196.

Meehan, W. R. (editor) 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. Special Publication 19. American Fisheries Society, Bethesda, MD.

Meffe GK, Minckley WL. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. American Midland Naturalist 117: 177-191.

Meyer, C.B. 2003. The importance of measuring biotic and abiotic factors in the lower egg pocket to predict coho salmon egg survival. Journal of Fish Biology (2003) 62, 534-548.
Mills D (1989). Ecology and Management of Atlantic Salmon. Chapman and Hall, London.

Mills D (1991). Strategies for the rehabilitation of Atlantic salmon.The Atlantic Salmon Trust, Pitlochry.

Minella, J.P.G., Walling, D.E., Merten, G.H., 2008a. Combining sediment source tracing techniques with traditional monitoring to assess the impact of improved land management on catchment sediment yields. Journal of Hydrology 348, 546–563.

Mohamed (2003) Measurement of sediment oxygen demand (SOD) 'in Situ' measuring chamber and its applications for stream water quality modeling and aquaculture management. Technical report - Institute of Environmental and Water resources management (IPASA), University of Technology, Skudai, Malaysia.

Moir HJ, Gibbins CN, Soulsby C, Webb J. 2004. Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (Salmo salar L.). Geomorphology 60: 21–35.

Moir, H.J., Soulsby, C. and Youngson, A.F., 1998. Hydraulic and sedimentary characteristics of habitat utilised by Atlantic salmon for spawning in the Girnock Burn, Scotland. Fish Manage Ecol 5, pp. 241–254

Moir, H.J., Soulsby, C., Youngson, A.F., 2002. Hydraulic and sedimentary controls on the availability and use of Atlantic salmon (Salmo salar) spawning habitat in the River Dee system, northeast Scotland. Geomorphology 45, 291–308.

Montgomery, D.R., Buffington, J.M., Petreson, N.P., Schuett-Hames, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Can. J. Fish. Aquat. Sci. **53**: 1061–1070.

Montgomery WL, McCormick SD, Naiman RJ, Whoriskey FG, Black GA. 1983. Spring migratory synchrony of salmonid, catostomid, and cyprinid fishes in Riviere la Truite, Quebec. Canadian Journal of Zoology 61: 2495-2502.

Montgomery,D. 2003. King of Fish, the thousand year run of Salmon. Westview Press.

Moore, J.E. 1961. Petrography of northeastern Lake Michigan bottom sediments. Journal of Sedimentary Research, 31(3): 402–436

Moss, B., Bennion, H., Carvalho, L., Demeester, L., Feuchtmayr, H., Friberg, N., Gessner, M.O., Hefting, M., Lauridsen et al. (2010). Interaction of climate change and eutrophication. In: Climate Change Impacts on Freshwater Ecosystems. Wiley, Chichester.

Motha, J.A., Wallbrink, P.J., Hairsine, P.B., Grayson, R.B., 2004. Unsealed roads as suspended sediment sources in an agricultural catchment in southeastern Australia. Journal of Hydrology 286,1–18

Murphy CA, Rose KA, Alvarez M, Fuiman LA. (2008) Modeling larval fish behavior: Scaling the sublethal effects of methylmercury to population-relevant endpoints Aquatic Toxicology 86 (2008) 470–484

NASCO (2008) Fisheries Management Focus Area Report European Union -UK (England and Wales).

Nechaev IV, Dikhnich AV, Kostin VV, Romanenko VO (2006) Dynamics of Cortisol and the Development of the Glucocorticoid Function in the Early Ontogenesis of Atlantic Salmon Salmo salar Journal of Ichthyology, 2006, Vol. 46, No. 4, pp. 328–341.

Nagaoka, H., and Ohgaki, S. (1990). Mass transfer mechanism in a porous riverbed. Water Research 24, pp. 417–425.

Natural Resource Council. 2000. Clean Coastal Waters- Understanding and Reducing the Effects of Pollution. National Academy Press.

Neal, C., H. P. Jarvie, et al. (2006). Nitrate concentrations in river waters of the upper Thames and its tributaries. Science of the Total Environment 365(1-3): 15-32.

Nelson, R. L., M. L. McHenry & W. S. Platts, 1991. Mining. American Fisheries Society (Spec. Publ.) 19: 425–457.

Nesler TP, Muth RT, Wasowicz AF. 1988. Evidence for baseline flow spikes as spawning cues for Colorado Squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5: 68-79.

Nicholls, D.J. 2000. The source and behaviour of fine sediment deposits in the River Torridge, Devon and their implications for salmoid spawning. Ph.D. thesis, University of Exeter, Exeter, UK.

Nilsson C. 1982. Effects of stream regulation on riparian vegetation. Pages 93-106 in Lillehammer A, Saltveit SJ, eds. Regulated rivers. New York: Columbia University Press

Oeurng, C.,Sauvage, S. and Sánchez-Pérez, J.-M. (2010), Dynamics of suspended sediment transport and yield in a large agricultural catchment, southwest France. Earth Surface Processes and Landforms, 35: 1289–1301

Oldfield, F. & Clark, R.L. (1990) Lake sediment-based studies of soil erosion. In: Soil Erosion on Agricultural Land, J. Boardman, I.D.L. Foster & J.A. Dearing (eds.), 201-228. Wiley, Chichester.

O'Connell M, Skibinski DOF & Beardmore JA (1995). Mitochondrial DNA and allozyme variation in Atlantic salmon(Salmo salar) populations in Wales. Canadian Journal of Fisheries and Aquatic Sciences 52, 171–178.

Ortuno J, Esteban MA, Meseguer J (2001) Effects of short-term crowding stress on the gilthead seabream (Sparus aurata L.) innate immune response. Fish Shellfish Immunol 11:187–197

Owens, P.N., Walling, D.E., Leeks, G.J.L., 2000. Tracing fluvial suspended sediment sources in the catchment of the River Tweed, Scotland, using composite fingerprints and a numerical mixing model. In: Foster, I.D.L. (Ed.), Tracers in Geomorphology. John Wiley & Sons, Chichester,pp. 291–308.

Owens, P. N., Batalla, R. J., Collins, A. J., Gomez, B., Hicks, D. M., Horowitz, A. J., Kondolf, G. M., Marden, M., Page, M. J., Peacock, D. H., Petticrew, E. L., Salomons, W. and Trustrum, N. A. (2005), Fine-grained sediment in river systems: environmental significance and management issues. River Research and Applications, 21: 693–717.

Packman, A. and MacKay, J. (2003). Interplay of stream-subsurface exchange, clay particle deposition, and streambed evolution. Water Resources Research 39(4).

Pander, J. and Geist, J. (2010), Seasonal and spatial bank habitat use by fish in highly altered rivers – a comparison of four different restoration measures. Ecology of Freshwater Fish, 19: 127–138

Petts GE. 1984. Impounded rivers: perspectives for ecological management. New York: John Wiley & Sons.

Petticrew E.M. Arocena, J.M. (2003) Organic matter composition of gravel stored sediment from salmon bearing streams. Hydrobiologia 949, 17-24

Petticrew, E.L. and Rex, J.F. (2006). The importance of temporal changes in gravel-stored fine sediment on habitat conditions in a salmon spawning stream, in Sediment Dynamics and the Hydromorphology of Fluvial Systems (Eds) J.S. Rowan, R.W. Duck and A. Werritty. International Association of Hydrological Sciences Press 306: 434-441.

Phillips RW, Campbell HJ. 1962. The embryonic survival of Coho salmon and steelhead trout as influenced by some environmental conditions in gravel beds. In 14th Annual Report of the Pacific Marine Fisheries Commission for the Year 1961. Pacific Marine Fisheries Commission, Portland, OR; 60–73.

Phillips, R. W., R. L. Lantz, E. W. Cliare, AND J.R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104:461-466.

Phillips,J.M. Russel, M. A. Walling, D. E. (2000) Time-integrated sampling of fluvial suspended sediment: a simple methodology for small catchments. Hydrol. Process. 14, 2589-2602 (2000)

Pickering, A.D., (1992). Rainbow trout husbandry: management of the stress response. Aquaculture 100, 125–139

Pickering AD, Pottinger TG (1989) Stress response and disease resistance in salmonid fish: effects of chronic elevation of plasma cortisol. Fish Physiol Biochem 7:253–258

Potter, E. C. E., Crozier, W. W., Schön, P-J., Nicholson, M. D., Prévost, E., Erkinaro, J., Gudbergsson, G., Karlsson, L., Hansen, L. P., MacLean, J. C., Ó Maoiléidigh, N. and Prusov S. (2004) Estimating and forecasting pre-fishery abundance of Atlantic salmon (Salmo salar L.) in the northeast Atlantic for the management of mixed stock fisheries. ICES Journal of Marine Science, 61: 1359-1369.

Portz, D.E., Woodley, C.M. and Cech, J.J. Jr (2006) Stress-associated impacts of short-term holding on fishes. Reviews in Fish Biology Fisheries 16, 125–170.

Portz, D.E. Fish-holding-associated Stress in Sacramento River Chinook Salmon (*Oncorhynchus shawytscha*) at South Delta Fish Salvage Operations: Effects on Plasma Constituents, Swimming Performance, and Predator Avoidance. PhD Thesis.

Power ME. 1992. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Archiv fiir Hydrobiologie 125: 385410

Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. J. Comp. Physiol. 137, 243-248.

Quinn,T. 2005. The Behaviour and Ecology of Pacific Salmon and Trout. Pub: Hopkins Fulfillment Services.

Randall, D. J. and T. K. N. Tsui (2002). "Ammonia toxicity in fish." Marine Pollution Bulletin 45(1-12): 17-23.

Reiser, D. W., and R. G. White. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. North American Journal of FisheriesManagement 8: 432-437.

Randall DJ, Perry SE (1992) Catecholamines. In: Hoar WS, Randall DJ (eds) Fish physiology, vol 12B. Academic Press, New York, pp 255–300

Richardson, K.. Benson, I. CARLING, P.A. An instrument to record sediment movement in bedrock channels (2003) *Erosion and Sediment Transport Measurement in Rivers: Technological and Methodological Advances* (Proceedings of the Oslo Workshop, June 2002). IAHS Publ. 283, 2003.

Rombough, P.J., (1988). Respiratory gas exchange, aerobic metabolism and effects of hypoxia during early life. In: Hoar,W.S., Randall, D.J. (Eds.), Fish Physiology, Vol. XI A. Academic Press, New York, pp. 59–161.

Robertson L. 1997. Water operations on the Pecos River, New Mexico and the Pecos bluntnose shiner, a federally-listed minnow. US Conference on Irrigation and Drainage Symposium.

Rood SB, Mahoney JM, Reid DE, Zilm L. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. Canadian Journal of Botany 73: 1250-1260.

Rounds, S.A. and M.C. Doyle. 1997. Sediment Oxygen Demand in the Tualatin River Basin, Oregon, 1992-96. U.S. Geological Survey Water-Resources Investigations Report 97-4103.

Roussel, J.M. (2007). Carry-over effects in brown trout (Salmo trutta): hypoxia on embryos impairs predator avoidance by alevins in experimental channels

Rosenbaum, M.S., 2007. A Geological Guide in front of the last glacier in South Shropshire. Shropshire Geological Society Special Publication, printed by Scenesetters, Bucknell SY7 0AL, UK

Roy, A.G., Buffin-Bélanger, T. & Deland, S. 1996. Scales of turbulent coherent flow structures in a gravel-bed river. In: Ashworth, P.J., Bennett, S.J., Best, J.L. & McLelland S.J. (Eds). Coherent Flow Structures in Open Channels. John Wiley. Chichester. 147-164.

Rubin J-F. and Glimsater C. (1996). Egg to fry survival of the sea trout in some streams of Gotland. Journal of fish Biology. 48: 585-606.

Rondeau, B., Cossa, D., Gagnon, P., Bilodeau, L., 2000: Budget and sources of suspended sediment transported in the St. Lawrence River, Canada. Hydrological processes, 14, 21-36

Rowan, J.S., Goodwill, P., Franks, S.W., 2000. Uncertainty estimation in fingerprinting suspended sediment sources. In: Foster, I.D.L. (Ed.), Tracers in Geomorphology. John Wiley & Sons, Chichester, pp. 279–290.

Russell, M.A., Walling, D.E., Hodgkinson, R.A., 2001. Suspended sediment sources in two small lowland agricultural catchments in the UK. Journal of Hydrology 252, 1–24

Ryan, P.A. 1991: Environmental effects of sediment on New Zealand streams: a review. New Zealand Journal of Marine and Freshwater Research 25:207-221.

Santiago, R.L. Thomas and R.L. McCarty et al.., Particle size characteristics of suspended and bed sediments in the Rhone river, Hydrol. Process. 6 (1992), pp. 227–240

Savant AS, Reible DO, Thibodeaux lJ. 1987. Convective transport within stable river sediments. Water Resources Research 23(9): 1763–1768.

Sayer, M.D., Reader, J.P., Dalziel, T.R. (1993) Freshwater acidification: effects on the early life stages of fish Reviews in Fish Biology and Fisheries Volume 3, Number 2, 95-132

Scheidegger KJ, Bain MB. 1995. Larval fish in natural and regulated rivers: assemblage composition and microhabitat use. Copeia 135.

Schreck CB (1981) Stress and compensation in teleostean fishes: Response to social and physical factors. In: Pickering A (ed) Stress and fish. Academic Press, New York, pp 295–321

Schreck, C.B. (1990). Physiological, Behavioural, and Performance Indicators of Stress. American Fisheries Society

Scott, ML, Auble GT, Friedman JM. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications 7: 677-690.

Scullion, J. 1983. Effects of impoundment on downstream bed materials of two upland rivers in mid-Wales and some ecological implications. Archiv fuer Hydrobiologie, 96: 329–344.

Sear D. A. (1993). Fine sediment infiltration into gravel spawning within a regulated river experiencing floods: Ecological implications for salmonids. Regulated Rivers Research and Management. 8: 373-390

Sear et al,(2008). Salmon Spawning Habitat in Rivers. American Fisheries Society Symposium 65

Sear, D.A. & DeVries, P.D. (editors) 2008, Salmonid spawning habitat in rivers: physical controls, biological responses and approaches to remediation, American Fisheries Society, Bethesda, Maryland, USA. 376p.

Sear, D.A., P.A. Carling and S.M. Greig. 2005. Fine sediment accumulation in spawning gravels and the effects on interstitial flow. Fifth international Symposium on Ecohydraulics: aquatic habitats: analysis and restoration. International Association of Hydraulic Engineering and Research, Madrid. Pgs: 808-812.

Seiki, T., H.Izawa, E. Date and H. Sunahara. 1994. Sediment Oxygen Demand in Hiroshima Bay. Water Research 28(2): 385-393.

Shang EH, Wu RS. (2004) Aquatic Hypoxia Is a Teratogen and Affects Fish Embryonic Development Environ. Sci. Technol. 2004, 38, 4763-4767

Sheridan GJ, Noske PJ, Whipp RK, Wijesinghe N. The effect of truck traffic and road water content on sediment delivery from unpaved forest roads. Hydrol Process 2006;20:1683–99.

Shirazi, M.A. and Seim W.K. (1981) Stream system evaluation with emphasis on spawning habitat for salmonids. Water Resources Research. 17: 592-549.

Shumway S.J., Warren, C.E. Doudoroff, P. (1964). Influence of oxygen and water movement on the growth of steelhead trout and Chinook salmon embryos at different water velocities. Transactions of the American fisheries society. 93: 342-356.

Sigler, J.W., Bjornn, T.C., Everest, F.H., 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. Transactions of the American Fisheries Society 113, 142–150.

Silver S. J., Warren C. E. Doudoroff P. (1963). Dissolved oxygen requirements of developing Steelhead trout and Chinook salmon embryos at different velocities. Transactions of the American Fisheries Society. 92(4): 327-343.

Silver, S.J., C.E. Warren, P. Doudoroff. (1963). Dissolved oxygen requirements of developing steelhead trout and Chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society. 92(4):327-343.

Sink TD, Kumaran S, Lochmann RT (2006) Development of a whole-body cortisol extraction procedure for determination of stress in golden shiners, Notemigonus crysoleucas Fish Physiol Biochem (2007) 33:189–193

Slattery et al.., 2000. M.C. Slattery, J. Walden and T.P. Burt, Use of mineral magnetic measurements to fingerprint suspended sediment sources: results from a linear mixing model. In: I.D.L. Foster, Editor, Tracers in geomorphology, John Wiley and Sons Ltd, Chichester (2000), pp. 309–322.

Smith, H.G. and Dragovich, D. (2008) Improving precision in sediment source and erosion process distinction in an upland catchment, south-eastern Australia. Catena, 72: 191-203.

Sophocleous, M. Interactions between groundwater and surface water: the state of the science (2002) Hydrogeology Journal (2002) 10:52–67

Soulsby C, Malcolm IA, Youngson AF. 2000. Groundwater in headwaters: hydrological and ecological significance. in Groundwater in Celtic Regions, Studies in Hard Rock and Quaternary Hydrogeology, Robbins NS, Minstear BDR (eds). Blackwell: London; 98–112.

Soulsby C., Malcolm I., Youngson A. 2001. Hydrochemistry of the hyporheic zone in salmon spawning gravels: a preliminary assessment in a small regulated stream. Regulated Rivers: Research and Management, 17, 651–665

Soulsby C, Neal C, Laudon H, Burns D, Merot P, Bonell M, Dunn SM, Tetzlaff D. 2008. Catchment studies, data collection and conceptualization: simply a case of less is more? Hydrological Processes 22(12): 2057–2061.

Soulsby C., Malcolm, I.A., Tetzlaff, D., Youngson, A.F. (2009) Seasonal and inter-annual variability in hyporheic water quality revealed by four years continuous monitoring in a salmon spawning stream. *Rivers Research Application.* 25: 1304–1319

Sparks RE. 1992. Risks of altering the hydrologic regime of large rivers. Pages 119-152 in Cairns J, Niederlehner BR, Orvos DR, eds. Predicting ecosystem risk. Vol XX. Advances in modern environmental toxicology. Princeton (NJ): Princeton Scientific Publishing Co.

Stanford JA. 1994. Instream flows to assist the recovery of endangered fishes of the Upper Colorado River Basin. Washington (DC): US Department of the Interior, National Biological Survey. Biological Report nr 24.

Stead S. M., and Laird L.M.,(2002) Handbook of salmon farming. Springer-Praxis Books :57 -59.

Strmac, M. Oberemm, A. Braunbeck, T. (2002) Effects of sediment eluates and extracts from differently polluted small rivers on zebrafish embryos and larvae. *J. Fish Biol.*, **61** (2002), pp. 24–38.

Stone, M. & English, M. C. 1993 Geochemical composition, phosphorus speciation and mass transport of fine-grained sediment in two Lake Erie tributaries. Hydrobiologia 253, 17-29

Storey RG, Williams DD. 2004. Spatial responses of hyporheic invertebrates to seasonal changes in environmental parameters. *Freshwater Biology* **49**: 1468–1486.

Stott TA, Leeks GJL, Marks SD, Sawyer AJ. 2001. Environmentally sensitive plot-scale timber harvesting: impacts on suspended sediment, bedload and bank erosion dynamics. Journal of Environmental Management 63(1): 3–25.

Stromqvist, J., Collins, A.L., Davison, P.S., and Lord, E.I. (2008). PSYCHIC – a process-based model of phosphorus and sediment transfers within agricultural catchments. Part 2. A preliminary evaluation. Journal of Hydrology 350, 303-316.

Stormer J, Jensen FB, Rankin JC., 1996. Uptake of nitrite, nitrate, and bromide in rainbow trout, Oncorhynchus mykiss: Effects on ionic balance. Can J Fish Aquat Sci 53: 1943–1950

Takle H.G. et al 2005. The effect of heat and cold exposure on HSP70 expression and development of deformities during embryogenesis of Atlantic salmon (Salmo salar). Aquaculture 249: 1-4. Pg. 515-524

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3:123-135.

Taylor DW. 1982. Eastern Sierra riparian vegetation: ecological effects of stream diversion. Mono Basin Research Group Contribution nr 6, Report to Inyo National Forest.

Tetzlaff D, Uhlenbrook S. 2005. Significance of spatial variability in precipitation for process-oriented modelling: results from two nested catchments using radar and ground station data. Hydrology and Earth System Sciences 9: 29–41

Tetzlaff D, Soulsby C, Bacon PJ, Youngson AF, Gibbins C, Malcolm IA.(2007) Connectivity between landscapes and riverscapes — a unifying theme in integrating hydrology and ecology in catchment science? Hydrol Process 2007;21:1385–9.

Theurer, F.D. Harrod T.R. Theurer, M. 1998. Sedimentation and salmonids in England and Wales. Report P2-103, Environment Agency, Bristol (1998), 70 pp.

Theurer, F.D., Harrod, T.R. and Theurer, M. (1998). Sedimentation and Salmonids in England and Wales. EA R&D report P194

Thibodeaux LJ, Boyle JD. 1987. Bedform-generated convective transport in bottom sediment. Nature 325(22): 341–343.

Thoms, M.C., and M. Parsons. 2002. Eco-geomorphology: an inter-disciplinary approach to river science. International Association of Hydrological Sciences 276: 113-120.

Thurston R, Russo R. (1983) Acute Toxicity of Ammonia to Rainbow Trout. Transactions of the American Fisheries Society, 1548-8659, Volume 112, Issue 5, 1983, Pages 696 – 704

Todd, C.D. Hughes, S.L. Marshall, C.T. M Clean, J.C. Lonergan, M.E. Martinbiuw, E. (2008) Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon Global Change Biology (2008) 14, 1–13

Tonina (2005) Interaction between river morphology and intragravel flow paths within the hyporheic zone PhD Thesis. University of Idaho.US

Tonina, D. Buffington , J.M. Hyporheic Exchange in Mountain Rivers I: Mechanics and Environmental Effects *Geography Compass* 3/3 (2009): 1063–1086.

Travnichek VH, Bain MB, Maceina MJ. 1995. Recovery of a warmwater fish assemblage after the initiation of a minimum-flow release downstream from a hydroelectric dam. Transactions of the American Fisheries Society 124: 836-844.

Triska, F. J., J. H. Duff, and R. J. Avanzino (1993), The role of water exchange between a stream channel and its Hyporheic zone in nitrogen cycling at the terrestrial-aquatic interface, Hydrobiologia, 251, 167-184.

Turnpenny A. W. H. and Williams R. (1980). Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology. 17: 681-693.

Turnpenny AWH, Williams R. 1980. Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology 17: 681–693.

Uusi-Kämppä, J., Braskerud, B., Jansson, H., Syversen, N., Uusitalo, R., 2000. Buffer zones and constructed wetlands as filters for agricultural phosphorus. Journal of Environmental Quality 29, 151–158.

USEPA (Environmental Protection Agency) 2010. Final Report on Acute and Chronic Toxicity of Nitrate, Nitrite, Boron, Manganese Fluoride, Chloride and Sulfate to Several Aquatic Animal Species.

USEPA (United States Environmental Protection Agency) 1984. Ambient water quality criteria for ammonia—1984. National Technical Information Service, Springfield, VA

USEPA 1999. Update of Ambient Water Quality Criteria for Ammonia—Technical Version—1999. EPA-823-F-99-024. USEPA, Washington DC, USA

USEPA (Environmental Protection Agency) 2010. Final Report on Acute and Chronic Toxicity of Nitrate, Nitrite, Boron, Manganese Fluoride, Chloride and Sulfate to Several Aquatic Animal Species.

Valentin S, Wasson JG, Philippe M. 1995. Effects of hydropower peaking on epilithon and invertebrate community trophic structure. Regulated Rivers: Research & Management 10: 105-119

Valett, H. M., S. G. Fisher, N. B. Grimm, and P. Camill. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. Ecology 75:548–560.

Valett, H.M., J.A. Morrice, C.N. Dahm, AND M.E. Campana. 1996. Parent lithology, surface-groundwater exchange, and nitrate retention in headwater streams. Limnology and Oceanography 41(2): 333-345

Vaughan IP, Diamond M, Gurnell AM, Hall KA, Jenkins A, Milner NJ, Naylor LA, Sear DA,Woodward G, Ormerod SJ. 2009. Integrating ecology with hydromorphology: a priority for river science and management. Aquatic Conservation: Marine and Freshwater Ecosystems 19: 113–125.

Verstraeten G, Poesen J (2001). Factors controlling sediment yield from small intensively cultivated catchments in a temperate humid climate. Geomorphology, 40: 123-144.

Vedel, N.E. Korsgaard, B. Jensen, F.B. (1998) Isolated and combined exposure to ammonia and nitrite in rainbow trout (*Oncorhynchus mykiss*): effects on electrolyte status, blood respiratory properties and brain glutamine/glutamate concentrations. *Aquat. Toxicol.*, **41** (1998), pp. 325–342.

Verspoor,E,,Stradmeyer,L, Nielsen,J.,(2005). The Atlantic Salmon- Genetics, Conservation and Management. Blackwell Publishing.

Webb, B.W. and Walling, D.E., 1993. Temporal variability in the impact of river regulation on thermal regime and some biological implications. Freshwat Biol 29, pp.167–182.

Whelan KF (1993). Decline of sea trout in the west of Ireland: an indication of forthcoming marine problems for salmon. In: Mills DH (ed). Salmon in the Sea. Fishing News Books, Oxford, 171–183.

Whitehead P. Wade A. Butterfield D. (2008) Potential impact of climate change on water quality in six UK rivers. BHS 10th National Hydrology Symposium, Exeter, 2008.
Wickett, W.P., 1954. The oxygen supply to salmon eggs in spawning beds. J. Fish. Res. Board Can. 11, 933-953.

Wade AJ, Butterfield D, Griffiths T,Whitehead PG. Eutrophication control in river-systems: an application of INCA-P to the River Lugg. Hydrol Earth Syst Sc 2007;11(1):584–600.

Walker, R.R. and W.J. Snodgrass. 1986. Model for Sediment Oxygen Demand in Lakes. Journal of Environmental Engineering 112(1): 25-43.

Wallbrink, P.J., Olley, J.M., Murray, A.S., Olive, L.J., 1996. The contribution of subsoil to sediment yield in the Murrumbidgee River Basin, New South Wales, Australia. In: Walling, D.E., Webb, B.W. (Eds.), Erosion and Sediment Yield: Global and Regional Perspectives. IAHS Publ., vol. 236. IAHS Press, Wallingford, pp. 347–355.

Walling, D. E., 1977: Limitations of the rating curve technique for estimating suspended sediment loads, with particular reference to British rivers. In: Erosion and solid matter transport in inland waters (Proceedings of the Paris symposium, July 1977), IAHS Publ., 122, 34-38.

Walling, D.E., and Kane, P. 1984. Suspended sediment properties and their geomorphological significance. In Catchment experiments in fluvial geomorphology. Edited by T.P. Burt and D.E. Walling. Geobooks, Norwich. pp. 311–334.

Walling, D.E. & Webb, B.W. 1987. Suspended load in gravel-bed rivers: UK experience. *In:* C.R.Thorne, J.C. Bathurst & R.D. Hey, eds. *Sediment transport in gravel-bed rivers*., 691-723.Chichester: Wiley.

Walling, D.E., Woodward, J.C., Nicholas, A.P., 1993. A multi-parameter approach to fingerprinting suspended sediment sources. In: Peters,N.E.,Hoehn, E., Leibundgut, Ch., Tase, N., Walling, D.E. (Eds.), Tracers in Hydrology. International Association of Hydrological Sciences Publication No. 215. IAHS Press, Wallingford, UK, pp. 329–337.

Walling, D. E. & C. M. Amos, 1999. Source, storage and mobilisation of fine sediment in a chalk stream system. Hydrol. Proc. 13:323–340.

Walling, D.E., Owens, P.N., Leeks, G.J.L., 1999. Fingerprinting suspended sediment sources in the catchment of the River Ouse, Yorkshire, UK. Hydrological Processes 13, 955–975.

Walling, D.E., Woodward, J.C., 1992. Use of radiometric fingerprints to derive information on suspended sediment sources. In: Bogen, J., Walling, D.E., Day, T.J. (Eds.), Erosion and Sediment Transport Monitoring Programmes in River Basins. IAHS Publ., vol. 210. IAHS Press,Wallingford, pp. 153–164.

Walling, D.E., Russell, M.A., Hodgkinson, R.A. and Zhang, Y. (2002). Establishing Sediment Budgets for Two Small Lowland Agricultural Catchments in the UK, Catena, 47, 323–353.

Walling, D.E., Collins, A.L., McMellin, G.K., 2003. A reconnaissance survey of the source of interstitial fine sediment recovered from salmonid spawning gravels in England and Wales. Hydrobiologia 497, 91–108.

Walling, D.E., Collins, A.L. and Stroud, R. (2008). Tracing suspended sediment and particulate phosphorus sources in catchments. Journal of Hydrology 350, 274-289.

Walsh C.L. Kilsby G.G. Implications of climate change on flow regime affecting Atlantic salmon Hydrology and Earth System Sciences 11, 3(2007) 1127-1143

Walters, T.F. 1995. Sediment in streams. American Fisheries Society, Bethesda, Md.

Walling, D.E. (2006). Human impact on land-ocean sediment transfer by the world's river. Geomorphology 79: 192-216

Wickett P. (1975) The oxygen supply to salmon eggs in spawning beds. Journal of the Fisheries Research Board of Canada. 11 (6): 933-953.

Wilby R.L., Whitehead P.G., Wade A.J., Butterfield D., Davis R.J., Watts G. Integrated modelling of climate change impacts on water resources and quality in a lowland catchment: River Kennet, UK (2006) Journal of Hydrology, 330 (1-2), pp. 204-220.

Williams RN, Calvin LD, Coutant CC, Erho MW, Lichatowich JA, Liss WJ, McConnaha WE, Mundy PR, Stanford JA, Whitney RR. 1996. Return to the river: restoration of salmonid fishes in the Columbia River ecosystem. Portland (OR): Northwest Power Planning Council.

Withers, P.J.A., Hodgkinson, R.A., Bates, A., Withers, C.M., 2006. Some effects of tramlines on surface runoff, sediment and phosphorus mobilization on an erosion-prone soil. Soil Use and Management 22, 245–255.

Wakeling, J.M. (2006). Fast-start mechanics. In R.E. Shadwick and G.E. Lauder (eds.), Fish Biomechanics. (pp. 333-368). New York: Academic Press

Wedemeyer GA, McLeay DJ (1981) Methods for determining the tolerance of fishes to environmental stressors. In: Pickering A (ed) Stress and fish. Academic Press, New York, pp 247–268

Wedemeyer GA, Barton BA, McLeay DJ (1990) Stress and acclimation. In: Schreck CB, Moyle PB (eds) Methods for Fish Biology. American Fisheries Society, Bethesda, MD, pp 451–489

Welker TL, Congleton JL (2009) Preliminary examination of oxidative stress in juvenile spring Chinook salmon Oncorhynchus tshawytscha of wild origin sampled from transport barges. J Fish Biol. 2009 Nov.75(7):1895-905.

Wesche, T.A., D.W. Reiser, V.R. Hasfurther, W.A. Hubert, and Q.D. Skinner. 1989. New technique for measuring fine sediment in streams. North American Journal of Fisheries Management 9:234-238.

Westin DT., 1974. Nitrate and nitrite toxicity to salmonid fishes. Prog Fish-Cult 36: 86–89

White, D. S. 1993. Perspectives on defining and delineating hyporheic zones. Journal of the North American Benthological Society 12:61–69.

Williams, E.M. Eddy, F.B. (1989). Effect of nitrite on the embryonic development of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences, 46:1726-1729.

Winter TC (1999) Relation of streams, lakes, and wetlands to groundwater flow systems. Hydrogeol J 7:28–45.

Withers, P.J.A., Lord, E.I., 2002. Agricultural nutrient inputs to rivers and groundwaters in the UK: policy, environmental management and research needs. Science of the Total Environment, 9–24.

Wootton JT, Parker MS, Power ME. 1996. Effects of disturbance on river food webs. Science 273: 1558-1561

Wu, F.-C., 2000. Modeling embryo survival affected by sediment deposition into salmonid spawning gravels: Application to flushing flow prescriptions. *Water Resources Research* 36 (6): 1595-1603.

WWF,2001. The Status of Wild Atlantic Salmon; A River by River Assessment.

Yamamoto,T.S.,Kobayashi,W.,Kuamoto,T., 1996. Twin malformation induced in chum salmon eggs by elevated water temperature, with a suggestion as to its mechanism. Can. J. Zool. 74, 48–491.

Youngson, A.F., Jordan, W.C., Hay, D.W., 1994. Homing of Atlantic salmon (Salmo salar L.) to a tributary stream in a major river catchment. Aquaculture 121, 259–267.

Youngson et al, 2003. Management of salmonid fisheries in the British Isles: towards a practical approach based on population genetics. Fisheries Research 62 (2003) 193–209.

Youngson, A.F. Malcolm, I.A. Thorley, J.L. Bacon, P.J. and Soulsby C. (2005) Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development and causes mortality. Canadian Journal of Fisheries and Aquatic Sciences 61: 2278-2287

Yin Z, Lam TJ, Sin YM (1995) The effects of crowding stress on the non-specific immune response in fancy carp (Cyprinus carpio L.). Fish Shellfish Immunol 5:519–529

Zimmerman, A.E. and Lapointe, M. (2005) Intergranular flow velocity through salmonid redds: Sensitivity to fines infiltration low low-intensity sediment transport events. River Res. Applic. 21: 865–881