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An assessment of factors influencing the ability of U.K. spawning gravels to support the respiratory requirements of Atlantic salmon (*Salmo salar*) embryos

by

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ABSTRACT

FACULTIY OF ENGINEERING SCIENCE AND MATHEMATICS

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Doctor of Philosophy

AN ASSESSMENT OF FACTORS INFLUENCING THE ABILITY OF UK SPAWNING GRAVELS TO SUPPORT THE RESPIRATORY REQUIREMENTS OF ATLANTIC SALMON (SALMO SALAR) EMBRYOS

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In recognition of the importance of oxygen availability to salmonid incubation success, a series of complementary field and flume experiments were undertaken to investigate the flux of oxygen through spawning gravels and its relationship to the respiratory requirements of Atlantic salmon embryos.

The key findings of the field and flume monitoring programme were:

1) Pre-emergent mortalities result from: (i) lethal oxygen concentrations (concentrations below which respiration is impeded), (ii) insufficient oxygen flux (product of concentration and discharge) to meet respiratory requirements, or (iii) critical intragravel flow velocities (flow velocities that are either insufficient to meet respiration independent of oxygen concentration or insufficient to remove metabolic waste).

2) Fine sediment accumulation restricted the flow of oxygenated water through spawning gravels. Based on the results of the field study, statistically significant linear relationships between sediment accumulation and intragravel flow were developed. However, due to site specificity, these relationships were restricted to environments of similar hydraulic and sedimentary character.

3) Sedimentary oxygen demands reduce intragravel oxygen concentrations. The oxygen demand of material deposited in the incubation environment was assessed at each field site. It was found that sedimentary oxygen demands varied between systems dependent on the proportion of organic material and the magnitude of the demand associated with that material.

4) Surface flow conditions influence the flux of oxygenated water through spawning gravels. In a series of flume experiments, it was shown that surface flow influences both subsurface flow paths (hydraulic head) and intragravel flow velocities. Furthermore, it was shown that flow through a sinusoidal bedform did not conform to simple Darcian principles. It was hypothesised that turbulent driven momentum exchange influenced intragravel flow velocities.

5) Clay particles potentially inhibit the exchange of oxygen across the egg membrane. The results of a laboratory study indicated that the presence of a thin film of clay at the egg surface severely restricted embryonic oxygen consumption. At present it is not possible to determine whether the clay particles are physically blocking micro-pore canals, or simple inhibiting the availability of oxygen at the egg surface.

It was recognised that these factors operate contemporaneously and that interactions between factors influence conditions within the incubation environment. Furthermore, the results of the field investigation indicated that the presence and magnitude of individual factors varied between the monitoring sites, indicating that the precise compound of factors influencing incubation success varies between systems dependent on channel and catchment characteristics.

Finally, in addition to investigating oxygen availability, the limitations of previously proposed indices of incubation success were recognised. To address these limitations, the principals of mass transport were applied to the problem of defining embryonic respiratory requirements. The results of this analysis were integrated with the oxygen concentration, intragravel flow velocity and embryonic survival data obtained during the field-monitoring programme, and three thresholds of embryonic survival based on oxygen availability were defined.

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A note on terminology

When referring to processes or factors that are applicable to all salmon and trout species, the term salmonid is applied. When discussing items pertaining to anadromous salmon species, the term salmon is adopted. Finally, when discussing matters that relate directly to a specific salmon species, including research findings in this project that can only be related directly to the study species (Atlantic salmon), the species is identified.

When referring to the rate of passage of water through the riverbed, a number of terms have been applied in the literature, including intragravel flow velocity, interstitial velocity, interstitial pore velocity and seepage velocity. In light of its frequent usage in salmonid related literature, the term intragravel flow velocity was adopted in this thesis.

Chapter 1. Introduction

This introductory section provides an overview of the plight of the Atlantic salmon and discusses the evolution of research into incubation success.

1.1 A species in decline

Wild Atlantic salmon (*Salmo salar*) populations are in decline. A recent study commissioned by the World Wide Fund for Nature (WWF) (WWF, 2001) reported that wild Atlantic salmon have been eliminated from over 300 of the world's 2000 historical Atlantic salmon bearing rivers, and that only 43% of the remaining rivers are recognised as having healthy populations. Within the U.K., seven of the 76 rivers in England and Wales previously believed to contain salmon runs are now classified as extinct, 10 are classified as critical and 19 are classified as endangered. Only 29 are classified as having healthy salmon populations[1]. Within Scotland and Ireland, the scale of the decline is less severe. However, recent reports indicate that populations within a number of historically productive rivers are also in decline (WWF, 2001; Youngson, 2002).

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[1] See WWF (2001) for a description of the classification system.

Population figures pertaining to other salmonid species indicate that declining stocks are not restricted to Atlantic salmon. Statistics from North America indicate that Pacific salmon (*Oncorhynchus spp.),* which are native to the western American coastline, are also in a period of recession, and a number of Pacific salmon populations have recently been placed on the endangered species list (Huntington *et al.*, 1996, Shea and Mangel, 2001). Concerns on both sides of the Atlantic have also been raised regarding declining trout numbers. Species under particular pressure include Brown trout (*Salmo trutta*), Cutthroat trout (*Salmo clarki*) and Steelhead trout (*Oncorhynchus mykiss*) (Harig and Fausch, 2002).

Declining salmon stocks have negative socio-economic and environmental implications. From a socio-economic perspective, wild salmon are an important food and recreational resource. The revenue and industry associated with commercial fishing, generates jobs and provides an economic base for many North American communities (Oregon Rivers Council, 1992). Furthermore, although in many countries the advent of fish farming has reduced the importance of wild salmon as a food resource, for many indigenous communities, particularly in North America, wild salmon remain part of an established diet (Cederholm *et al.*, 2001). The revenue generated from angling can also be an important source of income, particularly in rural areas. In the U.K., a survey of the value of angling to businesses in the Tweed catchment found that angling generates about £12.5 million annually (Deloitte and Touche, 1996). From a global perspective, hotels, fishing lodges, fishing tackle shops, water bailiffs and numerous others professions depend directly or indirectly on the revenue generated from angling.

In ecological terms, salmon are widely recognised as an indicator species. Subsequently, their decline may be indicative of a broader deterioration in marine and freshwater habitat quality. Additionally, wild salmon are an important food resource for various marine and freshwater species, including seals, cetaceans and otters (Cederholm, 2001). Consequently, declining populations may have implications at higher levels of the food chain. Finally, salmon, particularly Pacific salmon, have been identified as important nutrient vectors. The nutrients released by decomposing carcasses have been shown to form the basis of a cyclic ecosystem that supports a wide array of terrestrial organisms (Bormann and Likens, 1967; Cederholm *et al.*, 1999).

The causes of declining populations are complex and varied, however, three overarching factors can be identified: physical removal of fish through harvesting, impacts of aquaculture and reductions in the potential productivity of salmon habitats. Although these impacts are generic to all salmon species, the following section discusses impacts in relation to UK Atlantic salmon populations.

As discussed above, Atlantic salmon have traditionally been an important food resource. Prior to the twentieth century, harvesting of Atlantic salmon was generally small scale and driven by subsistence requirements. However, in the late 1960's and 70's, the expansion of commercial fishing and the identification of marine migratory paths, resulted in increased extractions from the freshwater and marine environment (Food and Agriculture Organisation, 1989). This resulted in harvesting quotas frequently exceeding one million fish (WWF, 2001). These yields were unsustainable, and dramatic declines in catch and stock were reported (WWF 2001).

In response to concerns regarding declining stocks, the North Atlantic Salmon Conservation Organisation (NASCO) was established in 1983 to manage and conserve wild Atlantic salmon stocks. With the aid of a number of non-governmental conservation organisations (Atlantic Salmon Federation [ASF], North Atlantic Salmon Federation [NASF]), NASCO has significantly reduced harvesting pressures on Atlantic salmon stocks, and developed a framework for promoting ecologically sustainable fishing quotas (WWF, 2001). However, mixed stock commercial fishing and drift netting continue to impose pressures, particularly at the local population scale (WWF, 2001; Solomon, 2003).

Over the past 40 years, aquaculture, which is broadly defined as the cultivation and harvest of captive fish, has expanded from a local industry into a global commercial enterprise and has been linked to declining salmon stocks (Black, 2001; Clifford et al. 1998). Although for many years evidence of a link between aquaculture and declining wild stocks was largely circumstantial - countries with the largest aquaculture industries experienced chronologically and geographically co-incident declines in wild Atlantic salmon returns - recent studies have identified direct linkages between commercial farming practices and declining salmon stocks (Hindar *et al.*, 1991; GESAMP, 1996; Einum and Fleming, 1997; Clifford *et al.* 1998). However, it should be noted that these linkages are contended by the commercial farming industry.

Many of the impacts attributed to aquaculture occur when farmed fish escape and interact with wild populations (Black, 2001). Interbreeding between farmed and wild Atlantic salmon erodes genetic adaptations to local environmental conditions, potentially reducing the fitness of progeny and resulting in lower survival rates (Hindar *et al.*, 1991; Einum and Fleming, 1997; Clifford *et al.* 1998). Interactions between farmed and native fish also allow harmful communicable parasites and diseases, which farmed salmon frequently host, to infect wild communities. Further to the detrimental impacts of population interactions, aquaculture practices may also affect the quality of wild salmon habitat. For example, effluent discharges, which often carry parasites and toxins, have been linked to aquaculture (GESAMP, 1996).

In addition to the impacts of harvesting and aquaculture, reports also indicate that in many systems the quality of the habitats utilised by Atlantic salmon have declined, often resulting in a consequent reduction in productivity (Crisp, 2000; WWF, 2001; Hendry, 2003). Typically, reductions in habitat quality can be linked to anthropogenic sources, for example, the encroachment of human activities on key salmon habitats. In the marine environment, shifting thermal regimes, potentially resulting from climatic change, have been linked to reductions in food availability and increases in predation (Jensen, 1992; Welch, *et al.,* 1998). In the freshwater environment, a variety of factors, ranging from migratory barriers to loss of juvenile rearing habitat, have been linked to poor productivity (Rimmer *et al.*, 1985; Bjorn and Reiser, 1991; Bergkamp *et al.,* 2000). In recent years, improved environmental regulations (Salmon and Freshwater Fisheries Act 1975, National Rivers Authority, 1990; Freshwater Fish Directive, European Union [E.U.], 1978; Habitats Directive, E.U., 1992) have alleviated some of the pressures on freshwater salmon habitats. Nevertheless, low productivity of key salmon habitats remains one of the principal factors associated with diminishing salmon stocks (Milan *et al.*, 2000; Solomon, 2003).

The recovery of declining Atlantic salmon stocks requires the development and execution of management strategies that target the multiple pressures currently affecting salmon populations. These pressures operate contemporaneously. Consequently, there is a requirement for the development of integrated management strategies that simultaneously target multiple identified pressures on salmon populations at all life stages and habitat zones. For instance, the promotion of sustainable fishing quotas and enforcement of tougher regulatory measures for aquaculture must be synthesised with the realisation of schemes aimed at enhancing the productivity of key habitats.

One of the principal habitat zones associated with poor productivity is the incubation environment (Meehan, 1991; Gibson, 1993; Soulsby *et al.*, 2001). Poor incubation survival is a consequence of (i) pressures on the ability of incubation environments to support physiological requirements and (ii) reduction in the availability of suitable spawning gravels, resulting in spawning occurring in zones of reduced incubation habitat quality. Increasing incubation survival of wild salmon populations through habitat restoration is currently one of the primary goals in fishery research and river management. Central to the development of appropriate restoration strategies is availability of detailed information pertaining to the processes and factors influencing the productivity of the incubation environment. This information will allow identification of wider catchment-scale processes that have the facility to influence factors identified as detrimental to incubation success.

1.2 Evolution of research into salmonid incubation success

Pioneering work into salmonid incubation success was carried out by fishery biologists who observed low survival of salmonids in spawning gravels with high proportions of fine sediment (Harrison, 1923; Hobbs, 1937). Laboratory-based research led by Harvey (1928), Krough (1941) and Hayes *et al.* (1951) advanced the premise that low dissolved oxygen concentrations and reduced water exchange, resulting from high levels of fine sediment in the incubation zone, increased embryonic mortalities. Field studies by Wickett (1954) Coble (1961) and Cooper (1965) verified that under natural conditions, fine sediment accumulation affected incubation success. Observations of emerging salmon fry also indicated that excess fine sediment inhibited the emergence of salmon from the incubation environment (White, 1942; Shelton, 1955).

Evidence of the detrimental impacts of fine sediments on the intragravel passage of oxygenated water initiated investigation into the oxygen requirements of salmon embryos. Investigative approaches were divided between experimental laboratory observation and theoretical modelling. Assessments of oxygen consumption rates were undertaken in a series of influential laboratory studies. These studies concluded that oxygen consumption was restricted below critical oxygen concentration thresholds, and by rates of oxygen supply that were insufficient to sustain respiratory demands (Alderdice *et al.*, 1958; Silver *et al.*, 1963; Shumway, 1964; Hamor and Garside, 1978). Theoretical models of embryonic oxygen consumption were developed around the theories of diffuse exchange of solutes across cell membranes (Krough, 1941; Hayes et al., 1951; Wickett, 1954). This area of research was advanced with the application of the theories of mass transport to the problem of fish respiration (Daykin, 1965; Wickett, 1975; Chevalier and Carson, 1985).

Physical scientists investigating the characteristics and processes governing fine sediment accumulation in riverbed gravels provided information to supplement observations of the impact of fine sediment on incubation success (Einstein, 1968; Beschta and Jackson, 1979; Meehan and Swanston, 1977; Lisle, 1980; Frostick, *et al.*, 1984; Carling, 1984). Flume and field studies demonstrated that fine sediment infiltration was controlled by the relationship between interstitial pore space and the size of fine particles (Einstein, 1968; Beschta and Jackson, 1979). Typically, particles in the clay to fine sand range were shown to deposit upward from the base of salmon redds, whereas larger particles were shown to deposit near the gravel surface (Einstein, 1968; Beschta and Jackson, 1979; Lisle, 1980; Frostick *et al.*, 1984). With respect to salmonid incubation success, the inference from these studies was that infiltration of fine sediment particles within the clay to fine sand region was an important factor controlling the passage of water through the riverbed, whilst deposition of larger sediment particles promoted the development of seals that inhibited the emergence of alevins from the gravel substrate (Chapman, 1988).

By the early eighties, poor embryonic survival was widely regarded as a key factor contributing to declining salmon stocks (Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Cederholm *et al.*, 1981; NCASI, 1981; Chapman 1988, Meehan, 1991). In response to this concern, environmental agencies (United States Department of Agriculture (USDA); United States Forestry Service (USFS)) promoted the development of practicable tools to predict survival and assess the quality of spawning gravels. This resulted in an active period of research, and the production of a variety of empirical relationships describing conditions within the incubation environment and survival to hatching or emergence of salmon progeny. Applying the simple premise that oxygen availability was the dominant factor influencing incubation success, a number of researchers utilised intragravel dissolved oxygen concentration as a metric of survival, and a range of oxygen concentration thresholds below which incubation success was impeded were reported (Philip and Campbell, 1963; Turnpenny and Williams, 1980; Hartmann, 1988; Maret *et al.*, 1993; Rubin and Gilmsater, 1996; Ingendahl, 2001) (Table 1.1).

Species	**Critical dissolved oxygen concentration mg l^{-1}**	**Reference**
Brown trout	8	Maret *et al.* (1993)
Trout	7.7	Hartmann (1988)
Rainbow trout	5.2	Sowden and Power (1985)
Rainbow trout	5	Turnpenny and Williams (1980)
Sea trout	10	Rubin and Gilmsater (1996)
Sea trout	7	Ingendahl (2001)
Steelhead trout	4.1	Philip and Campbell (1963)

Table 1.1 Dissolved oxygen concentrations below which survival in natural streams was negligible.

Other studies adopted the principle that the physical structure of the riverbed influenced oxygen availability and emergence form the incubation environment, and would therefore provide an indicator of the potential quality of the incubation environment. Based on this premise, a variety of granular determinants of survival were developed including percent fines, Fredle index and permeability (McNeil and Ahnell, 1964; Koski, 1966, 1975; Hall and Lantz, 1969; Bjorn, 1969; Phillips *et a*l., 197; McCuddin, 1977; Platts, 1979; Shirazi and Seim, 1981;

Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Cederholm *et al.*, 1981; National Council for Air and Stream Improvement (NCASI), 1981; Tappel and Bjorn, 1983, 1989; Tagart, 1976, 1984; McCrimmon Gots, 1986; Chapman, 1988; Young *et al.*, 1991; Kondou *et al..*, 2001) (Table 1.2).

Reference	Size of particles (mm)	Species	Impact on incubating salmon
McNeil and Ahnell (1964)	0.83	Pink Salmon	Decreases survival.
Koski (1966)	3.3	Coho salmon	Decreases survival.
Bjorn (1969)	6.35	Chinook salmon / Steelhead trout	Impedes emergence.
Hall and Lantz (1969)	1 - 3	Chinook / Steelhead	Impedes emergence
Koski (1975)	0.105 - 3.327	Chum salmon	Decreases survival
Tagart (1976, 1984)	0.85		Inversely related to dissolved oxygen (reduces permeability and/or increased biological oxygen demand). 32% survival to emergence at 20% fines 18% at > 20% fines.
McCuddin (1977) (artificial channel)	<6 and 6 - 12	Chinook salmon / Steelhead trout	Any percentage of 6-12mm particles above 10-15% reduced survival, as did any percent of particles < 6mm above 20-25%.
Cederholm *et al* (1981)	< 0.85	Coho salmon	30% survival at 15% fines, and 15% survival at 25% fines.
Tappel and Bjorn (1983)	< 0.85 and < 9.5	Chinook salmon / Steelhead trout	At fines (<0.85) survival varied from 20 to 80% as the amount of fines < 9.5mm varied from 60 to 25% (Sand Seal?)
Peterson and Metcalfe (1981)	0.06-0.5 and 0.5-2.2	Atlantic Salmon	Fine sand above 12% sharp decline in survival. Percent of coarse sand above 22% emergence dropped sharply.
McCrimmon and Gots (1986)	< 4	Rainbow trout	Survival ranged from 51-74% in gravels with 40-100% fines. More fines led to earlier emergence of smaller alevins. Survival equalled 87-92% in 0-20% fines
NCASI (1981)	< 0.8 <6.8	Rainbow trout	For each 1% increases in fines over the range 10-30% survival declined 1.3%. 90% survival at 20% fines < 6.4mm (larger fines may have prevented smaller fines from entering the incubation areas.
Phillips *et al.* (1975)	1-3	Coho salmon	Emergence declined at 10% fines. 20% fines reduced emergence 60-70

Table 1.2. Observations of the influence of fine sediment on survival to emergence.

In additional to oxygen concentrations, desktop and laboratory studies (Silver *et al.*, 1963; Shumway *et al.*, 1964, Daykin, 1965) identified intragravel flow velocity as an important factor influencing oxygen availability and incubation success. However, few field studies attempted to quantify intragravel flow velocities through spawning gravels, or reported survival in relation to interstitial flow characteristics. This was largely due to difficulties estimating intragravel flow. However, the application of simple dilution techniques allowed researchers to comment on the effectiveness of intragravel flow velocity as a determinant of survival, and a range of velocity thresholds were proposed (Coble, 1961; Cooper, 1965; Turnpenny and Williams, 1980).

In contrast to the empirical relationships highlighted above, process based information on the passage of water and oxygen through riverbeds was periodically provided from investigations of the intragravel environment of riverbeds. Key observations included the influence of streambed topography on the exchange of surface water with the streambed (Stuart, 1953; Vaux, 1968; Thibodeaux and Boyle, 1987), the role of organic matter in the consumption of oxygen from interstitial water (Chevalier and Murphy, 1985), and the influence of upwelling groundwater on intragravel oxygen concentrations (Sheridan, 1962, Soulsby *et al.*, 2001).

In addition to investigations into oxygen deficiency related incubation mortalities, researchers also recognised the influence of additional factors influencing incubation success. Observations of bed scour depths exceeding egg burial depths highlighted the potential impact of gravel entrainment on incubation success (Montgomery *et al.*, 1996; De Vries, 1997). Additionally, the accumulation of metabolic waste within the incubation zone was also proposed as a potential factor influencing embryonic survival (Burhalter and Kaya, 1977; Chapman 1988; Meehan, 1991; Crisp, 2000).

In recent years, awareness of the ecological significance of the subsurface environment of river corridors has prompted detailed investigation into the processes operating within riverbeds. Although the focus of these studies has not been to delineate the factors influencing incubation success, a number of observations of direct relevance to the availability of oxygen to incubating progeny have been provided. These include trends in sedimentary respiration (Whitman and Clark, 1982; Chevalier and Murphy, 1985; Sterba *et al.*, 1992), evidence of increased coupling of stream and hyporheic water during high flow events (Shimizu *et al.*, 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Soulsby *et al.*, 2001; Malcolm *et al.*, 2003) and the spatially and temporally variable influence of groundwater on the hydrochemical characteristics of hyporheic water (Rutherford *et al.*, 1993, 1995; Kaplan and Newbold, 2000; Packman and Bencala, 2000; Soulsby *et al.*, 2000, 2001, Malcolm *et al.*, 2003).

Recognition of the complex processes operating within riverbeds has raised concerns regarding the effectiveness of previously proposed metrics of survival (Chapman, 1988; Reiser, 1998). This has prompted the development of multi-factor analysis of embryonic survival and conceptual models of incubation success (Chapman, 1988; Lisle and Lewis, 1992; Alonso *et al.*, 1996; Wu, 2000; Crisp, 2000). There is a requirement to continue to promote awareness of the complex and dynamic nature of salmonid incubation environments, and to develop improved multi-factorial analyses of incubation success.

Chapter 2. Research theme and thesis structure

This section details the scientific context in which the thesis was developed, outlines the research theme of the thesis and summarises the thesis structure.

2.1 Project background

The thesis was developed within the remit of a larger research project funded by the Department for Environment, Food and Rural Affairs (DEFRA): Monitoring and modelling fine sediment accumulation and dissolved oxygen in experimental spawning gravels (Project Code: SF225). The overarching aim of the project was recalibration and assessment of a deterministic model of salmonid incubation success developed in North America for use in U.K. rivers (Sediment Intrusion and Dissolved Oxygen [SIDO]) (Alonso *et al.*, 1996). Calibration and validation of the revised model (termed SIDO-UK) required detailed field data pertaining to sediment dynamics, dissolved oxygen concentrations, and embryonic survival in U.K. spawning gravels. Acquisition of these data sets formed the template upon which the thesis was developed, and hence restricted the resources that could be apportioned to supplementary research areas. Additional outputs from the project included a flume investigation of deposition trends within salmonid redds and development and application of a passive tracer technique to quantify intragravel flow velocities.

2.2 Overview of scientific context and research approach

As highlighted in Section 1.1, global concern regarding declining productivity of salmon spawning gravels has produced a voluminous body of information pertaining to potential causes of poor pre-emergent survival. Among the composite of factors influencing pre-emergent survival (Figure 2.1), the infiltration of fine sediments into the incubation environment and its consequent effect on oxygen availability, has been identified as an important factor restricting embryonic survival (Harvey, 1928, Krough, 1941; Hayes *et al.*, 1951; Philip and Campbell, 1963; Turnpenny and Williams, 1980; Hartmann, 1988; Maret *et al.*, 1993; Rubin and Gilimsater, 1996; Ingendahl, 2001, Malcolm *et al.*, 2003). However, divergent research objectives and limited dissemination of information between scientific disciplines, has restricted the development of conclusive statements regarding sedimentation and the flux of oxygen through salmon spawning gravels. Furthermore, investigation into factors influencing the availability of oxygen to incubating salmon progeny has largely been limited to studies of individual factors within singular systems, for instance, intragravel oxygen concentration and measures of granular properties of the incubation environment (Table 1.1, 1.2). This contrasts with recent evidence, which indicates the flux of oxygen through riverbed gravels is influenced by a complex interaction of surface and subsurface factors (Chapman, 1988; Lisle and Lewis, 1992; Alonso *et al.*, 1996; Wu, 2000; Malcolm *et al.*, 2003). In response to these concerns, there is a requirement for (i) the development of a robust method of defining the quality of salmonid incubation habitats and (ii) improved awareness of factors influencing the flux of oxygen through salmon spawning gravels.

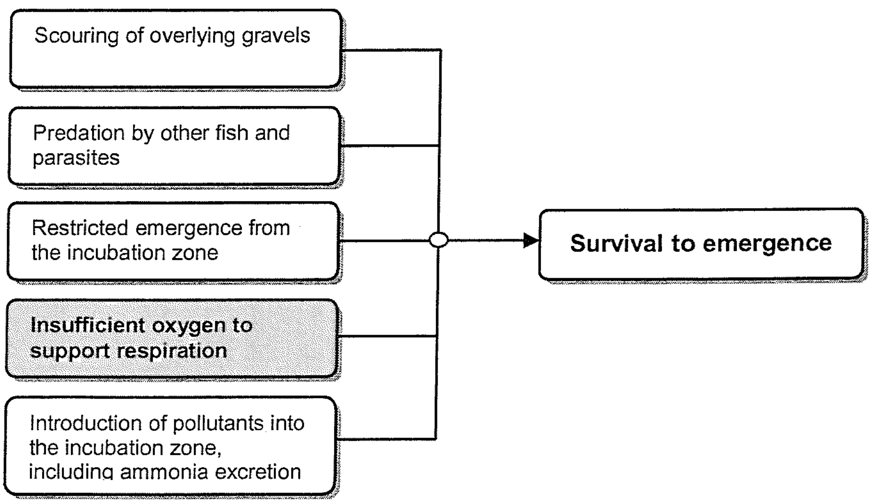

Figure 2.1 Summary of factors reported to influence survival to emergence of salmon progeny. Highlighted box identifies factor investigated in the thesis.

Within this research setting, the thesis was constructed around three broad aims (Figure 2.2). First, to investigate the availability of oxygen within salmon spawning gravels, second, to examine factors influencing the ability of incubation environments to support the respiratory requirements of Atlantic salmon embryos, and, third, to apply this information to develop tools to improve assessments of spawning and incubation habitat quality, thereby aiding managerial responses to poor incubation success.

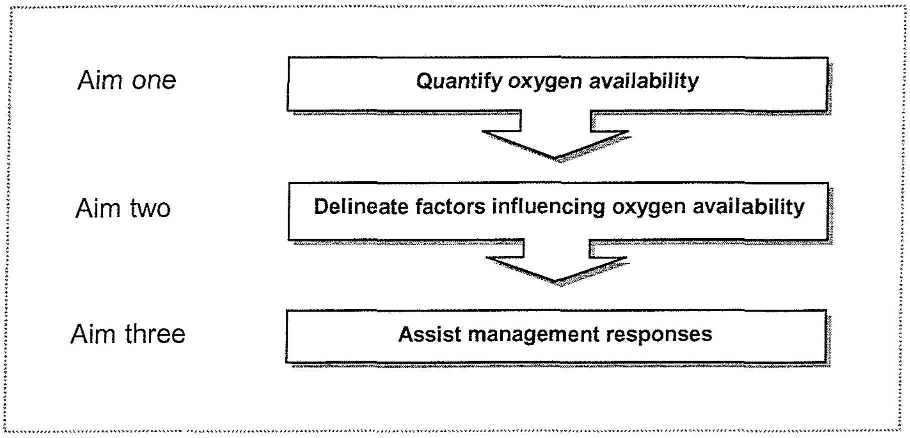

Figure 2.2. Summary of thesis aims.

To provide a scientific platform upon which to achieve these aims, the importance of adopting a multi-disciplinary approach to investigating incubation success was recognised. To date, investigation into incubation success has often failed to adequately integrate knowledge of embryonic respiratory requirements, with detailed information pertaining to the processes operating within the incubation environment. Therefore, one of the principal concepts underpinning the investigative approach adopted in this thesis, was identification of embryonic respiratory processes and requirements, and synthesis of this information with a detailed examination of associated processes operating within the incubation environment. Realisation of this investigative approach required assimilation of concepts and theories from three key research fields: fluvial dynamics, geomorphology and sedimentology, and embryonic biology (salmonid) (Figure 2.3).

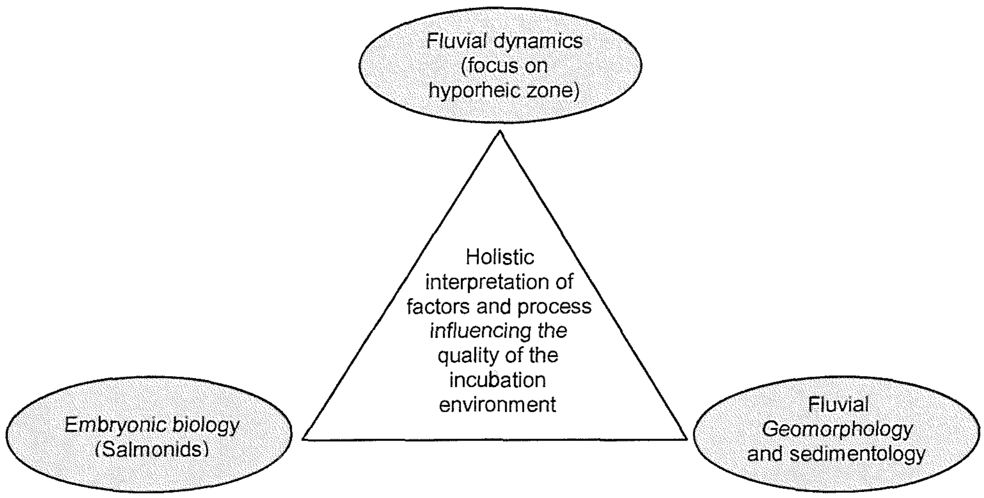

Figure 2.3 Overview of thesis research context.

Although providing the basis for a holistic interpretation of factors and processes operating within the natural environment, adopting a multidisciplinary research approach can limit the depth and detail of investigation within traditionally defined research fields. To overcome this limitation, a conceptual research boundary was defined. As highlighted in Section 1.2, the incubation environment is contained within an ecotone referred to as the hyporheic zone. The physical structure and hydro-chemical character of the hyporheic zone is influenced by a variety of physical and biological processes operating across a range of temporal and spatial scales (Section 3.2). As discussed above, the overarching aim of the thesis was to investigate the processes and factors restricting the ability of this environment to support the oxygen requirements of incubating embryos. Therefore, although consideration is given to the wider processes and factors influencing conditions within the incubation environment, the thesis focuses on those factors and processes that have a direct bearing on the availability of oxygen to incubating embryos, and its implications for their survival (Figure 2.4).

By defining this research boundary, it was possible to develop a multi-disciplinary research project that promoted awareness of the interactions between processes and factors influencing incubation success, and advanced scientific understanding of key physical and biological processes.

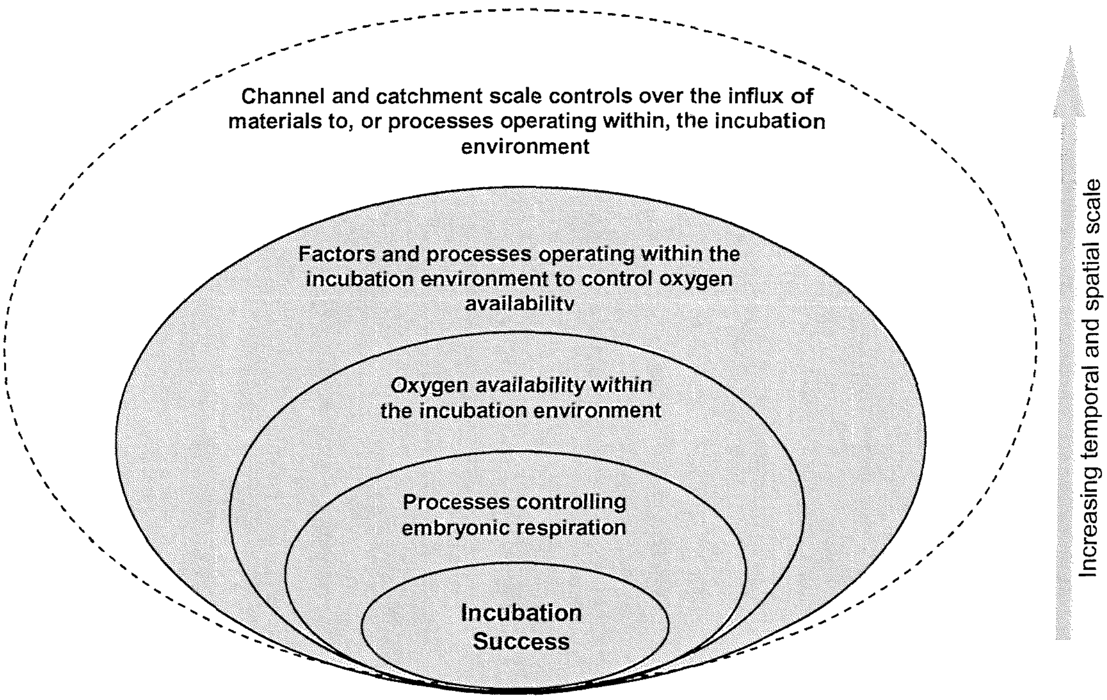

Figure 2.4 Identification of research boundaries. Shaded boxes represent the primary areas of investigation.

In additional to recognising the broad research boundaries, the operational limitations were also recognised. Many of these limitations resulted from project and resource constraints, however, others were self-imposed, and therefore must be rationalised. First, oxygen availability was defined as the dominant factor influencing survival, consequently, additional factors potentially influencing survival (Figure 2.1) were not directly assessed. Investigating oxygen availability as the primary mechanism influencing incubation success was a rational response to the weight of evidence provided from other studies of pre-emergent survival (Section 1.2). Additionally, excess fine sediment accumulation, which will have a consequent impact on oxygen flux, is recognised as a key environmental pressure in many U.K river systems (Sear, 1993; Wood and Armitage, 1997; Milan *et al.*, 2003).

Second, assessments of survival were based on rates of survival to hatching and, therefore, did not include an assessment of the period from hatching to emergence. The choice of focusing on survival to hatching was based on two findings presented in previous research: (i) observations that assessments of survival to emergence can be unreliable, and (ii) observations that hatchlings are less susceptible to oxygen deficiency related mortalities. A review of previous research indicated that accurate quantification of survival to emergence is frequently compounded by sampling difficulties (Philips and Koski, 1969; Hause and Coble, 1976; White, 1980). Potential problems include disturbance to the incubation zone by sampling equipment, and underestimates of survival resulting from emergence trap inefficiency (White, 1980). It was decided therefore, that robust measures of survival to hatching were preferable to unreliable estimates of survival to emergence. With respect to post hatching oxygen deficiency related mortalities, alevins are mobile, allowing them to migrate towards areas of high oxygen availability (Stober *et al.*, 1982; Fast and Stober, 1984). Consequently, alevins are better adapted than ova to survive in oxygen limiting environments. Similarly, alevins have been shown to consume less oxygen, thus reducing potential oxygen deficiency related mortalities (Rombough, 1988). In light of these observations, it was conjectured that assessments of survival to hatching provided a guide to the total number of oxygen deficiency related pre-emergent mortalities. However, as comparisons were not undertaken to validate this assumption, all survival rates are reported as survival to hatching.

Third, although the accumulation of metabolic waste (ammonia) excreted by incubating embryos has been identified as a factor potentially influencing survival (Burkhalter and Kaya, 1977), the equipment required to assess ammonia concentration within the incubation environment was unavailable. Therefore, it was not possible to distinguish between mortalities resulting from the toxic impact of ammonia accumulation and those resulting from oxygen deficiencies.

Fourth, although studies have discussed the impact of restricted oxygen availability on embryonic growth rates and potential post-hatching fitness (Silver *et al.*, 1963; Shumway *et al.*, 1964; Cooper, 1965; Garside, 1965; Mason 1969), the resources available to the project did not allow an assessment of sub-critical impacts of oxygen availability on incubation success.

Finally, in addition to reductions in the ability of incubation environments to support incubating embryos, in many systems, anthropogenic pressures have also reduced the availability of suitable spawning locations (Bjorn and Reiser, 1993). For instance, river engineering, which includes impoundment, canalisation, inappropriate bank protection and flood alleviation schemes, has influenced the availability of suitable spawning gravels and the availability of appropriate surface flow conditions (Bjorn and Reiser, 1993). Pressures on the availability of spawning habitat can result in spawning occurring in locations where incubation survival will be impaired (Bradford and Hubert, 1988; Bjorn and Reiser, 1993). Although, this indirect impact on incubation survival was recognised, assessments of pressures on the availability of suitable spawning locations were not undertaken. However, providing an indication of factors influencing the quality of incubation environments, promotes awareness of the suitability of spawning locations.

2.3 Overview of thesis structure

The remainder of the thesis is organised into five chapters and two appendices.

Chapter three provides a detailed literature review. The review is divided into two sections. Section one provides background information pertaining to Atlantic salmon spawning preferences and characteristic. Section two provides a detailed examination of the oxygen requirements of incubating embryos and discusses factors influencing the flux of oxygen through salmon spawning gravels. The broad aim of this review was to provide the scientific foundation required to develop the thesis and the associated project.

Chapter four details the thesis research objectives. Applying the conceptual model of oxygen flux outlined in the literature review, four key factors influencing oxygen availability to incubating salmonid embryos were identified. Based on these factors, a series of research objectives were proposed. Each objective was designed to target current limitations in our understanding of factors influencing the availability of oxygen to incubating salmon embryos. Also included in this chapter is a short section detailing the structure adopted to report scientific findings.

Chapter five summarises the methodological approach developed to investigate oxygen fluxes through salmon spawning gravels. Included in this section is (i) a review of the rationale underpinning the development of the monitoring programme, (ii) an overview of the characteristics of the selected field-sites, (iii) a summary of the field and laboratory monitoring strategies, and (iv) a rationalisation of the selection of sampling techniques.

Chapter six details the scientific findings of the monitoring programme. The chapter is divided into of series of concomitant sections, with each section based on a specific research objective outlined in Chapter 4. Individual sections are presented as distinct studies and include a summary of relevant literature, an overview of methods adopted and a discussion of results and observations.

Chapter seven summarises the information presented in Charter 6. The section (i) overviews the findings of the monitoring programme, (ii) details potential factors degrading incubation habitat quality at the monitoring sites, (iii) summarises the project limitations, and (iv) discusses areas requiring further research attention.

Appendices- The appendices contain important supplementary information. Included in the appendices are two research papers describing field techniques developed during the project.

2.5 External pressures on the project

The foot and mouth outbreak in the winter of 2000/2001 severely disrupted, and eventually terminated the first field season. Additionally, the data sets recovered during this period were adversely affected by high flow events (RI=1000) that resulted in restricted access to the field sites, and a series of equipment failures. Two field seasons were a contractual requirement of the DEFRA research grant, consequently, the second uninterrupted field season was undertaken in the third and final year of the project. Although the data recovered in the first field season was not of sufficient quality to present within the context of the thesis, the observations and sampling difficulties encountered during this period aided the design and implementation of the monitoring programme adopted in subsequent years.

Chapter 3. Literature Review

The literature review is divided into two principal sections. Section one summarises information pertaining to salmonid spawning and incubation habitats. Section two provides a detailed examination of the oxygen requirements of incubating embryos, and discusses factors influencing the flux of oxygen through salmonid spawning gravels.

3.1 Spawning preferences and characteristics

The section is divided into three subsections: (i) A review of the physical character of Atlantic salmonid spawning habitat, (ii) a summary of the construction and character of salmonid redds and (iii) a brief overview of incubation requirements.

3.1.1 Characteristics of spawning habitat

3.1.1.1Geographic isolation

Atlantic salmon migrate from marine feeding grounds to freshwater rivers to reproduce. Highly developed magnetic, celestial and olfactory senses, give salmon the ability to return to native rivers to spawn (Quinn, 1980, Groot and Margolis, 1991). This has resulted in the development of geographically isolated and self-sustaining populations (Rich, 1939). Reproductive isolation has promoted the evolution of genetically distinct populations, many of which may have developed physical and behavioural adaptations to local habitat conditions. Consequently, although many spawning characteristics are generic, precise spawning preferences and incubation requirements may vary between systems, or populations, dependant upon habitat availability (Miller and Brannon, 1982; Bjorn and Reiser, 1997).

3.1.1.2 Timing of spawning

Spawning traits and characteristics have evolved to maximise the potential survival of emergent fry (Brannon, 1972; Wilson, 1997). With respect to timing, spawning occurs at times that will promote the emergence of salmon fry at periods of favourable water flow conditions, temperatures and food supply (Heggberget, 1988, Jenson *et al.*, 1991). As the rate of development of incubating progeny is primarily controlled by temperature (Crisp, 1981, 1988, 2000), spawning generally occurs earlier in rivers with cooler thermal regimes. In the UK, spawning typically occurs in November and December in northern rivers, and in December and January in southern rivers.

3.1.1.3 Composition and size of spawning gravels

In broad terms, spawning gravels exhibit two distinct modes in the grain size distribution, although unimodal distributions have been reported in streams with limited fine sediment content (Kondolf *et al.*, 1991). Typically, the coarse mode is dominant and forms what is referred to as the 'framework', while a secondary mode, referred to as the 'matrix', consists of finer sediments (Carling and Reader, 1982). A study by Crisp and Carling (1989) suggested that spawning gravels in northeast England and southwest Wales were unimodal, whereas they were bimodal in Dorset chalk streams. With respect to fine sediment, salmonids have been shown to select sites with low fines content. In the U.K., percentages of fine sediments (< 1mm) reported in salmon spawning gravels range from 5% in a Scottish burn to 12% in a southern chalk stream, and spawning is seldom recorded in gravels exceeding 20% fines (Crisp and Carling, 1989; Moir, 1998). Reported percentages of fine sediments in U.K trout spawning gravels are outlined in Table 3.1.1.

Size fraction	**Upland streams (n=20)**	**Lowland chalk streams (n=11)**	**Lowland non-chalk streams (n=20)**
sand (0.063-2mm)	11 (6.5-16.5)	42 (28.0-64.1)	21.5 (9.5-43.0)
coarse sand (1-1.9mm	5	4	6
medium sand (0.125-0.99mm)	6	38	16
fine sand (0.063-0.124mm)	1	1	1.5
silt (0.004-0.062mm)	3.5 (0.6-7.3)	4.9 (0.9-8.1)	7.4 (2.0-18.0)
clay (<0.0039)	0.6 (<0.1-1.9)	0.6	1.7 (0.3-5.2)

Table 3.1.1 Percentage fine sediment in the upper 0.3m of the bed in three classes of U.K rivers (after Milan *et al.*, 2000).

Detailed studies of the composition of spawning gravels indicate that the precise size of gravels utilised by spawning fish is correlated to the length of the female fish (Crisp and Carling, 1989; Crisp, 1993; Kondolf *et al.*, 1993; Moir, 1998). As a general rule, larger fish construct redds in larger gravels. Two explanations for this observation have been proposed: (i) the ability of larger fish to lift more weight by virtue of the greater suction their tails can exert on the streambed and (ii) the ability of larger salmon, and trout, to maintain themselves in more powerful currents, where the greater force of the current assists in entrainment of particles (Arnold, 1974; Kondolf and Wolman, 1993; Kondolf, 2000). It is probable that a combination of both factors allow larger fish to use larger spawning gravels.

However, the ability of a large fish to spawn in a fast flowing reach with coarse gravel does not necessitate it to do so. Instead, she may choose a lower gradient reach with smaller gravel. Consequently, the relationship between fish size and spawning gravel size is best defined as an envelope curve, with the gravel sizes eventually adopted by fish determined largely by availability (Kondolf and Wolman, 1993). Fisheries scientists have adopted a variety of granular descriptors to characterise the size of salmonid spawning gravels, these are summarised in Table 3.1.2.

Descriptor	**Equation**	**Reference**	**Eq. No.**
Geometric mean$_1$	$dg^1 = [\ (D_{84})(D_{16})^{0.5}\ ]$	Shirazi and Seim, 1979	3.1
Geometric mean$_2$	$dg^2 = [D_1 w_1 \times D_2 w_2 \ldots\ldots D_n w_n]$	Lotspeich and Everest, 1981	3.2
Graphic mean	$mg = [(D_{84})(D_{50})(D_{84})^{0.333}$	Folk, 1980)	3.3
Standard deviation	$sg = [\ (D_{84})/(D_{16})^{0.5}\ ]$		3.4
Skewness	$sk = \log [\ (dg_1/ [D_{50})\ / \log (sg)$	Inman, 1952,Vanoni, 1975	3.5
Fredle index	$fi = dg/So$ (where $So = \sqrt{D_{75}} / D_{25}$)	Lotspeich and Everest, 1981	3.6

Table 3.1.2 Summary of granular descriptors used to describe the size of salmonid spawning gravels. Where D_{50} is the median particle diameter, D_{84} is the grain size at which 84% of the sample is finer, D_{16} is the size at which 16% of the sample is finer, D_n is the midpoint diameter of particles retained by a given sieve and w_n is the decimal fraction weight of particles retained by a given sieve.

Mean and median grain sizes are measures of central tendency, standard deviation is a measure of how well the bed material is sorted, skewness is a dimensionless term describing the shape of the grain size distribution and the Fredle index (Lostpeich and Everset, 1981) is a measure of central tendency and spread. Table 3.1.3 summarises information pertaining to the physical character of spawning gravels utilised by U.K. salmonid species. Information from other countries has been used to supplement a lack of information pertaining to U.K. rivers.

Species	Location	Fish length (cm)	n	D_{50}	Dg	mg	sg	sk	Reference
Atlantic salmon	Maine	49	23	16.5	7.2	9.5	4.8	-0.52	Warner (1963)
Atlantic salmon	Maine	53	10	15	7.0	9.0	4.7	-0.49	Warner (1963)
Brown trout	England	29	22	50	21	27.9	5.2	-0.52	Carling (1987) published in Kondolf and Wolman (1993)
Brown trout	England	29	35	19	10.3	12.6	8.6	-0.29	Carling (1987) published in Kondolf and Wolman (1993)
Rainbow trout	North Carolina	21	14	24.6	16.5	18.7	3.8	-0.30	Kondolf and Wolman (1993)
Rainbow trout	North Carolina	21	14	46.3	26.6	31.9	4.0	-0.40	Kondolf and Wolman (1993)

Table 3.1.3 Properties of spawning gravel size distributions (after Kondolf and Wolman, 1993)

3.1.1.4 Flow characteristics

Although salmon and trout may attempt to spawn in still water, they show preferences for particular depths and water velocities (Jones, 1959). Generally, larger fish spawn in faster flowing, deeper water than smaller fish (Crisp and Carling, 1989). Table 3.1.4 summarises reported velocity and depth preferences for UK salmonid species.

Species	Velocity (m s^{-1}) at 0.6 depth	Depth (m)	Reference
Atlantic salmon	0.25-0.90	0.38	Beland *et al.* (1982)
	0.15-0.1		Crisp and Carling (1989)
	0.54	0.24	Moir *et al.* (1998)
Brown trout	0.39	0.26	Shrival and Dungey (1983)
Rainbow trout	0.49-0.91	0.34	Shrival and Dungey (1983)

Table 3.1.4 Summary of preferred flow characteristics at U.K. salmonid spawning sites.

In general, spawning salmon and trout display an ability to adapt to available flow conditions. Therefore, although Atlantic salmon display preferences for water depths and flow velocities of between 0.15 and 0.6 m, and 0.3 and 0.6 m s^{-1} respectively, the range of water depth and velocity options is larger, and the precise preference may vary between systems dependent on habitat availability. This was highlighted by Crisp and Carling (1989), who reported that spawning grounds in Britain display a degree of variance in mean water velocity, ranging from 0.1- 0.15 m s^{-1}. Closer inspection of Crisp and Carlings' (1989) results indicates that similar sized salmon in Dorset chalk streams tend to spawn in faster flowing water than salmon in north east England, which may be indicative of different available flow conditions.

3.1.1.5 Interchange of surface and subsurface flow

Within the realm of feasible spawning sites indicated thus far, female salmonids have been shown to apply a second set of criteria to select final spawning locations (Jones and King, 1950; Crisp and Carling, 1989; Leman, 1993). Spawning sites often occur where channel and streambed morphology create surface or subsurface flow patterns that enhance intragravel flow velocities. Favourable sub-surface flow conditions occur where the interchange of surface waters is enhanced by a combination of increasing surface velocity, convex bed profile and high gravel permeability. Such zones are generally found on the upstream interface between pools and riffles (Briggs, 1953; Hoopes, 1972; Hunter, 1953; Kondolf, 2000) (Figure 3.1.1).

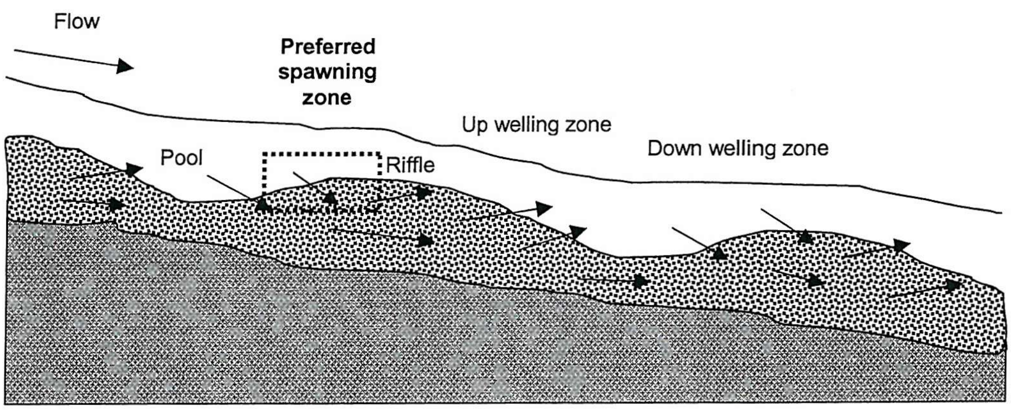

Figure 3.1.1 Preferred spawning zone. The lower elevation of the water surface in the riffle creates a hydraulic gradient that induces downwelling at the tail of the pool.

However, although salmonids have been shown to prefer spawning sites located on the interface between pools and riffles, in many river systems, particularly in lowland chalk streams, such zones are often poorly defined. In these systems, salmonids will generally spawn in areas of suitable gravel, flow velocity and water depth. Within chalk streams located in southern England, which lack defined pool/riffle sequences, spawning often occurs on discrete patches of gravel located within large runs or glides (Personal communication, Mark Fidebottom (Environment Agency)).

3.1.1.6 Upwelling groundwater

The use of spring or groundwater upwelling sites has been documented for a number of salmonid species (Heimer, 1965; Hansen, 1975; Lister *et al.,* 1980, Sowden and Power, 1985; Lorenz and Eiler, 1989; Curry *et al.,* 1994). However, at present no studies have reported the use of upwelling sites by U.K. Atlantic salmon, although this may be indicative of a lack of information, rather than a spawning characteristic of Atlantic salmon.

Upwelling groundwater may enhance embryo survival by providing a more stable thermal environment and/or increasing the supply of oxygen to incubating embryos (Bjorn and Rieser, 1991; Berrie, 1992; Acornley, 1999). As highlighted by Acornley (1999), during winter months, groundwater inputs increase and stabilise the thermal regime of rivers. This increase in temperature accelerates the development of incubating salmonid progeny and reduces intragravel residence time, potentially increasing the probability of survival (Crisp, 2000). Sowden and Power (1985), in a study of incubation success of Rainbow trout, discussed the importance of groundwater as a supplementary supply of dissolved oxygen. They observed incubation success and fry quality to be less dependent on substrate quality in areas of groundwater upwelling with sufficient dissolved oxygen. In contrast, a study of Alaskan spawning riffles recorded reduced dissolved oxygen concentrations and higher water temperatures at zones of upwelling groundwater (Sheridan, 1962). Low incubation success at these sites was attributed to the presence of low oxygen concentration groundwater (Sheridan, 1962). From these observations, of spawning preferences and incubation success, it may be concluded that, dependent on the oxygen content of the groundwater inputs, groundwater can have either a detrimental or beneficial affect on incubation success. Consequently, the use of zones of upwelling groundwater may be a population specific trait that has evolved in the presence of high oxygen content groundwater.

3.1.2 Salmonid redds: construction and characteristics

3.1.2.1 Redd construction

In common with all salmonid species, female Atlantic salmon reproduce by depositing eggs in a series of clusters (egg pockets) within one or more nests (redds) excavated in the gravel substrate of rivers and streams (Burner, 1951; Chambers *et al.*, 1955; Jones and Ball, 1954). The redd construction process is an intricate cycle of digging motions and courtship interactions. For the purposes of this review, a simplified overview of important features of the spawning process is presented.

The hen salmon (or trout) constructs her redd by turning on her side, at an angle of roughly 45°, and vigorously bending and straightening her tail in a vertical flapping motion. The tail intermittently strikes the gravel substrate, producing strong boiling currents that lift the gravel into the stream. Surface flow then displaces the lifted materials, with the finer fractions travelling well downstream and larger particles moving into a loose pile termed the tailspin (Jones and Ball, 1954). The maximum size of particles displaced by the female is dependent on body size and localised flow conditions (Chambers, 1955; Everest *et al.,* 1985). Particles that are either too large for the female to dislodge or too large for the flow to displace, are left in the bottom of the excavated pit, forming the egg pocket centrum (Burner, 1951, Gustafson-Marjanen and Moring, 1984, Chapman, 1988). The centrum commonly consists of a grouping of two to four large gravel or cobble particles, which typically derive from the armour layer and gradually assume a deeper position as finer material is excavated (Hobbs, 1937; Burner, 1951; Jones and Ball, 1954; Gustafson-Marjanen and Moring, 1984, Peterson and Quinn, 1996). The female deposits her first batch of eggs (500-1000 eggs per pocket) in the centrum while the male simultaneously fertilises them. Currents at the bottom of the pocket help deposit the eggs around the lower upstream edges of the centrum particles (Hobbs, 1937).

Once the eggs are fertilised, the female commences digging directly and obliquely upstream from the first pocket[2]. The excavated gravels and sands from this new pit are carried downstream, some being deposited into the first egg pocket creating a permeable protective barrier over the fertilised eggs. The female then prepares a new egg pocket and the egg

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[2] Observations of Chum salmon (Oncorhynchus keta) populations have shown that prior to recommencing the cutting process, the female performs a series of soft 'covering' digs, which mobilise fine pea sized material that settle over the centrum particles. This layer has been termed a bridging layer, and it has been suggested it may act as a barrier, excluding the infiltration of fine material into the egg pocket. At present, the presence of a bridging layer within Atlantic salmon redds has not been reported (Peterson and Quinn (1996).

fertilisation process continues. When the female has prepared the final upstream pocket, she makes several shallow upstream excavations, which fill the most recently created pocket, and the spawning process is completed. Typically, two to four egg pockets are prepared by female Atlantic salmon (Figure 3.1.2).

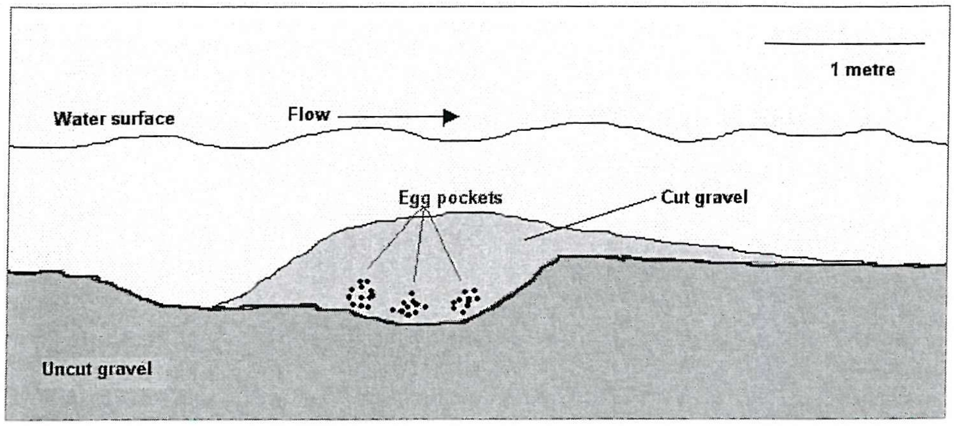

Figure 3.1.2 Completed redd, showing position of eggs and area of cut gravel.

3.1.2.2 Redd dimensions

The size of salmonid redds are closely related to fish length, with larger fish constructing larger redds. This relationship is a result of both the ability of larger fish to displace greater amounts of gravel and by their ability to construct redds in higher energy areas of flow in which greater particle displacement may occur (Bjorn and Reiser, 1997). Variations in redd dimensions between rivers has been reported (Crisp and Carling, 1989), suggesting that between systems, local river hydrology and geomorphology influence redd dimension and structure (Section 3.1.1). Further factors potentially effecting redd dimensions are the availability of gravel and the degree of concretion or compaction of the riverbed (Burner, 1951; Stuart, 1953).

Crisp and Carling (1989) showed that regressions of logarithmically transformed data could be used to estimate redd tail length from female fish length. Although these relationships were defined using data from different salmonid species (Brown trout, Sea trout, Atlantic Salmon), all species shared similar physiological and redd building characteristics. Subsequently, the relationships defined are interchangeable between the species sampled. The terminology and reference points are shown in Figure 3.1.3 and the equations developed are described below.

$$In\ q = b\ \ ln\ x + ln\ a \qquad (3.1.1)$$

$$ln\ x = b^1\ ln\ q + ln\ a^1 \qquad (3.1.2)$$

Where q is the redd tail length (cm), x is the female fish length (cm), b =1.18 , b^1 = 0.06, a = 0.453, and a^1 = 0.860.

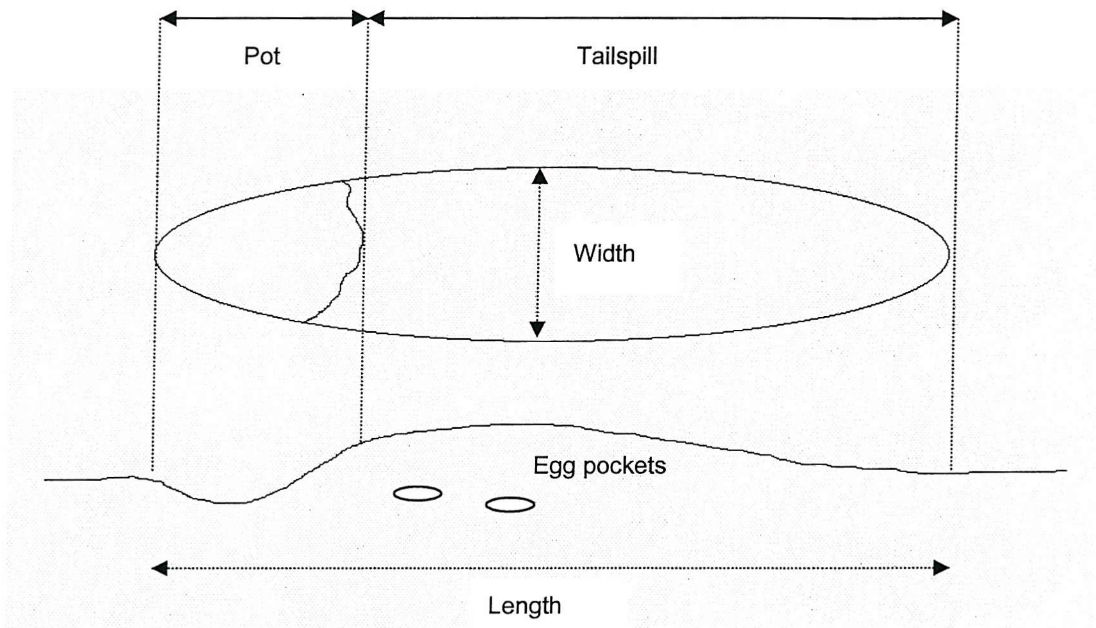

Figure 3.1.3 Plan and longitudinal profile of a salmonid redd. Lines represent dimension described by equations presented in Table 3.1.5 (Crisp and Carling, 1989).

Crisp and Carling (1989) also showed that after logarithmic transformations of all variables, the relationships between tail length and the other three horizontal redd dimensions (pot length, pot width and tail width) could be summarised as four linear regressions (Table 3.1.5).

X	y	n	Ln a ± 95% C.L.	Ln b ± 95% C.L	r^2
tail length (q)	pot length (c)	65	0.462 ± 0.658	0.795 ± 0.128	0.71
tail length (q)	pot width (c)	65	0.349 ± 0.709	0.799 ± 0.138	0.68
tail length (q)	tail width (d)	65	0.426 ± 0.714	0.811 ± 0.139	0.68
tail width (d)	tail length (q)	65	1.259 ± 0.664	0.842 ± 0. 145	0.68

Table 3.1.5 Summary of linear regressions relating natural logarithms of various horizontal dimensions of redds (cm). Each regression is in the form Ln y = b lnx + ln a, and r^2 is the coefficient of variation (after Crisp and Carling, 1989).

Although there is little evidence to support relationships between fish length and vertical redd dimensions, a number of observation of typical egg burial depths have been recorded (Table 3.1.6). Generally, the average egg burial depth for U.K. salmonids varies from 0.4 body lengths for a 0.2 m female to 0.3 body lengths for a 0.7 m fish (Crisp, 1996).

Reference	Burial depth (m)	Point measured to	Datum
Belding (1934)	0.15-0.3	top of pocket	original level
White (1942)	0.150.-30	top of pocket	original level
Ottaway *et al.* (1981)	0.18 (mean)	bottom of pocket	top of tail
Balaup *et al.* (1994)	0.27 (mean)	bottom of pocket	top of tail
Heggerget *et al.* (1988)	0.18 (mean)	centre of pocket	top of tail
Ottaway *et al.* (1984)	0.1-0.18	eggs	top of tail
Crisp and Carling (1989)	0.17-0.23	eggs	original level
Carling (1990)	0.12-0.22	eggs	top of tail
Jones (1954)	0.3-0.6	unknown	unknown
Crisp (1996)	0.08-0.21	unknown	unknown
Chapman (1988)	0.08-0.22 (Brown trout)	unknown	unknown

Table 3.1.6 Atlantic salmon egg burial depths (uncompensated for variations in fish length).

3.1.2.4 Effect of redd cutting on gravel composition

The cutting action of the female salmon modifies the size distribution of riverbed gravels (Table 3.1.7). The principal factor influencing the distribution of gravels is the ejection of fine sediments (Chambers, 1954; McNeil and Ahnell, 1964; Koski, 1987; Everest *et al.*, 1987; Kondolf *et al.*, 1993). A reduction in the proportion of fine sediments contained in the redd zone, increases the mean particle size of spawning gravel relative to the size of adjacent gravels (Kondolf and Wolman, 1993; Kondolf *et al.*, 1993). Where spawning salmonids frequent the same area on a yearly basis, the spawning reach may retain a coarser mean particle size than the surrounding gravels that remain unused (Kondolf *et al.*, 1993).

It should be noted that conclusive evidence demonstrating the cleansing properties of salmonid spawning activities has been hindered by both sampling difficulties and the heterogeneous nature of gravel substrates. Crisp and Carling (1989), in a study of UK spawning gravels, proposed that low levels of fines could be explained by the natural propensity of fine materials to filter through clean gravels. Crisp and Carling (1989) concluded that the jiggling action of cutting results in finer sediment sinking deeper into the redd, resulting in increased siltation at the basal interface.

Reference	Species	location	Investigation	Results
Chambers *et al.* (1954, 1955)	Chinook, Sockeye salmon	Washington, Idaho, British Columbia	Bulk core samples from redds and adjacent undisturbed gravels; some sites sampled pre and post spawning.	Average dg was 24.4mm in undisturbed gravels, 32.7 in redds, percent < 4mm was 12.9 in undisturbed, 8.3 in redds.
McNeil and Ahnell (1964)	Pink salmon	Southeast Alaska	Bulk core samples from Harris River before and after spawning in 1959 and 1960 (n not reported)	Average percent < 0.83 mm was reduced by spawning from 16.7 to 13.2 in 1959, and from 14.8 to 11.5 in 1960
Rukhlov (1969)	Pink salmon	Sakhalin, Siberia	Grab samples of spawned and undisturbed gravels (n= 109)	Average percent < 2mm was 13.5 in undisturbed gravels , 11.6 in redds
Ringler (1970)	Coho salmon	Oregon	Freeze core samples of redds and undisturbed gravels ("former redds") in needle Branch (n=48)	Average percent <0.83 mm was 38 in former redds (undisturbed) 24 in redds: Average percent < 3.3 mm was 51 in disturbed 36 in redds.
Helle (1970)	Pink salmon	Southeast Alaska	Bulk core samples from mass spawning areas before and after spawning (n=34:22prespawning 12 post spawning)	On average, dg increased from 6.8 to 7.6 mm after spawning percent < 0.83 mm decreased from 11.0 to 7.4, and percent < 2mm decreased from 22 to 18
Shrivell and Dungey (1983)	Brown trout	New Zealand	Bulk core samples from redds and adjacent undisturbed (n= 140)	" mean diameter " in redds was 1mm coarser than adjacent gravel(11.5 versus 10.5mm. Percent < 0.5mm was as much as 8% (of total) lower in redds.
Porter (1985)	Brown trout	North Carolina	Freeze core samples of redds and undisturbed gravels unpaired samples (n=9: 4 redds, 5 undisturbed)	No significant differences in dg, sg, or percent fines, between redd and undisturbed samples.
Everesr *et al.* (1987)	Chinook salmon Steelhead trout	Oregon	Freeze core samples of spawning areas pre-and-post spawning (n not reported)	Chinook salmon in Evans creek reduced percent < 1mm from 30 to 7.2; steelhead trout in Sams creek reduced percent <1mm from 14.5 to 7.5)
Crisp and Carling (1989)	Brown Trout, Atlantic salmon	United Kingdom	Freeze core samples of redds and adjacent, undisturbed gravel (n not reported).	No significant differences in dg, sg, or percent fines, between redd and undisturbed samples
Koski cited by Everest *et al.* 1987)	Pink salmon	Southeast Alaska	Freeze core and bulk core samples of spawning areas pre- and post spawning(n not reported)	Average percent < 0.83mm decreased from 8.2 to 6.5 after spawning.
Porter cited by Everest *et al.* (1987)	Pink salmon	Southeast Alaska	Freeze core samples of spawning areas pre-and-post-mass-pawning (n not reported)	Average percent < 1mm decreased from 14.2 to 7.4 in Montana Creek, from 9.5 to 4.4 in Tap Bay Creek.

Table 3.1.7 Reported gravel size modifications by spawning salmonids (after Kondolf and Wolman, 1993).

In addition to filtering fine sediments, the cutting action also modifies the vertical structure of redd gravels (Peterson and Quinn, 1996; Chapman, 1988). As described in Section 3.1.1, particles that are either too large to be evacuated into the flow by the spawning salmonid, or too large to be displaced by critical shear velocities at the redd site, will remain at the base of the egg pocket. This interaction between the cutting action of the female salmonid and local substrate and hydraulic conditions, results in a zone of coarse larger particles at the basal interface (Hobbs, 1937; Burner, 1951; Jones and Ball, 1954; Peterson and Quinn, 1996). The size of these larger particles is dependent on surface and subsurface substrate characteristics, particularly the presence of an armour layer. It has been suggested that the presence of larger particles in the base of the redd creates a zone of high permeability within the egg pocket, potentially promoting the flux of water through the redd (Chapman, 1988; Bjorn and Reiser, 1997).

It is also important to consider the impact of redd cutting on the susceptibility of redd gravels to bed entrainment or scour events (Section 3.1.3). The removal of fine material and resultant reduction in packing density of gravels overlying the egg pocket, combined with the loss of any surface armour layer, will reduce the hydraulic stability of these gravels (Furniss *et al.*, 1993), resulting in increased susceptibility to bed entrainment and gravel scouring.

3.1.2.5 Redd hydraulics

The distinctive redd morphology promotes the exchange of surface water into the redd (Stuart, 1965.) Localised areas of high hydraulic pressure are created in the substrate below zones of deeper flow (Cooper, 1965; Thibodeaux and Boyle, 1987). Such zones are created on the upstream side of the redd. At these areas of high hydraulic pressure, water flows into and through the substrate towards areas of lower pressure associated with zones of lower depth (Stuart, 1965; Vaux 1962). The zone of lowest depth is situated above the apex of the redd and beyond this point water is re-routed to the surface (Figure 3.1.4).

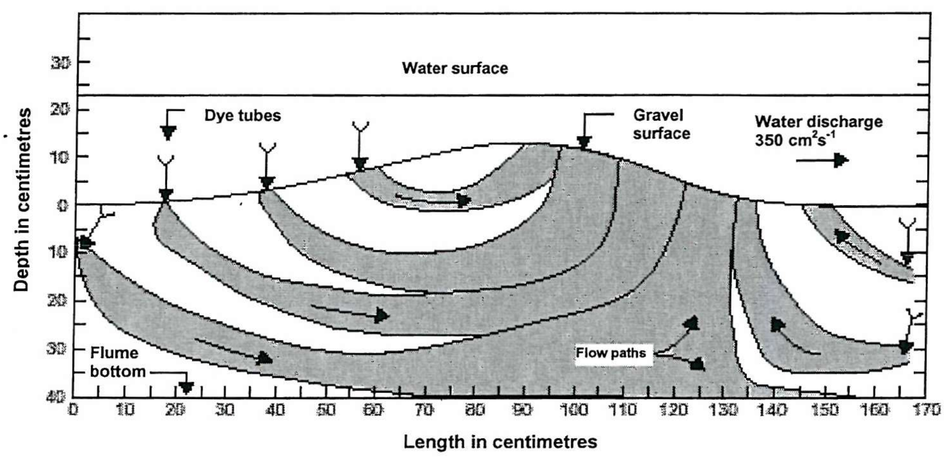

Figure 3.1.4 Flow through a homogenous gravel substrate with a bed morphology similar to a new salmonid redd (after Cooper, 1965).

Although a number of studies have commented on the benefits of increased surface-subsurface exchange induced by the distinctive redd morphology, in many systems these enhanced exchanges are of short duration. During high flows, bed material may become entrained resulting in loss of the distinctive redd morphology. In freshet rivers, flows capable of entraining over loose redd gravels are frequent, consequently the redd morphology may be lost shortly after creation. However, in systems with stable hydrological regimes, for instance groundwater-dominated chalk streams, bed movement is infrequent (Sear *et al.*, 1999), consequently, redds may remain intact for the duration of the incubation period (Personal communication, Mark Fidebottom (Environment Agency).

3.1.3 Incubation requirements

Although the characteristics of the spawning and incubation environment are similar, the incubation requirements of salmonid progeny are distinct from those of adult salmonids. Successful incubation of embryos and alevins is dependent on a series of extragravel and intragravel variables including oxygen availability, water temperature, stability of the incubation environment, and the presence of toxins and/or other aspects of water quality (Bjorn and Resier, 1997). Section 3.2 details the oxygen requirements of salmonid embryos and alevins and the factors influencing oxygen availability, the following brief section discusses additional important incubation requirements.

Salmonid embryos and alevins can tolerate a wide range of water temperatures. Typically, the upper and lower lethal temperature limits for Atlantic salmon embryos are 12°C and < 0°C, although short periods outside of this temperature range may be endured if freezing or drying out does not occur (Gunnes, 1979). Temperature is also the principal factor influencing the rate at which embryos and alevin develop, although other environmental factors, such as dissolved oxygen concentration and mechanical shock, have also been reported to influence development to a lesser extent (Alderice *et al.,* 1958; Burns, 1970; Combs, 1965; Crisp, 1982, 1988; Garside, 1966; Gunnes, 1979; Hamour and Garside, 1976, 1977, 1979).

If daily mean water temperatures (T) are available, predictions of the occurrence of eyeing, hatching and swim up can be made (Crisp, 1981, 1988, 2000). Such predictions are for median development times, where half the eggs are expected to reach eyeing (D_1), hatching (D_2) and swim-up (D_3) respectively (Crisp, 1988). Although the model for the Atlantic salmon is based on relatively few data points and a narrow range of temperatures, it has been validated in the field for temperatures down to 1°C (Wallace and Heggberget, 1988; Crisp 1988, 2000). The empirical relationship defining median hatching is given by:

$$\text{Log10}D_2 = [-2.6562\log_{10}(T + 11.0] + 5.1908 \qquad \text{(Crisp 1981)} \qquad (3.1.3)$$

This relationship can also be used to determine median eyeing and emergence. The quantity of $100/D_2$, where D_2 is the number of days to reach median hatch, is the percentage daily increment towards median hatch. From the date of oviposition (fertilisation) onward, daily mean water temperatures can be used to calculate the percentage increment for each day. The predicted day of median eyeing, hatch and emergence will be the day upon which the cumulative sum of daily increments reaches 50%, 100% and 150% respectively.

Physical disturbance of salmonid redds during high flow events can also cause mortalities or reduce the probability of survival of embryos and alevins (Chapman, 1988). Salmonid embryos require a stable incubation environment in which to develop. If this environment is disturbed, eggs and alevins may be damaged, potentially resulting in mortalities. The most common disturbance to the incubation environment occurs as a result of riverbed scouring (Montgomery *et al.*, 1996; De Vries, 1997). Scouring takes place when the entrainment threshold of riverbed gravels is exceeded. If scour depth reaches or exceeds egg burial depth, incubating embryos may be disturbed or released into the flow, reducing the probability of survival

Once salmonid eggs have hatched, the hatchlings (alevins) remain in the gravel substrate until they are fully developed fry. Once developed, the fry must escape from the gravel substrate to begin feeding. Fine sediments that deposit within and above the incubation zone have been shown to restrict emergence from the gravel substrate causing pre-emergent mortalities (White, 1942; Philips *et al.*, 1975; Crisp, 1993). Typically, sediments in the sand to coarse sand range have been shown to impede emergence (Philips *et al.*, 1975; Crisp, 1993).

Aspects of water quality, for instance, the presence of toxins within the incubation environment, can also influence the survival of salmonid embryos. Under low intragravel flow velocities, excreted metabolic waste, which includes ammonia, can be toxic to incubating embryos (Burkhalter and Kaya, 1977; Bjorn and Reiser, 1991). At present little data exists concerning lethal concentration limits or intragravel flow velocities required to flush waste from the microenvironment surrounding incubating embryos. Finally, the introduction of toxins, including agro-chemicals and heavy metals, and the acidity of freshwaters can aversely affect survival. The lower pH limits for embryos and alevins are 4.8 and 5.4 respectively (WWF, 2001).

The factors discussed above have been shown to influence incubation success. However, the most frequently cited cause of incubation mortalities is insufficient availability of oxygen to support respiratory requirements (Section 1.2). The following section (Section 3.2) provides a detailed examination of the respiratory requirements of salmonid embryos and alevins and discusses factors influencing the flux of oxygen through salmonid spawning gravels. Special attention is given to the requirements of Atlantic salmon embryos.

3.2 Review of factors influencing the availability of dissolved oxygen to incubating salmon embryos

The following section provides an overview of the respiratory requirements of incubating salmon progeny and discusses factors influencing the ability of the incubation environment to support respiratory requirements.

3.2.1. Introduction

The availability of oxygen to incubating salmonid embryos is dependant on the exchange of oxygenated water with the riverbed and the ability of the riverbed gravel medium to transport this water at a rate and concentration appropriate to support embryonic respiratory requirements (Figure 3.2.1). Applying this simple model of oxygen flux through salmon spawning gravels, the following section provides an examination of the principal processes and factors influencing the availability of oxygen within salmonid spawning gravels. The review is organised into four sub-sections: (i) an overview of the respiratory requirements and characteristics of incubating salmon embryos and alevins, (ii) a summary of factors influencing the exchange of oxygenated water with the riverbed, (iii) an examination of surface and subsurface factors influencing the passage of oxygenated water through riverbed gravels, and (iv) the development of a holistic model of factors influencing the availability of oxygen to incubating salmon progeny.

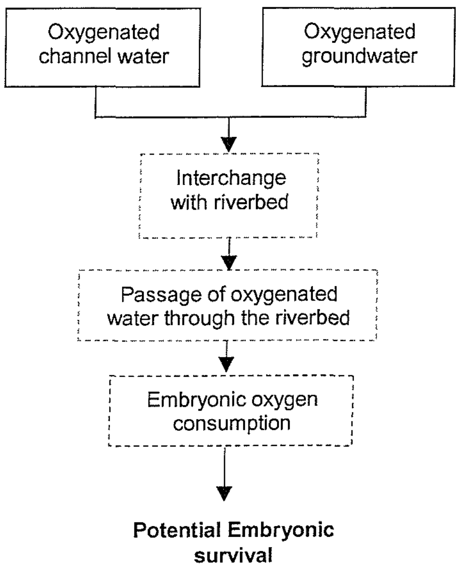

Figure 3.2.1 Summary of the dominant factors (solid boxes) and processes (dotted boxes) controlling the availability of oxygen to respiring salmonid embryos.

3.2.2. Pre-emergent oxygen consumption

3.2.2.2 Basic processes

Knowledge of the metabolic characteristics of pre-emergent embryos promotes understanding of the relationship between oxygen supply and demand, and improves awareness of potentially deleterious factors impacting on the incubation environment. Prior to hatching, the oxygen available to incubating eggs is contained within a thin film of water at the egg surface; termed the boundary layer (Daykin, 1965) (Figure 3.2.2). Oxygen is transported from the boundary layer across the egg membrane by diffusion. This requires a concentration gradient between the internal egg environment and the boundary layer. If oxygen concentration in the boundary layer drops, the concentration gradient is reduced, potentially resulting in restricted consumption and growth deficiencies (Silver *et al.*, 1963; Shumway *et al.*, 1964; Cooper, 1965; Garside, 1965; Mason 1969). If the concentration in the boundary layer drops below a critical threshold, the concentration gradient will be insufficient to support metabolic activity, and mortalities will occur (Daykin 1965; Rombough, 1988).

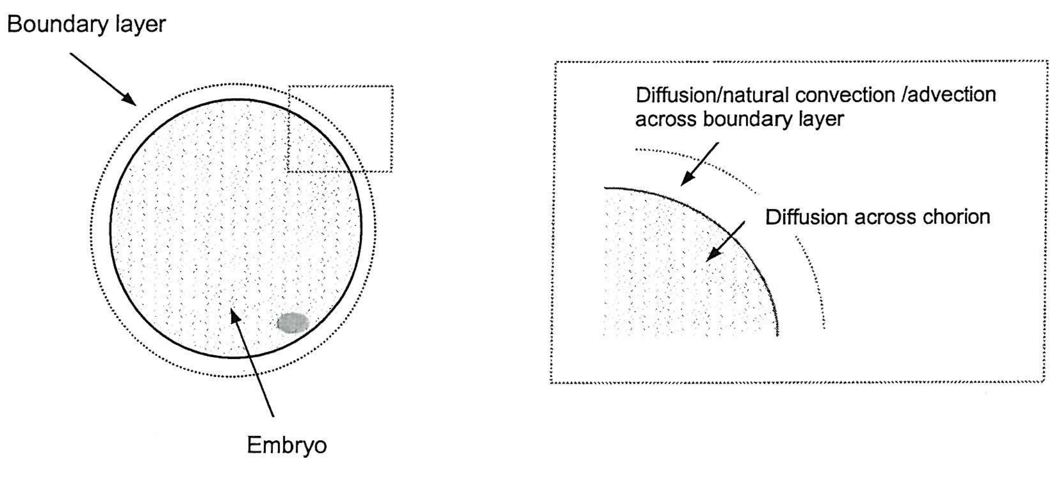

Figure 3.2.2 Schematic representation of boundary layer and zone of oxygen exchange.

The availability of oxygen to the boundary layer is dependent on the rate of supply of oxygenated water from the macroenvironment (Daykin, 1965). Oxygen is transferred to the boundary layer from the surrounding environment primarily by diffusion, although natural convection and advection have also been reported to influence supply (Daykin, 1965; O'Brien *et al.*, 1978; Rombough, 1988). Therefore, if oxygen concentrations in the macroenvironment drop, oxygen supply to the boundary layer will also drop. If incubating embryos consume oxygen at a greater rate than can be supported by the macroenvironment, oxygen concentrations within the boundary layer will decline, influencing the availability of oxygen to incubating embryos. If the oxygen concentrations in the macroenvironment result in restricted consumption, they are termed 'oxygen limiting', and if mortalities occur, they are termed critical (Davis, 1975). Theoretical and experimental examination of critical oxygen concentrations (Davis, 1975), suggest a critical oxygen concentration threshold of around 5mg l^{-1}, although survival at lower concentrations has been reported (Silver *et al.*, 1993; Shumway *et al.*, 1964).

Reductions in intragravel flow velocity, or a combination of reduced intragravel flow and oxygen concentration also restrict the availability of oxygen to the boundary layer. If the rate of oxygen supply is insufficient to support the oxygen requirements of incubating embryos, restricted consumption and mortalities may occur (Silver *et al*, 1963; Shumway *et al*, 1964; Cooper, 1965; Daykin, 1965).

Post hatching, oxygen consumption switches from cutaneous (across the cell membrane) to branchial (through respiratory gills) gas exchange (Rombough, 1981). The transition is gradual, subsequently cutaneous exchange remains an important source of oxygen beyond swim-up (Rombough, 1988). At this stage of development, embryos become mobile, allowing them to migrate from areas of low oxygen availability (Stober *et al.*, 1982; Fast and Stober, 1984). Therefore, hatchlings may be less susceptible to mortalities resulting from oxygen deficiencies, and critical oxygen concentrations or supply rates become more difficult to define.

3.2.2.2 Factors influencing oxygen consumption

Prior to emergence, rates of oxygen consumption are influenced by the stage of embryonic development, ambient water temperature and the availability of oxygen within the incubation environment (Wicket 1975; Hamor and Garside, 1977, 1979; Silver *et al.*, 1963; Shumway *et al.*, 1964; Cooper, 1965; Rombough, 1987; Hayes *et al.*, 1951).

Stage of development is the factor most commonly associated with changes in oxygen consumption (Hayes, 1951; Wickett, 1954; Hamor and Garside, 1978) (Figure 3.2.3). In broad terms, prior to hatching, consumption increases with development (Crisp, 2000). However, within this general trend researchers have observed two peaks in metabolism. The first peak occurs early in development, and has been attributed to proliferation of the blastodisc (Hamor and Garside, 1978). The second peak occurs at hatching and has been ascribed to the exertion of breaking free form the egg capsule, which must be supported by increased oxygen uptake (Hamor and Garside 1978). Post-hatching developmental consumption trends have received less research attention. Rombough (1987) performed a detailed laboratory study on growth, aerobic metabolism and dissolved oxygen requirements of embryos and alevin of Steelhead trout from fertilisation beyond hatching. The results indicated that consumption increased towards hatching, before declining post-hatching.

Intragravel water temperature influences the rate of development of salmon embryos and alevins (Alderdice *et al.,* 1958; Burns, 1970; Combs, 1965; Crisp, 1981; Garside, 1966; Hamor and Garside, 1976, 1977, 1979) (Figure 3.2.3). As water temperature increases, metabolic activities increase and, as a result, consumption increases. Consequently, all other factors being equal, at any given temperature, the development rate and the rate of oxygen consumption are directly related. Few studies have directly investigated the influence of temperature on oxygen consumption. However, results presented by Garside (1959) and Hamor and Garside (1977), indicate that a two-fold increase in temperature halves the development time of Atlantic salmon embryos. Assuming a direct relationship between temperature and development, this would result in a two-fold increase in oxygen consumption. Data supplied by Hamor and Garside (1978) support this premise.

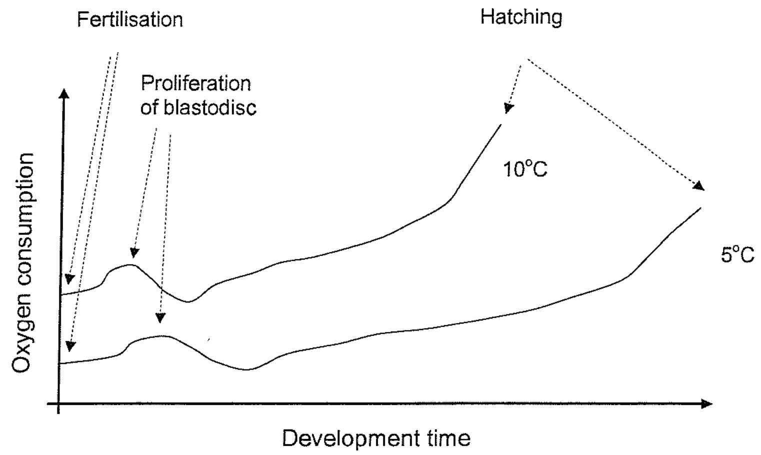

Figure 3.2.3 Summary of the influence of temperature and stage of development on rates of oxygen consumption.

Finally, embryonic oxygen consumption is also a function of oxygen availability (Hayes *et al.*, 1951; Silver *et al.*, 1963; Alderdice *et al*, 1958; Shumway *et al.*, 1964), Hamor and Garside 1977, Garside, 1965; and Rombough, 1987). Hayes *et al.* (1951), in a laboratory study investigating the influence of oxygen supply on consumption for pre-hatch Atlantic salmon, concluded that at low levels of oxygen supply, consumption was dependent upon supply, however, at higher levels, consumption is independent of supply. Studies carried out by Silver *et al.,* (1963), Shumway *et al.* (1964), Hamor and Garside (1977), Garside (1965) and Rombough (1987) support this observation.

3.2.2.3 Rates of oxygen consumption

Research generally concurs on the factors influencing oxygen consumption, however, disparity exists regarding precise rates of consumption (Table 3.2.1). Explanations for the discrepancies in reported consumption rates include variations in sampling techniques, interspecies variations in consumption and differences in consumption between small and large groups of eggs (Ryzhkoz, 1968; Hamor and Garside, 1978; Chevalier *et al*, 1984).

Of particular significance is the order of magnitude difference in consumption reported by Hamor and Garside (1979) and a number of other studies (Alderice, 1958; Lindroth, 1942; Hayes, 1951; Eimum et al., 2003). Hamor and Garside were aware of the disparity between their results and those of previous studies and provided a potential explanation for this discrepancy. Early assessments of oxygen consumption rates were carried out in closed systems in which the oxygen concentration of the ambient water declined over time as oxygen was consumed by incubating embryos. Hamor and Garside (1979) suggested that this decline in concentration may have reduced the oxygen available to incubating embryos, resulting in reduced consumption. Hamor and Garside (1979) circumvented this problem by incubating eggs in an open system in which the water was continually re-aerated. However, the data presented by Eimum *et al.* (2003), which supports the lower rates of consumption, was based on an experimental set-up that avoided the development of oxygen gradients. Without further details pertaining to the experimental procedures adopted by previous researchers, it is difficult to provide a comprehensive assessment of the accuracy and precision of reported rates of oxygen consumption.

Temperature (°C)	**Stage of development**	**Oxygen consumption (mg O_2 egg^{-1} h^{-1})**	**Reference**
10	Early	0.0013	Hamor and Garside (1979)
10	Eyed	0.02	Hamor and Garside (1979)
10	Eyed	0.00104	Hayes (1951)
5.5	'Domed' Eyed	0.0014	Lindroth (1942)
4.4	Well Eyed	0.0012	Eimum et al. (2003)
10	Hatch	0.048	Hamor and Garside (1979)
10	Hatch	0.0048	Hayes (1951)
17	Hatch	0.0067	Lindroth (1942)

Table 3.2.1 Reported rates of oxygen consumption for Atlantic salmon at various stage of embryonic development.

3.2.2.4 Modelling consumption

Early attempts to theoretically assess embryonic oxygen consumption utilised simple models of oxygen diffusion across cell membranes (Harvey, 1928; Krough, 1941; Hayes, 1951; Wickett, 1954). These early models were superseded with the application of the theories of mass transport, an established and tested theoretical model of solute and heat transfer, to the problem of embryonic respiration (Daykin 1965). The original model proposed by Daykin was refined by Wicket (1975) who integrated oxygen transport from the microenvironment to the egg capsule with transport from the surrounding macroenvironment to the microenvironment. Additional amendments to the model were carried out by Chevalier and Carson (1985) who, applying knowledge of factors influencing oxygen consumption, modified the model to assess consumption under varying internal egg conditions, and Alonso *et al.*, (1996) who added a function describing the influence of natural convection.

Although based on recognised theories of molecular transport, and integrating multiple aspects of oxygen supply and consumption, the theories of mass transport have received only limited application to the problem of estimating incubation success and habitat quality (Chevalier and Carson, 1985; Alonso *et al.*, 1996). Consequently, limited information exists on the ability of the theories of mass transfer to accurately define oxygen consumption or habitat suitability. One concern regarding the application of the theories of mass transfer is a lack of reliable information pertaining to important parameters utilised by the model, for instance the oxygen diffusion coefficient of the egg capsule and the oxygen concentration of the privitelline fluid. Section 6.5 contains further information regarding mass transport theory, and discusses its application to define intragravel flow velocity and oxygen concentration thresholds.

3.2.3. Exchange of oxygenated water with gravel riverbeds

3.2.3.1 Identification of hyporheic zone

The intragravel incubation environment of salmonid ova is contained within an ecotone referred to as the hyporheic zone. In addition to providing incubation habitat, the hyporheic zone offers refuge for complex communities of interstitial fauna, is an important zone for nutrient cycling and acts as a zone of mediation between catchments, underlying groundwater and surface water (Triska *et al.,* 1989; Findlay *et al.*, 1993; Findlay, 1995; Valett *et al.*, 1996; Brunke and Grosner, 1997). In recent years, the hyporheic zone has received research attention from a range of scientific disciplines, including freshwater ecology and biology, hydrology and fishery sciences. Investigation into the processes operating within the hyporheic zone is providing important insights into the processes and factors influencing the flux of oxygen through spawning gravels.

The hyporheic zone is typically defined as: the saturated interstitial area beneath and adjacent to the streambed that comprises some proportion of channel water, or that has been altered by channel water infiltration (White, 1993). With respect to the incubation zone of salmonids, it is the zone of saturated gravels below the streambed that is of direct relevance. Therefore, for the purposes of this review, the hyporheic zone refers to the riverbed substratum (Figure 3.2.4).

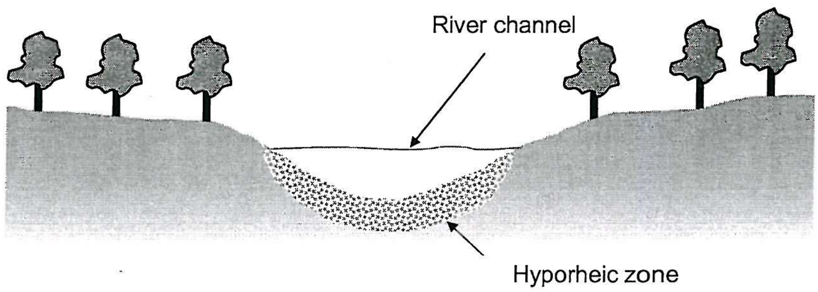

Figure 3.2.4 Delineation of area of hyporheic zone of interest to salmonid incubation.

Typically, water within the hyporheic zone is composed of upwelling groundwater and advected surface water. The influx of water from these zones is controlled by dynamic processes operating over a variety of spatial and temporal scales (Edwards, 1998; Brunke and Grosner, 1997; Boulton *et al.*, 1998; Malard, 2002). In complex landscapes, hyporheic exchanges are typically composed of localised hyporheic processes embedded within larger hill slope groundwater systems (Harvey and Bencala 1993, Malard, 2002). Therefore, the riverbed can be viewed as a mosaic of spatially distinct surface-subsurface exchange patches in which the timing and magnitude of exchange is temporally variable (Brunk and Grosner, 1997; Malard, 2002; Sophocleous, 2002).

3.2.3.2 Groundwater inputs

In channels flowing above a sediment layer overlying an impermeable stratum, water within the hyporheic zone will be composed solely of surface derived water (Gordon *et al.*, 1992; Sophocleous, 2002). However, if the riverbed is composed of an extended sediment layer overlying a zone of permeable substratum, groundwater may contribute to the hyporheic zone. Based on the regularity of groundwater inputs, streams are defined as perennial, intermittent or ephemeral. In perennial streams, groundwater is continually supplied to the stream. In intermittent streams the exchange of groundwater with the streambed fluctuates between exfiltration and infiltration, dependent on the height of the water table. Ephemeral streams continually lose water to zones of groundwater storage (Gordon *et al.*, 1992, Malard *et al.*, 2002).

Groundwater moves within three-dimensional flow fields that are controlled by gradients in hydraulic head, and hydraulic conductivity (Winter *et al.*, 1998). Hydraulic head is a measure of the mechanical energy per unit mass of water and is simply described as the sum of elevation above sea level and water pressure. Hydraulic conductivity is a measure of a mediums ability to transport water and for saturated porous media is determined by the size and interconnectivity of pore spaces. The direction of subsurface flow is controlled by gradients in hydraulic head, with flow moving from zones of higher to lower pressure along flow paths that are perpendicular to hydraulic contour lines. Flow velocity is controlled by the relative difference in hydraulic head over a given distance and the hydraulic conductivity of a medium (Freeze and Cherry, 1979). Darcy's law is a commonly adopted empirical equation that uses hydraulic conductivity and hydraulic gradient to describe the rate of laminar flow through a confined porous medium. Details of Darcian theory of groundwater flow can be found in (Freeze and Cherry, 1979).

Within complex catchments composed of variable geology, lithology and topographic relief, multiple groundwater flow paths may exist over a variety of spatial scales (Toth, 1963; Sophocleous, 2002). This will result in a subsurface network of groundwater flow systems (Figure 3.2.5). Water contained within these systems will be of varying age and hydrochemical composition, dependent on the length of flow path and character of the storage medium (Freeze and Cherry, 1979). With respect to dissolved oxygen concentration, groundwater is typically of lower quality than surface waters (Winter *et al.*, 1998; Fraser and Williams, 1998). A number of studies have reported that oxygen concentrations within the hyporheic zone reflect changes in the relative contribution of groundwater and surface water (Fraser and Williams, 1998, Soulsby *et al.*, 2000, 2001; Malcolm *et al.,* 2003). Typically this results in conditions synonymous with surface oxygen levels at the riverbed interface, and conditions similar to those of underlying groundwater at depth.

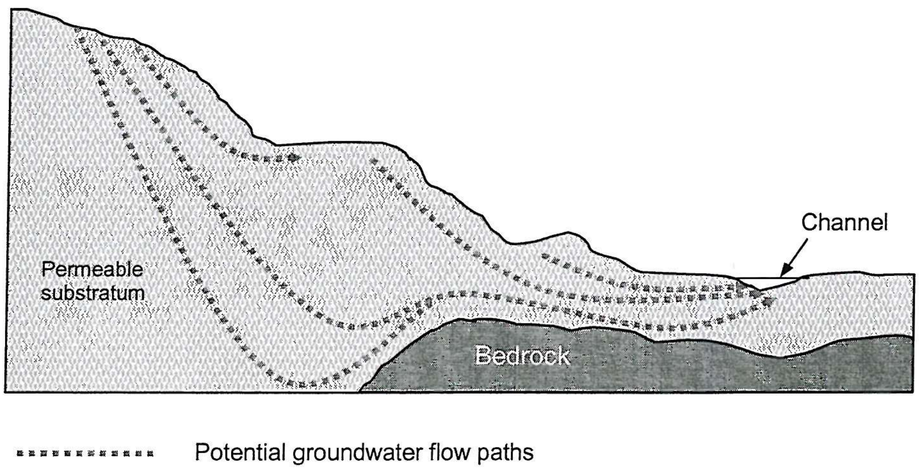

Figure 3.2.5 Summary of potential groundwater flow paths to a receiving waterbody.

The flux of groundwater into the hyporheic zone may occur diffusely or at discrete locations. The precise location of groundwater upwelling in the hyporheic zone is typically dependent on localised geologic features and topographic characteristics (Winter *et al.*, 1998 Dole-Olivier, 1998). Enhanced areas of upwelling may occur within subsurface geologic units of increased permeability, for instance, ancient channels below the hyporheic zone (Brunke and Gosner, 1997). Similarly, localised topographic features within the catchment may induce pressure differentials that drive upwelling into the hyporheic zone (Freeze and Cherry, 1979; Sophocleous, 2002). The relative contribution of groundwater and surface water to the hyporheic zone is also a function of surface water exchange. Evidence suggests that the zone of mixing between groundwater and surface water migrates towards the bed surface under low flow conditions and migrates downward during high flow conditions (Soulsby *et al.*, 2001; Malcolm *et al.*, 2003) (Section 3.2.3.3).

Studies have reported detrimental influences of groundwater on intragravel oxygen concentrations and incubation success (Sheridan, 1962; Soulsby *et al.*, 2001; Malcolm et *al.*, 2003). However, salmon populations have also been shown to display preferences for spawning in zones of groundwater upwelling (Heimer 1965; Lister *et al.*, 1980; Sowden and Power 1985; Curry *et al.*, 1984; Geist, 2002), indicating that in some systems groundwater inputs provide functional benefits to incubating embryos. For example, elevated water temperatures associated with groundwater inputs may induce development and promote emergence at periods conducive to fry survival. Furthermore, enhanced oxygen availability has been reported in zones of groundwater upwelling (Sowden and Power, 1985). Therefore, it seems appropriate to consider the influence of groundwater incubation success on a system-to-system basis.

3.2.3.3 Surface water inputs to the hyporheic zone

The exchange of surface water with the hyporheic zone is controlled by the physical character of the streambed and surface flow dynamics. Exchange is driven by pressure gradients, variations in bed permeability and turbulent coupling of surface-subsurface water. The processes that drive these exchanges operate over a variety of spatial scales; consequently, surface-subsurface interactions are typically classified into spatial units that represent the features associated with the exchange processes (Brunke and Gosner, 1997; Boulton *et al.*, 1998, Edwards, 1998).

A variety of spatial classifications have been proposed to describe the linkage between process and the landscape (Frissell *et al.*, 1986; Turner *et al.*, 1989; Townsend, 1996). Of the proposed classifications, an approach proposed by Frissell *et al.* (1986) is frequently adopted. The framework presented by Frissell *et al.* (1986) classifies streams and associated habitats within the context of geomorphic features and events, and spatio-temporal boundaries. Five spatial boundaries are defined: stream system, segment system, reach system, pool riffle system and microhabitat system. For the purpose of this review, a spatial hierarchy modified from Frissell *et al.* (1986) is adopted. The amendments to Frissells approach are (i) the term system is omitted, (ii) stream system is replaced by catchment scale, and (iii) pool/riffle system is integrated with reach system and termed reach scale (Figure 3.2.6)

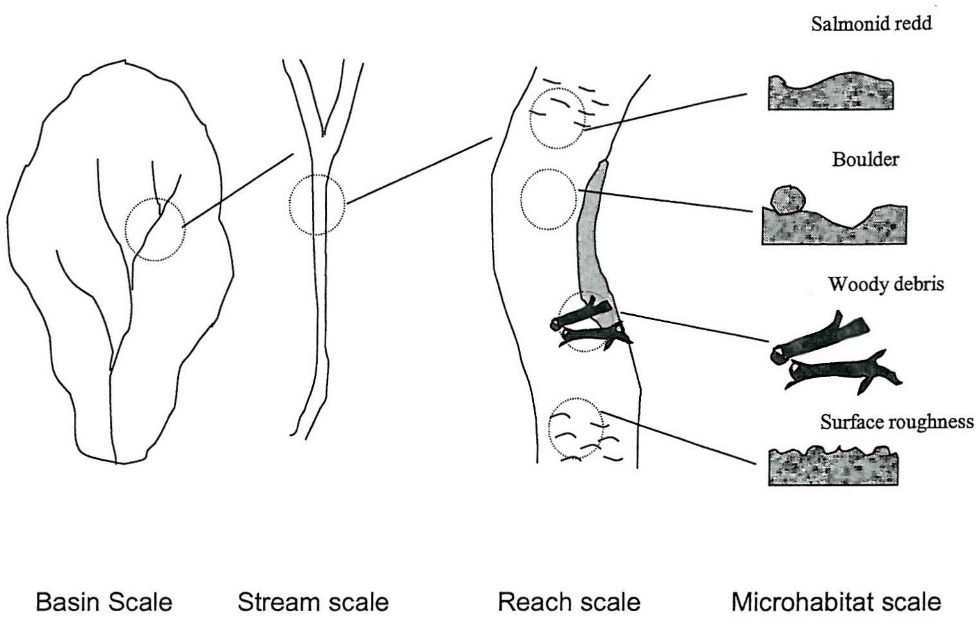

Figure 3.2.6 Spatial hierarchy adopted to describe exchange processes (modified from Frissell *et al* 1986)

Basin and stream scale exchange processes are primarily controlled by variations in subsurface lithology. For instance, as streams move from zones of bedrock constriction into zones of permeable alluvial deposits, deep penetration of surface water into the alluvium may occur. Upwelling back to the channel will occur as the channel re-enters a zone of constriction (Stanford and Ward, 1988). Subsurface flow of this nature will penetrate deep into the substratum, and result in extended flow paths and long residence times of water within the subsurface environment (Brunke and Gosner, 1997; Edwards, 1998).

At the reach-scale, exchange of surface water with the riverbed is driven primarily by topographic features and changes in bed permeability (Vaux, 1968; Savant *et al.*, 1987; Thibodeaux and Boyle, 1987; Harvey and Bencala, 1993). Streambed topography induces surface-subsurface exchange by creating pressure differentials above the bed. Down-welling is associated with local areas of high to low pressure change, for instance the interface between a pool and a riffle, and up-welling is associated with local areas of low to high pressure change, for instance at the interface between a riffle and pool (Figure 3.2.7 (a)). Reach scale changes in substrate permeability also create areas of up-welling and down-welling, with down-welling occurring in areas of decreasing permeability, and up-welling in areas of increasing permeability (Vaux, 1968). In zones of well defined bed topography and heterogeneous substrate composition, reach-scale exchange processes will result in mosaics of subsurface flow paths of variable flow path length and depth although, typically, flow paths are shallower and shorter than those operating at the basin and stream scale (Brunke and Gosner 1997; Edwards, 1998). Flow path lengths are closely associated with the size of geomorphic features and are typically measured in tens of metres (Edwards, 1998).

Microhabitat scale exchange processes are driven by localised changes in bed topography and permeability, and by roughness at the bed surface. At this scale, topographic features generally result in shallower penetration of surface water and shorter flow paths than reach scale driven exchange (Edwards, 1998; Malard *et al.*, 2002). Obstacles in the streambed, for instance, log jams and boulders, cause pressure differentials that induce surface-subsurface exchange with the hyporheic zone (Vaux 1968, White, 1990). Similarly, freshly created salmon redds contain gravels of enhanced permeability and have a distinct morphology that induces downwelling of surface water into the redd (Figure 3.2.7 (b)) (Chapman, 1988, Carling *et al.*, 1999).

The influence of surface roughness on the coupling of surface-subsurface flow has been investigated in a number of flume studies (Shimuzu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Packman and Bencala, 2000). Tracer experiments investigating flow through a flat bed under varying discharges, have shown that intragravel pore water velocities increase towards the bed surface; suggesting a coupling of surface and subsurface flow (Shimizu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993). This surface-subsurface coupling has been attributed to turbulence induced by roughness at the bed surface. This turbulence promotes a slip velocity and an exchange of momentum with subsurface water (Figure 3.2.7 (b)) (Shimizu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Packman and Bencala, 2000).

Under laboratory conditions, surface flow has been shown to influence the upper 0.1 m of the gravel substrate (Mendoza and Zhou, 1992; Zhou and Mendoza, 1993). This penetration depth would not typically affect conditions within the egg pocket, which is typically located at a depth of between 0.15 and 0.3m (White, 1942; Ottoway *et al.,* 1981; Crisp and Carling, 1989). However, periods of surface gravel entrainment may allow turbulent mixing to penetrate deeper into the riverbed. Additionally, only relatively small changes in surface flow have been assessed under flume conditions. At discharges commonly reported in natural river systems, it is possible that the penetration depth of surface water into the hyporheic zone may increase. Field evidence indicating increased surface-subsurface exchange during periods of high flow has been provided in a number of studies (Wickett, 1954; Bretschko, 1992; Vervier *et al.*, 1992; Panek, 1994; Brunke and Grosner, 1997; Angradi and Hood, 1997; Fraser *et al.*, 1998; Soulsby *et al.*, 2001, Malcolm *et al.*, 2003). Fraser and Williams (1998) observed a seasonally variable influence of groundwater within the hyporheic zone and concluded that downwelling surface water during high flow events lowered the hyporheic-groundwater interface. Malcolm *et al.* (2003) reported similar results and concluded that deeper penetration of surface water occurred during high flow events.

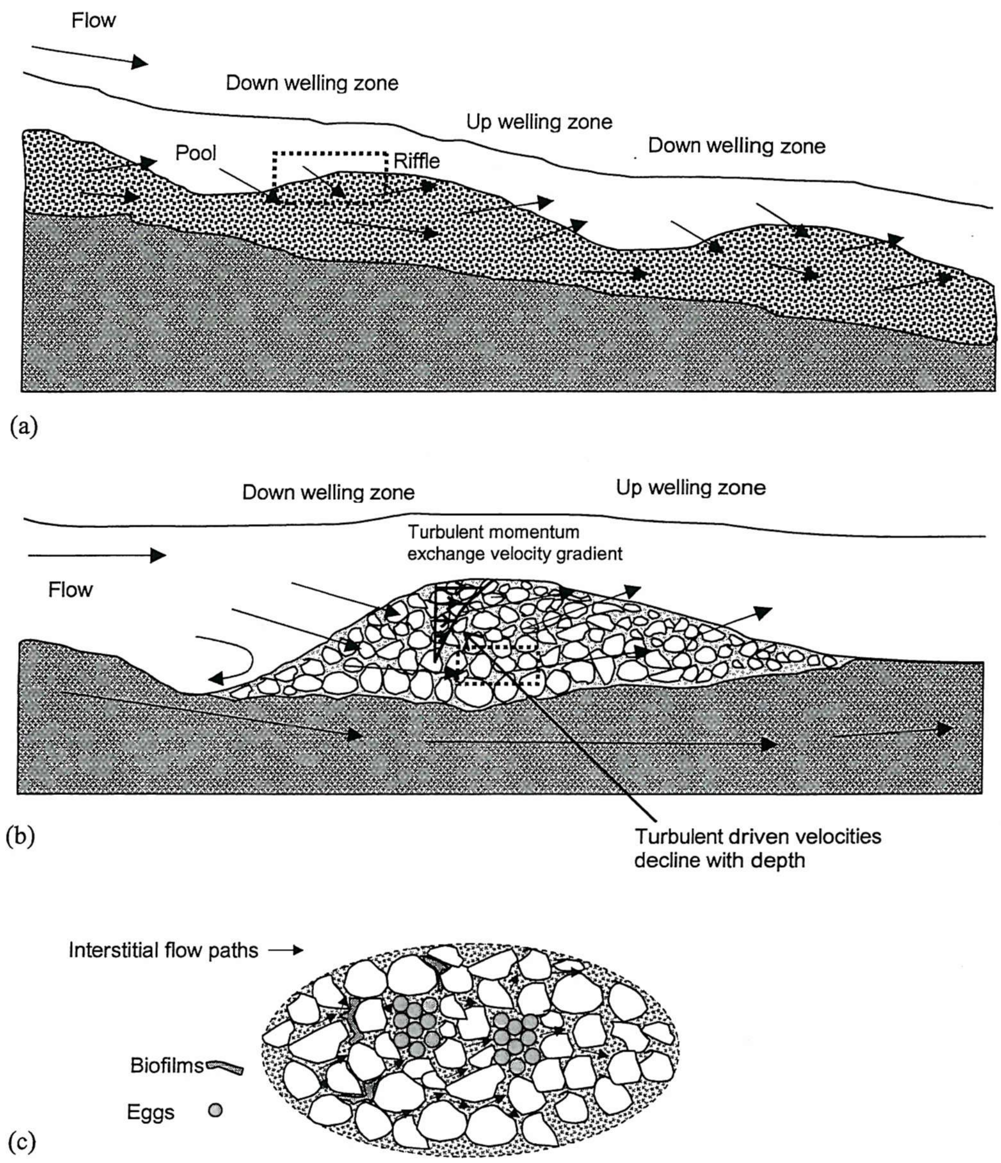

Figure 3.2.7 (a) Reach-scale surface subsurface exchange flows. **(b)** Micro-scale exchange flows (redd). **(c)** Interstitial flow paths within the egg pocket (Section 3.2.4).

3.2.4 Hyporheic controls on the flux of oxygenated water

3.2.4.1 Intragravel flow velocity

Once water has entered the hyporheic zone, its oxygen content and progress through the riverbed is influenced by characteristics of the riverbed substratum and surface flow conditions. The oxygen content of hyporheic water is influenced by the oxygen concentration of surface and groundwater inputs, and the contact time of water with oxygen consuming materials within the hyporheic zone, including salmonid embryos. Intragravel flow is influenced by the permeability of riverbed gravels, pressure differentials induced by surface topography and the coupling of surface and subsurface flow.

The processes controlling the passage of water through the riverbed are similar to those of groundwater flow, with intragravel flow velocity primarily influenced by hydraulic gradient, substrate permeability and surface driven turbulent momentum exchange (Section 3.2.3.3). The pressure gradients driving subsurface flow are determined by bed topography. Consequently, zones of high topographic relief induce higher subsurface flow. As described above, permeability is determined by the interconnectivity and size of pore spaces. The principal factor influencing the availability of interconnected pore space in riverbed gravels is the infiltration of fine inorganic and organic particles. Fine particles block interstitial pore spaces and restrict the flow of water through the riverbed (Chapman, 1988). The impact of fine particles on intragravel flow is determined by the size of infiltrated particles and the size and structure of framework gravels. Typically, as particle size decreases, its impact on permeability and intragravel flow increases. It has been shown that a one percent increase in silt and clay can result in a drop in intragravel flow equivalent to a 22 percent increase in sand (Chevalier and Carson, 1985).

Fine sediment deposition and infiltration processes have been covered extensively in the literature. In summary, infiltration rates and variations in the particle sizes of infiltrated sediments are governed by a complex interaction of processes, including sediment supply and transport mechanisms (Carling and McCahon, 1987), local hydraulics (Einstein, 1968; Carling, 1992; Sear, 1993), the relationship between particle size and surface and subsurface interstitial pore spaces (Besheta and Jackson, 1979; Frostick et al., 1984, Reid, 1992), scour and fill sequences during floods (Lisle, 1989), and reach morphology (Jobson and Carey, 1989; Diplas and Parker, 1992).

For the purposes of this review, a précis of infiltration characteristics of relevance to intragravel flow velocities is provided. With respect to trends in accumulation, it has been demonstrated that infiltration is largely controlled by the relationships between sediment size and available pore space. In short, the ratio of pore size to fine sediment size determines whether a particle is obstructed, becomes trapped near the surface, or penetrates deeper into the riverbed. Fine sediments that infiltrate upper gravels layers, but are too large too pass through the sub-layer gravels, become trapped near the surface of the riverbed (Besheta and Jackson, 1979; Frostick *et al.*, 1984, Lisle, 1989). These sediments reduce interstitial pore spaces and trap successively smaller matrix particles. As a result, the subsurface layer becomes plugged (often referred to as a surface or sand seal), preventing deeper penetration of fine sediments particles (Besheta and Jackson, 1979). Conversely, fine sediments that are smaller than the interstitial gaps in the surface and sub-surface gravels will pass through the riverbed gravels and settle at the base of the permeable gravel layer (Einstein, 1968) (Figure 3.2.8 (a)). Infiltration of this nature is often referred to as 'bottom up' sediment accumulation. Importantly, as the formation of 'seals' at the bed surface can inhibit deeper deposition of finer material, the mixture of fine sediment size classes exert an important control over the amount of fine sediment that accumulates in riverbed gravels (Figure 3.2.8 (b)).

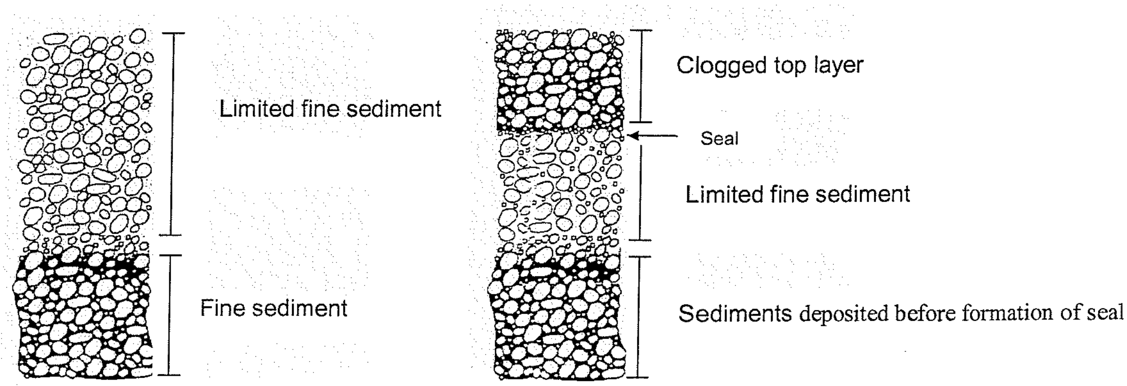

Figure 3.2.8 Trends in fine sediment accumulation. (a) 'bottom up' sediment deposition. (b) formation of a seal near the bed surface (after Alonso *et al.*, 1996).

With respect to salmon redds, the granular and morphological character of the redd may influence infiltration of fine sediments. First, an important control over the depth and rate of fine sediment deposition is the overlap of substrate particle sizes with sediment in transport (Frostick *et al.*, 1984; Lisle, 1989). The removal of fines during the cutting process reduces the overlap in particle sizes with sediments in transport; consequently, before the intrusion of coarse fine sediments, which potentially inhibit the downward penetration of finer material, they are susceptible to deep intrusion of fine sediments. Secondly, the vertical redistribution of substrate particles during the cutting process results in the loss of the surface armour layer and an increase in large particles within the egg pocket zone. As highlighted by Frostick *et al.*, (1984), if the sub-surface gravel is coarser than the surface layer gravel, fine sediment intrusion is increased. Third, by loosening the gravel substrate, the cutting action of the female may potentially increase the pore space between gravel particles (Crisp and Carling, 1989). This increased pore space, particularly in the egg pocket, which contains large centrum particles, may potentially result in increased intrusion of fine sediments into salmon redds. Finally, although it has been suggested that fine sediments may preferentially deposit in the redd pit (Everest *et al.*, 1987), the topographic form of the redd also promotes exchange of surface water with the riverbed. It has been suggested that downwelling surface water could provide a mechanism to increase the influx of fine sediments into redd gravels (Kondolf *et al.*, 1993).

The implications of these observation on intragravel flow can be summarised as follows: (i) fine sediments that penetrate deep into the riverbed will reduce gravel permeability and intragravel flow velocity, (ii) the accumulation of coarse fine sediment particles towards the bed surface may inhibit deeper penetration of fine sediments, thereby retaining a zone of high permeability at depth into the riverbed, potentially increasing the flow of water at egg incubation depths, and (iii) although initially cleansed of fine sediments, due to their granular and morphological properties, salmon redds may be susceptible to enhanced infiltration of fine sediments and the associated impacts on intragravel flow velocities.

In addition to inorganic substances, the infiltration of organic detritus into riverbed gravels must also be considered. The infiltration of organic material will also block interstitial pore spaces and reduce gravel permeability, however, the accumulation of organic material within the riverbed may also promote the formation of biofilms. Biofilms form around sediment particles during the breakdown of organic material; potentially resulting in the formation of cohesive matrices that may further reduce gravel permeability and intragravel flow (Chen and Li, 1999).

3.2.4.2 Intragravel oxygen concentration

The oxygen concentration of subsurface water is controlled by the oxygen content of surface and groundwater inputs (as described above), and the contact time of water with oxygen consuming materials within the hyporheic zone (Whitman and Clark, 1982; Chevalier and Murphy, 1985; Sterba *et al.*, 1992). Oxygen demands within riverbeds, which are commonly referred to as either sediment oxygen demands (SOD's) or sedimentary respiration, develop as microbial communities breakdown organic and inorganic materials deposited in the riverbed. Based on the cycle driving oxygen consumption, the total sediment oxygen demand can be divided into biological oxygen demands (BOD) and nitrogen oxygen demands (NOD). A third component, referred to as the chemical oxygen demands (COD), is more commonly associated with anaerobic conditions and is therefore not thought to significantly influence the availability of oxygen within zones of salmonid incubation (Chevalier and Murphy, 1985).

In many river systems, BOD's are the primary driving force for oxygen consumption. BOD's develop when organic material within subsurface gravels are broken down by micro-organisms in a carbon oxidation processes that consumes oxygen from the surrounding environment. Principally, these oxygen demands take place at the sediment water interface that is coated by microbial biofilms. NOD's are similar to BOD's except that the driver for the oxygen demand is a nitrogen oxidation process. Nitrogen sources are typically inorganic, for instance fertilisers, although the aerobic or anaerobic conversion of proteins may provide an organic source of nitrogen. Based on temporal characteristics, the total oxygen demand can be simplified into two stages. Stage one is driven by the carbon demand (BOD) and generally peaks at between 10 and 14 days. Stage two is driven by nitrifying bacteria (NOD), and typically lags the BOD demand. Generally nitrogen driven demands occur around 10 days into the consumption cycle, and peak at around 25 days (Figure 3.2.9) (Chevalier and Murphy, 1985). These time tends are provided as general markers; in reality oxygen demand curves are composed of multiple overlapping consumption cycles that are controlled by the specific chemical composition of oxidising materials.

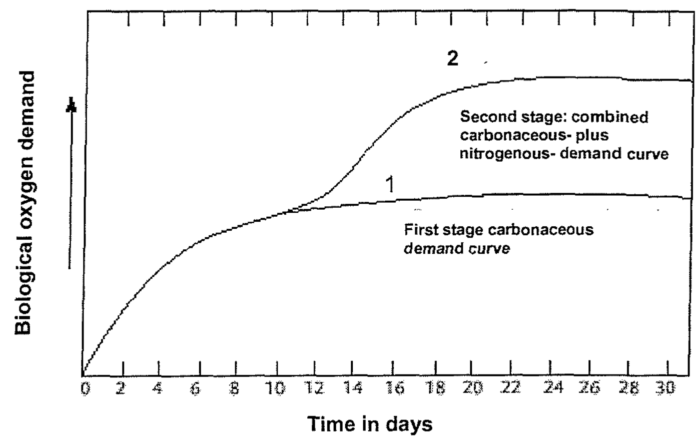

Figure 3.2.9 Typical oxygen demand response curve. (1) first stage BOD curve for oxidation of organic matter, (2) second stage NOD, influence of nitrification (after United States Geological Society, 2000).

Oxygen demands require the presence of nutrients to support the oxidation processes. Within streams, organic matter is the principal nutrient input (Jones *et al.*, 1994). The dominant forms of organic matter are particulate organic matter (POM) and dissolved organic matter (DOM). Inputs of particulate organic matter can be described as autochthonous (in-stream source) and allochthonous (terrestrial source). Typical autochthonous material includes dead and necrotic macrophyte vegetation, and small macro-invertebrate faeces. Typical allochthonous material includes leaf litter, cattle faeces, agricultural waste and effluent discharges (Jones *et al.*, 1994; DEFRA, 2002). DOM is input from groundwater and surface water sources and is typically the largest source of organic carbon in running waters (Hynes, 1983). DOM often originates naturally from soils, terrestrial plants or aquatic organic matter, although non-natural sources, for instance fertilisers may also provide a source.

As respiration is strongly dependent on the availability of organic matter, sedimentary respiration will increase as the pool of organic matter increases (Jones *et. al.*, 1994). Increases in the availability of organic matter occur during succession, when algal biomass is at a maximum, and when inputs of leaf litter and other natural occurring allochthonous organic detritus are high, for instance in autumn (Bunn, 1986) or during periods of clear cutting (Cederholm *et al.*, 1981), and when localised sources of organic material are washed into the river, for instance during periods of overland flow across arable land. Two mechanisms have been reported to control the influx of particulate organic matter into the hyporheic zone (Jones *et al.*, 1995). First, organic matter retained in the stream is continually deposited into the substratum. Therefore, resultant deposition is greatest in zones of downwelling and during periods of high organic availability. Second organic matter is buried during flood events that disturb surface gravels. Both mechanisms are potentially present within a river system, although the dominant mechanism of deposition will depend on catchment characteristics and will typically reflect trends in inorganic sediment deposition. DOM is transported into the streambed by surface water exchanges and upwelling groundwater (Kaplan and Newbold, 2000). The availability of organic carbon resulting from particulate deposition and surface and groundwater sources of dissolved organic carbon within riverbeds, has been closely related to gradients in dissolved oxygen concentration (Findlay et al., 1993 Kaplan and Newbold, 2000).

The impact of oxygen demands on the oxygen concentrations of hyporheic water is controlled by the magnitude of the oxygen demand and the residence time of interstitial water, with increased residence time resulting in greater contact times and larger reductions in dissolved oxygen (Chevalier and Murphy, 1985; Chevalier *et al* , 1984). At present, there are limited data sets pertaining to the oxygen demands associated with materials deposited in spawning gravels. Typical SOD rates, as reported in the literature, are outlined in Table 3.2.2. In view of the limited availability of data regarding sedimentary oxygen demands, it is suggested that further information is required before conclusive statements on its importance to intragravel oxygen concentration are drawn. Of particular interest is the potential oxygen demand of sediments in agriculturally intensive catchments, where the timing of farming practices, for instance the application of fertiliser and silage, may provide a source of nutrient rich organic and inorganic material.

Substrate	**SOD** **mg $O_2g^{-1}h^{-1}$**	**Reference**
Sand	0.0055	Hargrave (cited in Chevalier and Murphy,
Lake mud	0.74	1985)
Detritus	0.33	
Organic muck (30% organic)	2.45	Sylvester and Seabloom (1965)
Silt loam (9% organic)	0.0054	
Gravel loam with wood fragments (17% organic	0.31	
Pasture loam with dead grass (20% organic)	12.08	

Table 3.2.2 Review of reported sedimentary oxygen demands.

Intragravel residence time is a function of flow path length and intragravel flow velocity, with long flow paths and low intragravel flow velocities resulting in maximum contact times. Consequently, as intragravel flow velocities are impaired by the infiltration of fine sedimentary material into the riverbed, the impact of any associated oxygen demand will be exacerbated. Evidence of the influence of sedimentary respiration and residence time on the depletion of oxygen from hyporheic waters has been provided by studies of oxygen concentration through riffles (Findlay, 1995). These studies have shown that oxygen concentration gradients exist between the zones of downwelling at the head of riffles, and subsequent zones of upwelling (Findlay, 1995; Franken *et al.*, 2001). Based on the mosaic of hyporheic flow paths discussed in Section 3.2.3.3, it is possible to conceptualise a hyporheic zone that is characterised by oxygen gradients that are spatially defined by distinct flow systems or interactions between flow systems (Figure 3.2.10).

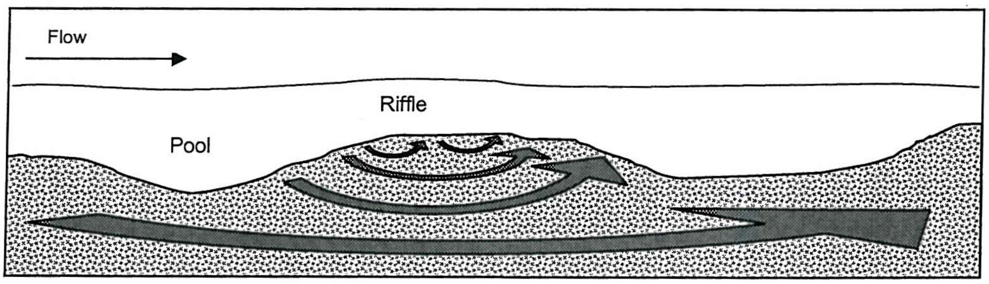

Figure 3.2.10 Summary of hyporheic flow paths. The thickness of the lines schematically represents the potential depletion in oxygen concentration of water within that flow path.

3.2.5 A holistic interpretation of factors influencing oxygen availability

Based on the simple model of oxygen availability presented in Section 3.2.1, and on the information presented in the preceding sections, Figure 3.2.11 provides an overview of factors influencing the availability of oxygen to incubating embryos. To summarise, pre-emergent mortalities are induced when oxygen concentrations drop below critical oxygen concentration thresholds or when oxygen supply rates are insufficient to support metabolic demands. Therefore, mortalities may occur as a consequence of periods of low oxygen concentration or as a result of combinations of oxygen concentrations and intragravel flow velocities that produce oxygen supply rates that are insufficient to support respiratory requirements at a given temperature and stage of development. Additionally, the spatial distribution of eggs within the incubation zone may also influence potential survival. For instance, as water passes through an egg pocket, oxygen will be removed from the ambient water by the incubating embryos, consequently eggs located at the downstream end of an egg pocket may receive lower oxygen concentration. Similarly, as fine sediments frequently accumulate from the base of the redd upwards, eggs located towards the bed surface may remain within zones of higher permeability and will potentially benefit from increased through flow of oxygenated water.

Factors influencing oxygen availability, as described in this review, operate contemporaneously and over a variety of spatial and temporal scales. Therefore, awareness of environmental conditions that can result in oxygen deficiencies within spawning gravels requires identification of potentially harmful factors and awareness of how these factors interact to influence oxygen availability. Furthermore, the presence and relative influence of factors influencing oxygen availability, and the degree of interaction between factors, will be determined by physical and biological characteristics of the river channel and its surrounding catchment. Consequently, the precise factors influencing oxygen availability within spawning gravels may vary significantly between and within river systems. For instance, in agriculturally degraded catchments, excessive sedimentation resulting from bank failure and inappropriate land drainage systems may be coupled with inputs of organic rich material associated with over winter grazing or poorly timed application of fertilisers or silage. Deposition of these materials within spawning gravels will reduce intragravel flow velocities, which in turn will exacerbate the impact of oxygen demands associated with the deposited materials, potentially resulting in oxygen limiting conditions within the riverbed. In over managed systems with moderated flow regimes, for instance as a consequence of impoundment or abstraction, the impact of sedimentation and its consequent effect on intragravel flow may be exacerbated by extended periods of low flow that reduce the exchange of surface water within the riverbed. In zones of low oxygen content groundwater, reductions in the exchange of surface water with the riverbed may increase the relative influence of groundwater on intragravel oxygen concentrations.

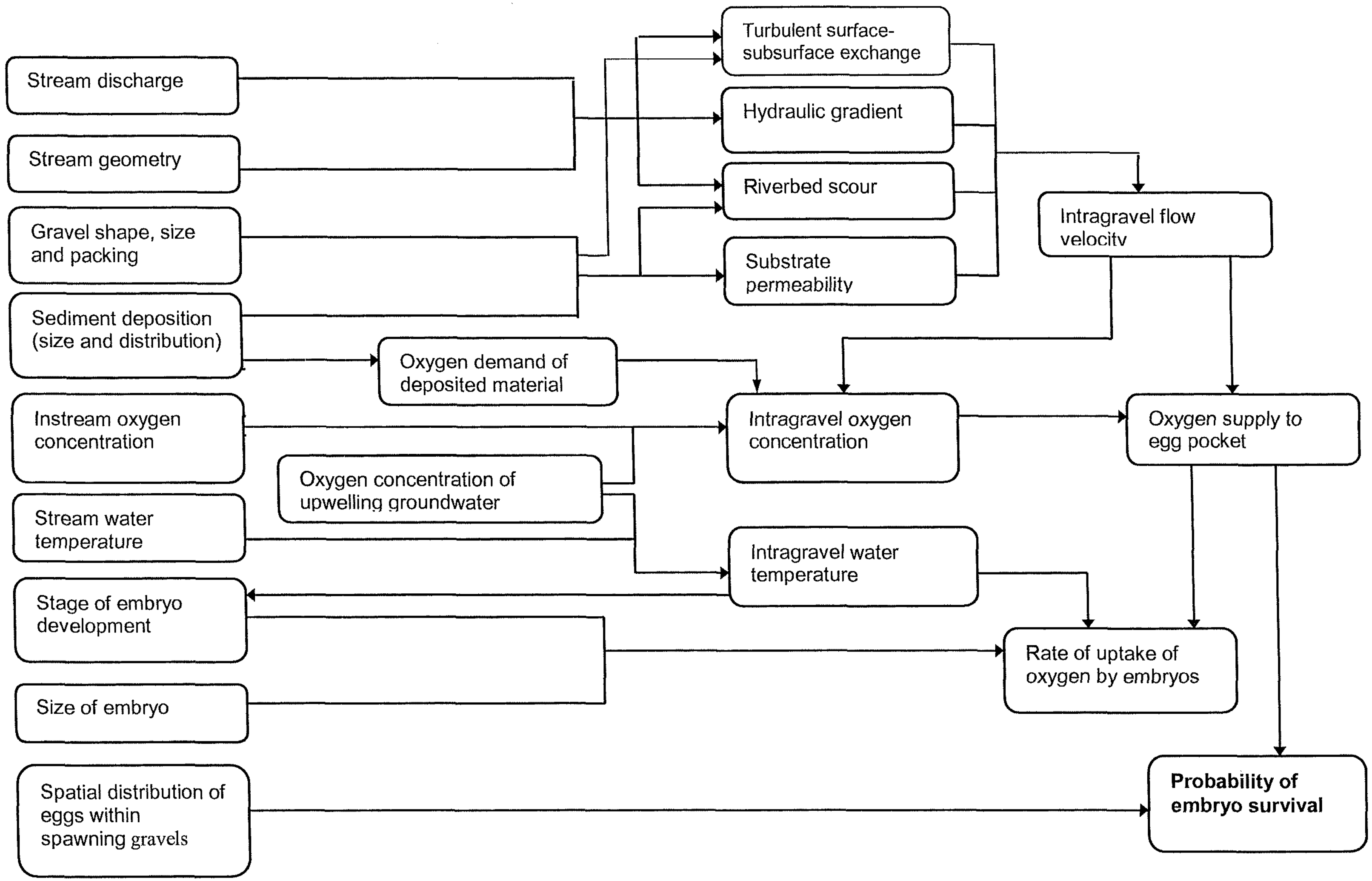

Figure 3.2.11 Overview of factors influencing the availability of oxygen to incubating salmon embryos.

3.2.6 Summary

An overview of factors and process influencing the availability of oxygen to incubating salmonid embryos was presented. The processes controlling oxygen availability were divided into four key sections. First, embryonic respiratory processes and characteristics were detailed. Fundamental principles governing oxygen exchange from the macroenvironment to the egg surface and across the egg membrane were discussed and it was shown that an interaction of advective and diffuse oxygen exchange controlled oxygen consumption. It was also shown that oxygen consumption varied with temperature stage of development and oxygen availability. Second, a summary of processes controlling the exchange of oxygenated water with gravel riverbeds was provided. The review detailed the importance of groundwater inputs and discussed the primary process driving the exchange of channel water with gravel riverbeds. It was shown that the exchange of oxygenated water is controlled by pressure driven and turbulent momentum driven processes. Third, the factors influencing the oxygen concentration and rate of transport of oxygenated water through riverbed gravels were described. The influence of surface flow conditions and oxygen consuming materials were outlined. Finally, the information presented in the previous sections was synthesised to produce a holistic overview of the processes and factors influencing the availability of oxygen to incubating embryos.

Chapter 4. Research objectives

The following chapter details the thesis research objectives and summarises the framework developed to report scientific findings.

4.1 Development of research objectives

As outlined in Section 1.2, increasing the productivity of spawning and incubation habitats is recognised as an integral component in the recovery of U.K. salmon populations. Increasing the productivity of salmonid spawning gravels will require the development of appropriate and measured remediation strategies, which target the sources and pathways of factors degrading the quality of spawning habitats. Central to the development of such strategies, is an appreciation of the physiological requirements of salmon embryos and alevins, and identification of the physical, biological and chemical processes influencing the ability of spawning gravels to support these demands (Section 3.2).

Previous investigations into factors influencing incubation success have often been limited to observations of intragravel oxygen concentrations and sediment accumulation (Section 1.2). Furthermore, assessments of habitat quality, or potential incubation success, are typically based on simple empirical relationships between incubation success and measures of the physical structure of the riverbed or oxygen concentration (Table 1.1 and 1.2). However, based on the information presented in Section 3.2, these assessments of habitat quality and incubation success may be inadequate to describe the range of environmental pressures influencing embryonic survival. Further investigation into the multiple processes and factors potentially affecting the quality of salmon incubation environments is required to elucidate the compound pressures affecting salmonid incubation success.

Section 2.2 identified oxygen availability as a primary factor influencing incubation success. It is proposed therefore that the relationship between oxygen flux and embryonic respiratory demand provides a process-based foundation upon which to investigate pressures affecting incubation success. Applying a process-based approach to assessing incubation success will improve delineation of the multiple factors potentially influencing survival and provide a scientifically robust foundation for determining the quality of spawning gravels. Additionally, improved understanding of these factors and processes will aid identification of wider catchment scale sources of factors degrading the quality of salmon spawning gravels.

As discussed in Section 3.3, multiple interacting processes and factors influence the availability of oxygen to incubating salmonid embryos. Therefore, investigation into the flux of oxygen through salmonid spawning and incubation environments, and assessment of the implications for incubation success, requires the development of a research project capable of assessing multiple processes across a variety of research disciplines. As discussed in Section 2.2, undertaking this type of multi-factorial assessment of incubation success limits the depth and detail of investigation into individual factors or processes. However, in terms of practicable research outputs, adopting a multifaceted research approach will: (i) promote appreciation of the complex interacting processes affecting the quality of spawning and incubation environments, thus highlighting a requirement to shift current research impetus away from simple single factor investigations, and (ii) allow identification of potential variations in the principal pressures on incubation success, thus promoting identification of management treatments that address the specific causes of poor embryonic survival within individual river systems.

4.2 Research objectives

The literature review (Section 3.2) provided a detailed discussion of factors and processes influencing the flux of oxygen through gravel riverbeds (Figure 3.2.7). For the purposes of delineating incubation success, the complex interaction of processes described in Section 3.2 can be divided into four key elements:

(i) *Impact of sediment on the passage of water through the riverbed.*

(ii) *Impact of sedimentary oxygen demands on intragravel oxygen concentrations.*

(iii) *Influence of surface flow on intragravel flow patterns and velocities.*

(iv) *Influence of upwelling groundwater on intragravel oxygen concentrations.*

With reference to these key factors, five research objectives were defined (Figure 4.1). These objectives were designed to meet the overarching thesis objectives defined in Section 2.2 and to: (i) enhance understanding of the interaction of processes and factors influencing the availability of oxygen to incubating salmon embryos, (ii) improve theoretical knowledge of key processes influencing oxygen fluxes through gravel riverbeds, and (iii) allow identification of the causes of poor incubation survival in four U.K river systems.

Importantly, it was recognised that in the natural environment additional factors can influence incubation success, for instance bed scouring and the accumulation of toxins in the incubation zone. However, as described previously (Section 1.2, 2.2, 3.2), the availability of oxygen to incubating embryos is regarded as one of the key factors restricting incubation success. Therefore, although it is not the only factor influencing the quality of spawning and incubation gravels, investigation into oxygen availability will provide valuable information regarding potential causes of poor embryonic survival in U.K. rivers.

Thesis aim one

Assess oxygen availability within salmon spawning gravels

Research objective

1) Quantification of oxygen fluxes through salmon spawning gravels and assessment of oxygen flux as a potential measure of incubation success.

Thesis aim two

Investigate factors influencing oxygen availability

Research objectives

2) Investigation of the impact of clay particles on oxygen consumption by Atlantic salmon embryos.

3) Assessment of the influence of surface-subsurface interaction across topographic features and under varying discharges.

4) Investigation of the influence of fine sediment on the flux of oxygenated water through salmonid incubation environments.

Thesis aim three

Assist management responses

Research objectives

5) Development of a new method of assessing the quality of salmonid spawning and incubation environments.

Figure 4.1 Summary of research objective and their relationship to the thesis aims.

Objective one

To improve process-based understanding of the causes of oxygen deficiency related embryonic mortalities, there is a requirement for improved information regarding spatial and temporal trends in the flux of oxygen through salmonid incubation environments. This information should provide a strong scientific foundation upon which to delineate the causes of oxygen deficiency related mortalities. Additionally, detailed information on oxygen fluxes through spawning gravels will aid assessments of the quality of salmon spawning gravels. As highlighted in the Section 3.2, the availability of oxygen within the incubation environment is one of the dominant factors influencing incubation success. Therefore, oxygen flux should provide a robust method of assessing potential incubation success. Based on this rationale, the first research objective was:

Quantification of oxygen fluxes through salmon spawning gravels and assessment of oxygen flux as a potential measure of incubation success.

Objective two

In addition to assessing the flux of oxygen through salmon spawning gravels, assessments of oxygen availability must also consider factors influencing the respiratory response of incubating embryos. A factor often discussed in relation to respiration is the potential impact of very fine sediments (clay) on the exchange of oxygen across the egg membrane. However, to date, no study has directly attempted to delineate the physical impact of fine sediment particles on the exchange of oxygen across the egg chorion. Based on principles of embryonic biology, it was hypothesised that fine sediments may block respiratory pore canals within the egg chorion, thereby restricting the passage of oxygen across the egg membrane. Based on this hypothesis, the second research objective was:

Investigation of the impact of clay particles on exchange of oxygen across the membrane of Atlantic salmon eggs

Objective three

In addition to the impact of sediment on the flux of oxygen through gravel riverbeds, surface flow has also been identified as a potential factor influencing the rate and pattern of subsurface flow (Section 3.2). This observation may have implications for environments experiencing altered hydrological regimes, for instance as a result of impoundment, abstraction or land drainage. At present investigations into the influence of surface flow on the subsurface environment has been restricted to simple flume observations of flatbed conditions, and field observation based on the hydrochemical composition of interstitial water. In order to advance scientific understanding of the interaction of surface and subsurface flow and to improve awareness of the implications for embryonic survival, the third research objective was:

Assessment of the influence of surface flow on subsurface flow patterns and intragravel flow velocities

Objective four

Among the factors influencing oxygen availability identified in Section 3.2, sediment accumulation is frequently cited as a dominant factor influencing incubation success (Chapman, 1988; Sear, 1993; Wood and Armitage, 1997; Milan *et al.*, 2003). However, investigation into the impact of fine sediment accumulation is generally restricted to the development of empirical relationships between granularmetric properties of the incubation zone and incubation success (Section 1.2). Within the context of oxygen availability, there are two mechanisms by which sediment accumulation influences oxygen flux. First, restricting the passage of water by physical blocking of pore spaces and second, the physical removal of oxygen by oxygen consuming materials associated with deposited sediments. Based on this observation the fourth research objective was:

Investigation of the impact of fine sediment on the flux of oxygen through salmon spawning gravels.

Objective five

The previous research objectives were designed to advance scientific understanding of oxygen availability and factors influencing oxygen fluxes through salmon spawning gravels. The final research objective related to the practical application of this knowledge to aid managerial responses. In view of the limitations associated with current methods of assessing habitat quality and factors degrading incubation habitats, the final research objective was:

Development of a new method of assessing the quality of salmon spawning and incubation habitats.

4.3 A note on the influence of groundwater inputs

It should be noted that although groundwater inputs have been recognised as a potential factor influencing oxygen fluxes within gravel riverbeds, project limitations did not allow a detailed assessment of the influence of groundwater. However, during the monitoring programme measurements of thermal profiles, hydraulic gradients and hydrochemical parameters allowed an assessment of the potential presence of groundwater inputs at each monitoring site. This and other project limitations are discussed further in Chapter 5.

4.4 Overview of structure adopted to report findings

As detailed in the previous section, the remainder of this thesis is formed around a series of interrelated research objectives, that, when integrated, form the basis of a holistic representation of factors influencing oxygen availability and incubation survival. In view of the complexities arising from investigating and reporting findings based on discrete research objectives that exist concomitantly within a broader framework, the remainder of the thesis is formed around a nucleus of concurrent sections divided between two chapters (Figure 4.2).

Chapter 5 provides an overview of the rationale underpinning the selection of the sampling methods; specific methodological details and sampling protocols are contained at appropriate junctures in Chapter 6. In addition to providing methodological details, Chapter 5 also provides detailed field-site descriptions, including a review of the potential groundwater inputs at the field sites. Further to the methodological details described in Chapters 5 and 6, some expanded sampling descriptions are contained in the appendices.

Applying the research objectives as a template, Chapter 6 is divided into five parallel sections. Although developed within the broad framework outlined in Chapter 2, each section is presented as a discrete study. Therefore, individual sections include a brief appraisal of associated literature, a description of monitoring techniques, a summary of important results, and a discussion of scientific and/or managerial implications. Section 6.1 reports the findings of the field assessment of embryonic survival and oxygen availability within salmon spawning gravels of four U.K. rivers. Section 6.2 reports the findings of the laboratory-based investigation of the impact of clay particles on the exchange of oxygen across the egg chorion of Atlantic salmon eggs. Section 6.3 discusses laboratory observations of the influence of discharge on subsurface flow paths and intragravel flow velocities. Section 6.4 reports the findings of the field-based assessment of the impacts of fine sediment on embryonic survival and oxygen flux. Finally, Section 6.5 integrates the information presented in section 6.1 with a theoretical model of oxygen consumption to develop a method of assessing potential incubation success.

Chapter 7 summarises the scientific information presented in chapter 6. A summary of the potential causes of poor incubation success at the field sites is also presented. Finally, the analytical limitations of the study are recognised, and recommendations for future research are proposed.

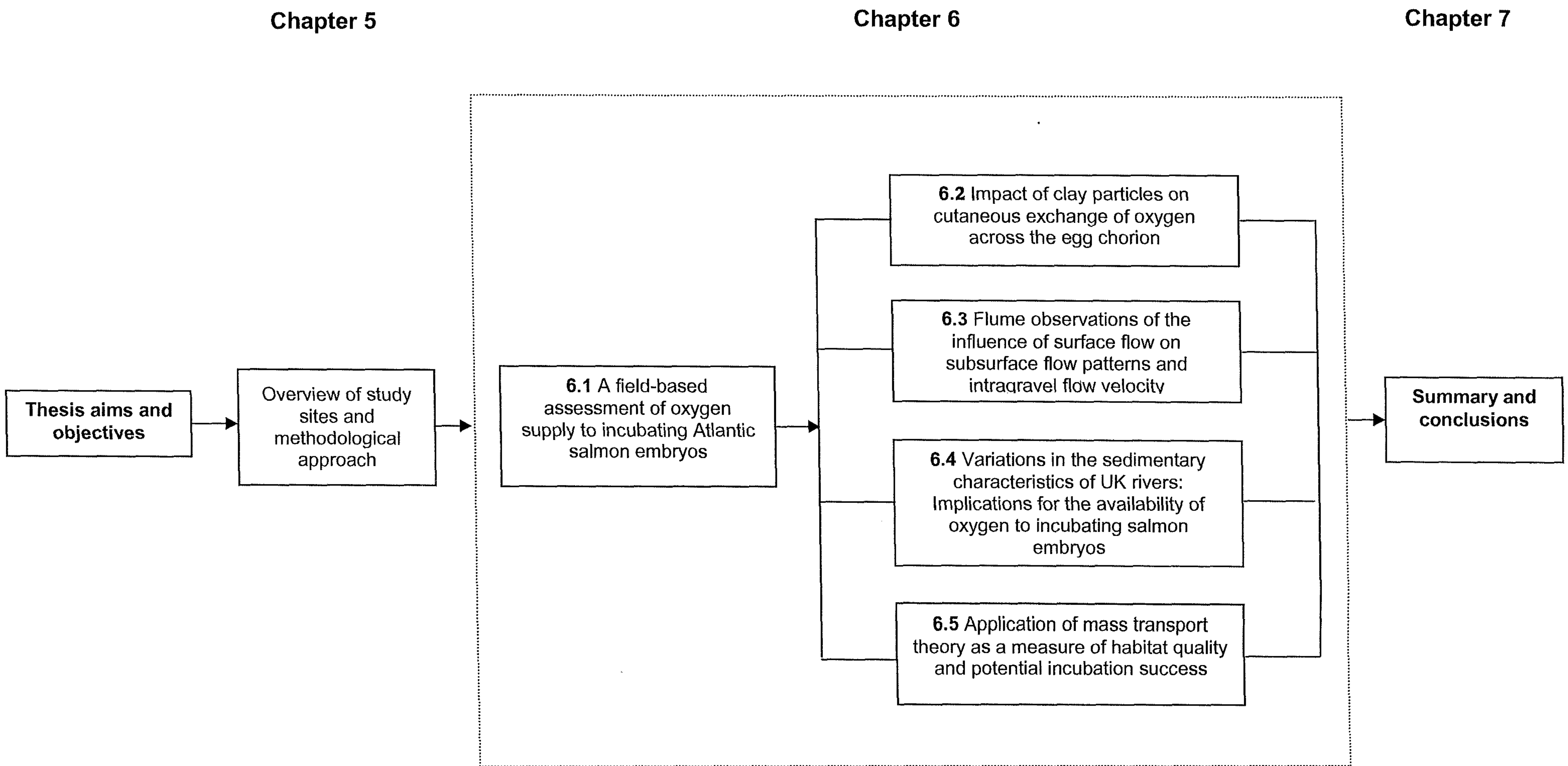

Figure 4.2 Overview of structure used to present scientific findings.

Chapter 5. Overview of study sites and monitoring strategy

The following chapter outlines the general principles underpinning the monitoring program. The chapter is divided into four sections: (i) an overview of the broad rationale and sampling objectives underpinning the development of the monitoring programme, (ii) an overview of selected field sites, including a discussion of U.K. river types and (iii) a summary of the rationale underpinning the selection of monitoring techniques.

5.1 Overview of methodological approach

The following section provides an overview of the monitoring strategy. With respect to habitat quality, the principle purpose of monitoring is the production of robust scientific data that allows: (i) investigation of relationships between organisms and their environment, (ii) evaluation of current environmental conditions and (iii) assessment of factors potentially degrading environmental conditions (Barbour *et al.*, 1999). This information provides a scientific basis for the development of appropriate or adaptive management strategies that target identified causes of habitat deterioration. Reductions in aquatic habitat quality may result from direct interference with the river channel, for instance channelisation, impoundment or gravel extraction, or from indirect activities occurring within riparian margins, floodplains or catchments, for example, forestry, agriculture or municipal activities. Effective assessment of habitat quality requires the development of spatially appropriate monitoring strategies that apply common measures of aquatic environments to identify and define levels of disturbance. Potential measures of habitat quality include, water quality, pollutant concentrations or loads, temperature, channel structure and habitat heterogeneity (Rankin, 1995; Barbour *et al.,* 1999). These collective measures of disturbance can be concomitantly, or subsequently, linked to in-stream or catchment sources of habitat deterioration.

Applying these principles, two approaches to defining appropriate levels of habitat quality are commonly adopted: comparative analysis and process-based analysis (McCullough and Espinosa, 1996, Spence *et al.*, 1996). Comparative analysis evaluates habitat quality by comparing degraded systems with perceived undegraded, or ecologically stable, systems. Assessments of degradation are typically based on species abundance, although historical analysis of pristine conditions may be undertaken. The physical, chemical and biological character of undegraded systems is assessed to define a suite of key characteristics that can be compared with degraded systems. Degraded systems are then assessed on their resemblance to pristine conditions. Potential problems arising from this approach to assessing habitat quality are the omission of potentially important habitat features that have the capacity to alter habitat quality, difficulties selecting or defining pristine conditions and problems delineating potential ecological responses to altering selected habitat features.

Process-based approaches to defining habitat quality are based on assessments of the physiological and behavioural requirements of identified species. Habitat assessments are then performed to determine the ability of a habitat zone to support defined physiological or behavioural requirements (McCullough and Espinosa, 1996). Subsequent analysis of factors influencing the ability of a habitat zone to support species requirements is undertaken to identify potential causes of poor habitat quality. Problems associated with this approach include a requirement for detailed scientific awareness of biological or behavioural requirements, and integration of this knowledge with awareness of the processes operating within the physical environment. The acquisition of information pertaining to the factors and processes influencing habitat quality requires either complex modelling or thorough field analysis.

The monitoring strategy adopted in this study combined aspects of both approaches to assessing habitat quality to develop process-based *modus operandi* that utilised comparative analysis to aid delineation of factors influencing habitat quality. As discussed in Chapter 4, oxygen supply has been defined as the critical process influencing survival. To allow investigation of oxygen supply and factors impacting on oxygen supply, a complementary set of field and laboratory studies were developed.

A field-monitoring programme that allowed examination of the flux of oxygen through salmon spawning gravels, assessment of incubation success, and investigation of the impact of sediment on oxygen flux, was developed. Assessments were carried out at four physically distinct river systems, and detailed site characterisations were undertaken. Each field site represented a range of physical habitat features and a range of levels of habitat quality. Assessing the primary process influencing incubation across a range of physically distinct field sites of varying levels of habitat deterioration provided a basis for a comparative assessment of habitat quality and enhanced elucidation of factors influencing the flux of oxygen through salmonid incubation environments.

Although providing important information pertaining to oxygen availability within natural salmon spawning gravels, the field study could not provide definitive information pertaining to the exchange of water with the riverbed and the direct impact of sediment on oxygen consumption by salmon embryos. Therefore, two laboratory studies were undertaken to provide supplementary, process-based information pertaining to factors influencing oxygen availability.

5.2 Contextual field site information

Field sites were selected to represent: (i) a range of physical characteristics associated with U.K. salmon habitats and (ii) range of levels of habitat quality. The following section describes the hydrological and geomorphological character of the two river types studied in this project, and discusses the deterioration of U.K. river habitats.

5.2.1 U.K. Atlantic salmon bearing rivers

In broad terms, two major UK Atlantic salmon bearing river types can be identified: groundwater dominated and freshet. Freshet streams are typically located within montaine regions, where the underlying geology is predominately composed of impermeable materials, for instance, metamorphic rocks (Lewin, 1981). These impermeable substances have a low capacity to store water, consequently, stream water is predominately derived from overland flow, although shallow groundwater may be present above impermeable layers. Groundwater-dominated streams are contained within catchments dominated by porous surface and subsurface materials, for instance, chalk, limestone and Permo-Triassic sandstones (Sear *et al.*, 1999). These porous materials have a high capacity to store water, therefore, when precipitation falls on these pervious layers, it drains downward until it reaches an impervious layer, reducing the potential for overland flow. Above the impervious layers, the overlying material becomes saturated and aquifers are formed. These aquifers provide an influent flow of groundwater to the stream channel (Berrie, 1992).

The hydrology of freshet streams is characterised by intermittent flashy discharges. These discharges are predominately composed of quickflow (overland flow and throughflow) associated with precipitation events within the catchment (Burt, 1992). Typically, the precipitation response of freshet upland streams has three distinctive features. First, a quick response, resulting from quickflow inputs, second, a short duration, associated with the length of precipitation event and, third, a swift return to baseflow after the precipitation event has ceased (Burt, 1992). The annual hydrological regime of freshet rivers is controlled by seasonal weather patterns. During summer months, the hydrological regime is characterised by low flows, occasionally interrupted by flashy discharges, associated with localised storm events. Over the winter months, a similar hydrological pattern is evident, although rain events are more frequent, and a higher base flow is maintained.

In contrast to freshet rivers, groundwater-dominated rivers are typically characterised by a stable flow regime; although limestone rivers with cave systems may display hydrological characteristics similar to freshet rivers (Sear *et al.*, 1999). This stable regime is a product of the pervious catchment geology, and consequent reduction in overland flow that characterises groundwater-dominated streams (Burt 1992; Sear *et al.*, 1999). The precipitation response of groundwater-dominated streams is characterised by a long lag before response occurs, a slow rising limb to peak groundwater discharge and a low rate of recession (Burt, 1992). The annual hydrological regime of groundwater-dominated streams is primarily controlled by annual fluctuations in aquifer levels (Berrie, 1992). As the aquifer is recharged in winter, water flows from springs located in the upper reaches of the stream, and the river lengthens. Conversely, in the summer months, the aquifers dry and the river returns to its shortened form. The slow rate of recession after rain events results in elevated discharges over winter months. In the summer, discharge recedes, and baseflow is maintained by groundwater inputs (Figure 5.1).

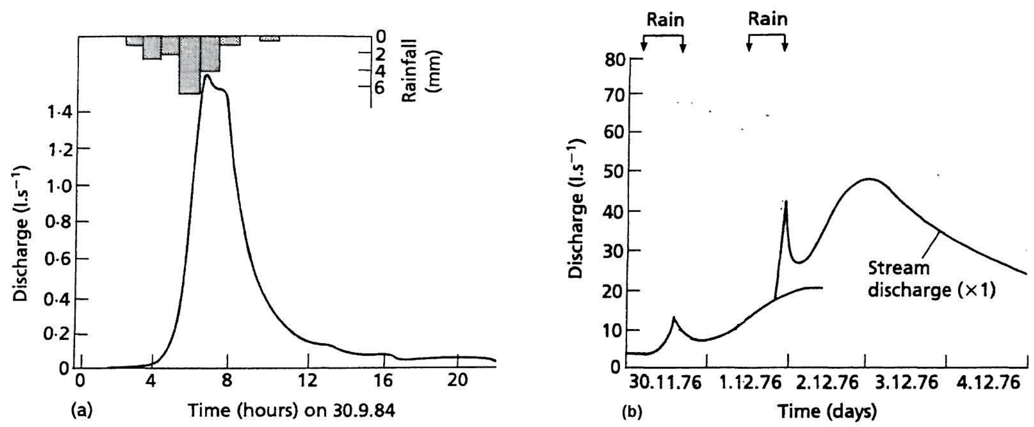

Figure 5.1 Summary of the characteristic hydrological response of (a) freshet and (b) groundwater-dominated rivers (after from Burt, 1992).

The hydrological regime of freshet rivers typically results in episodic sediment transport events (Walling and Webb, 1992). Sediment transport is composed of both suspended load and bedload, although bedload is typically restricted to higher flow events. Fine sediments (<1mm) are derived from surface material that is washed into the river during periods of overland flow or through catchment drainage systems and, in degraded streams, from riverbank erosion (Walling and Webb, 1992; Walling and Amos, 1999). During the rising limb of highflow events, a large proportion of this sediment is washed downstream, however, as the flow recedes sediments infiltrate riverbed gravels. The residence time of infiltrated fine sediments is controlled by the mobility of the bed, the depth of penetration of sediment fractions and the timing and magnitude of the subsequent highflow event (Carling, 1992, Knighton, 1998).

Generally, the more stable hydrological regime of groundwater-dominated streams results in a less peaky sediment transport regime than in freshet rivers, although increases in suspended sediment load will be recorded during precipitation events. Bed movement is infrequent and sediments are predominantly transported in suspension (Sear *et al.*, 1999; Walling and Amos 1999). Typically, sediments are derived from catchment sources, although large macrophyte beds provide a source of in-stream organic detritus (Burt 1992; Sear *et al.*, 1999). As bed disturbance is infrequent, deposited sediments may remain in the gravel for extended periods, promoting the accumulation of large quantities of fine sediment (Acornley and Sear, 1999). Some typical geomorphological and sedimentological features associated with U.K. groundwater-dominated and freshet streams are highlighted in Tables 5.1 and 5.2.

River	Lithology	Sediment Yield (T km^{-2} yr^{-1})	Reference
Test	Chalk	11.9	Essaney (1993)
Piddle	Chalk	6.5	Walling & Amos (1994)
Headwater streams (chalk)	Chalk	1-12	Collins (1981)
Frome	Chalk	10.2	Farr & Clark (1984)
Fenland rivers	Mixed clay /Chalk	3-14	Wilmot & Collins (1981)
Headwater streams (clay)	Wealden clay	16-201	Collins (1981)
Headwater streams (mixed sandstones)	Mixed greensand / clay	6-46	Collins (1981)
Western Rother	Mixed greensand / clay	19-30	Sear (1996)
Devon rivers	Mixed clay / sandstone	24-90	Walling (1978
Gt Eggleshope/Carl Beck	Carboniferous sandstone	12-24	Carling (1983)

Table 5.1 Field estimates of suspended sediment yields from UK rivers (after Acornley and Sear, 1999).

Aquifer/ Lithology	Power (W/km^2)	Bankfull width (m)	W:D	Riffle Spacing/ width bf	Mean number VSSF/ 500m	Mean number DSSF/ 500m	Sinuosity	n
Chalk	6.1 (17.8)	8.7 (4.4)	18.4 (14.0)	51.0	0.1	0.1	1.29 (0.47)	98
Soft limestone	15.6 (31.6)	7.7 (4.5)	11.0 (7.1)	27.2	0.8	1.0	1.24 (0.41)	91
Permo-Triassic sandstone	6.8 (13.9)	10.8 (8.3)	9.2 (6.3)	29.0	0.6	0.6	1.25 (0.24)	50
Clay	6.3 (19.3)	6.1 (3.80	7.8 (5.4)	31.0	0.4	0.5	1.31 (0.33)	200
Hard limestones	72.1 (236)	9.2 (7.9)	11.7 (8.5)	15.4	0.7	1.2	1.22 (0.26)	96
Impermeable lithology	25.4 (81.8)	10.3 (10.6)	10.0 (9.3)	15.1	1.4	1.5	1.20 (0.25)	486

Figures in brackets are standard deviations of sample population.

W:D = 'Form ratio' of bankfull channel width to bankfull depth.
VSSF = Vegetated sediment storage features (point bars, mid channel bars and side bars).
DSSF = Dynamic sediment storage features (point bars, mid channel bars and side bars).
Bf = Bank full.

Table 5.2 Geomorphological features associated with U.K. aquifer and impermeable catchment lithologies. Data derived from RHS and Clark *et al,* 1995 (after Sear *et al,* 1999).

The composition and size of substrate materials found in freshet rivers and groundwater-dominated streams are distinct. Typically, spawning zones of freshet rivers contain coarser gravels and lower levels of fine sediment (<1mm) than in UK groundwater dominated streams. Reported substrate characteristics of spawning reaches within southern chalk streams and UK freshet rivers are highlighted in Tables 5.3 and 5.4.

Location	Mean values (mm)	Min value (mm)	Max value (mm)
NE England	62.2	2.20	190
SW Wales	21.84	3.30	60
Dorset (Chalk)	18.18	6.00	54
River Test (Chalk) 1990	11.3	0.92	42
River Test (Chalk) 1991	18.51	0.40	90
All sites	40.03	2.20	190

Table 5.3 Median grain data for the River Test spawning gravels and for other UK locations (after Carling1990).

Location	Mean	Max	Min
NE England	11.17	39.11	2.40
SW Wales	7.86	28.64	0.89
Dorset (Chalk)	12.51	32.38	3.91
River Test (Chalk) 1990	27.25	53.00	3.00

Table 5.4 Percentage of fines (<1mm) in spawning gravels (after Carling 1990).

Freshet water temperatures are primarily controlled by air temperature and typically range from 0°C in winter to 20+ °C in summer (Walling and Webb, 1992). Within the riverbed, temperatures are similar to those of overlying surface water, although a temperature lag will often be present. At depth, localised areas of groundwater may influence subsurface water temperature (Malcolm *et al.*, 2002).

Groundwater-dominated stream temperatures, are moderated by the stabilising effect of groundwater inputs (Acornley, 1999; Berrie, 1992), the magnitude of which is proportional to quantity of groundwater entering the stream (Webb and Zhang, 1999). In southern England, spring water from chalk aquifers emerges at around 11°C throughout the year (Berrie, 1992). This has a warming effect on the annual temperature regime in winter and a cooling effect in summer. Consequently, chalk stream temperatures in southern England are seldom less than 5°C or greater than 17°C (Acornley, 1999). Within the riverbed, the effect of groundwater inputs are more localised and of larger magnitude. A number of studies have shown that water temperatures within riverbeds of groundwater-dominated streams are distinct from stream water temperatures, typically being higher than those in the stream during the winter and lower during the summer (Acornley, 1999; Crisp 1990; Evans, 1995; Ringer and Hall, 1975;). The temperature within a specific zone of the riverbed is a function of stream temperature, groundwater temperature, proximity to zone of groundwater upwelling, and rate and depth of penetration of surface derived water (Acornley, 1999; Webb and Zhang, 1992). With respect to intragravel oxygen concentrations, in view of the greater inputs of groundwater associated with groundwater dominated systems, the influence of groundwater on intragravel oxygen concentrations is potentially greater in groundwater-dominated systems. However, as in freshet systems, the influence of groundwater on intragravel oxygen concentrations will largely be dependent on the character and magnitude of spatially discrete inputs.

5.2.2 Pressures on U.K. rivers

Anthropogenic pressure has impacted on the quality of many U.K. freshwater systems (DEFRA, 2002). These impacts have occurred, and continue to occur, across a variety of spatial and temporal scales, and have influenced physical, chemical and biological aspects of habitat quality. Common anthropogenic pressures on U.K watercourses include poor forestry practices, urban generated runoff, effluent discharges, and point source pollutant inputs. However, the field sites were located in agriculturally dominated catchments (Section 5.3), consequently, the following discussion focuses on pressures relating to agricultural practices.

Within the U.K., rivers are characterised by varying landcover and landuse activities. Land cover and landuse influence the physical structure of the channel environment, control the influx of materials into rivers and modify hydrological regimes. Historically, mature forests dominated land cover in the U.K. (Woodland Trust, 2000). However, as populations have expanded, much of this land has been converted for agricultural use and urbanisation[1], resulting in varying levels of habitat degradation. Impacts on freshwater systems associated with agriculture include the loss of riparian margins, altered hydrological regimes, increased inputs of fine sediments and excess nutrient inputs (Platts *et al.*, 1985; Meehan, 1991; Platts, 1991; Theurer *et al.,* 1998).

The riparian margin is the zone where aquatic ecosystems interface with the terrestrial environment. Typically riparian margins are composed of emergent aquatic plants, trees,

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[1] As the impacted study sites were contained in agriculturally dominated catchments, the following discussion focuses on agricultural pressures.

shrubbery and grasses. Riparian vegetation provides inputs of leaf detritus and insects that add to the aquatic food web (Cushing and Allen, 2001; Wetzel, 2001; Murphy and Meehan, 1991) Similarly, inputs of woody debris, which can influence channel morphology, create retention zones for organic matter and provide cover for aquatic species, are also associated with riparian margins (Binns and Eisermann, 1979; Platts *et al.*, 1985; Platts, 1991). The rooting matrix associated with riparian vegetation stabilises stream banks and maintains undercut banks; a prime salmonid habitat (Platts, 1981). Riparian vegetation also provides a protective cover that helps maintain cool temperatures in winter and insulate the stream in winter (Claire and Storch, 1983; Cushing and Allen, 2001). However, it should be noted that dense canopy cover can also restrict light penetration to streams and reduce primary production, thereby limiting food availability (Murphy and Meehan, 1991; Cushing and Allen, 2000). Additionally, riparian margins act as buffer strips between the terrestrial and channel environments. Riparian vegetation slows surface runoff allowing deposition of sediments before reaching stream channels (Manci, 1989; Muphy and Meehan, 1993; USDA, 1998). Additionally, the canopy reduces the initial impact of precipitation on the land surface, reducing potential inputs of surface runoff associated sediments (USDA, 1995, 1998). The removal of pollutants has also been attributed to riparian margins. The pollutant removal occurs as a result of infiltration, deposition, filtration, adsorption and absorption. These processes operate synergistically; infiltration of overland flow reduces velocities, which results in increased deposition and increased soil water contact time and, therefore, the opportunity for adsorption (Manci, 1989; Quinn, 1992; Murphy and Meehan, 1993).

The loss of riparian margins to agriculture has removed the beneficial influences associated with riparian land. Resultant impacts include loss of bank stability, resulting in channel widening, greater inputs of sediments and loss of important salmonid habitat, loss of canopy cover, resulting in elevated stream temperatures in summer, reduced temperatures in winter and loss of important allochthonous inputs of organic detritus, insects and woody debris and finally, greater inputs of surface runoff and associated sediments and pollutants (Platts, 1991).

In additional to the loss of riparian habitat, agricultural drainage systems have also impacted on many U.K. rivers (Sear *et al.*, 2000). Agricultural drainage can be defined as the use of surface ditches and subsurface permeable pipes to remove standing or excess water from poorly drained lands. In the U.K., drainage systems are often supplemented by secondary treatments (Theurer *et al.,* 1998). Typical secondary treatments comprise mole ploughing (the drawing of semi-permeable, continuous, cylindrical channels through stable, clay soils) and subsoiling (the disruption of dense impermeable soils to increase their porosity). One of the primary concerns pertaining to agricultural drainage is its influence on stream hydrology (Robinson, 1986, 1990). Evidence also suggests that as a consequence of the land drainage, streams and ditches have become "flashier" over time. A review of land drainage studies from several countries concluded that subsurface drainage generally decreases peak flows in fine textured soils but often increases those flows in coarser, more permeable soils (Robinson, 1986, 1990). Further research is necessary to improve understanding of the impacts of land drainage at the catchment and reach scale.

Land drainage also provides a pathway for increased delivery of sediments and nutrients and pollutants (Theurer *et al.*, 1998). Drainage networks act as bypass routes for water, sediments and nutrients. When these bypass routes are coupled with natural bypass flow, for instance soil fissures or animal burrows, a direct pathway for sediment and other contaminants to nearby surface water is created (Theurer *et al.*, 1998). Additionally, agricultural drainage has resulted in the loss of important wetland ecosystems, although its direct affect is difficult to quantify.

Excess sedimentation is also a feature of many U.K river systems (Theurer *et al.* 1998, DEFRA 2002). Recognised sources of fine sediment include the loss of surface vegetation and resultant physical disturbance of surface soils by grazing cattle and sheep, areas of bank failure resulting from cattle poaching, and poorly-timed or implemented ground preparation, ploughing and harvesting operations (Walling, 1995; Walling and Amos, 1999; DEFRA, 2002). Additionally, as described above, the loss of riparian vegetation increases surface runoff inputs of fine sediments and reduces bank stability, potentially resulting in exacerbated rates of bank erosion.

Finally, excess nutrient inputs to freshwater systems have also been attributed to agricultural practices. The principal nutrient inputs associated with agriculture are nitrogen and phosphorous. The Royal Society (1983) estimated that 70% of the nitrogen input to the UK's inland surface water originated from diffuse sources, particularly agriculture. The primary source of nutrients to freshwater systems is excessive fertiliser application, although, animal waste provides an additional source (Platts, 1993; Evans, 1996, Theurer and Harrold, 1998; Harrold and Appleby, 2000, Environment Agency, 2002; DEFRA, 2002).

5.3 Field site characterisation

As discussed in Section 5.1, one of the principal factors influencing site selection was the acquisition of data that would allow a comparative analysis of factors influencing oxygen fluxes and incubation success. Therefore, field sites were selected to represent (i) the two dominant salmonid UK river types, (ii) a range of potential levels of habitat quality and (iii) a variety of distinct physical features that, in light of information presented in section 3.2, may influence oxygen availability and incubation success. In total, four field sites (Table 5.5, Figure 5.2) were monitored over two field seasons (2001-2002 and 2002-2003 spawning and incubation periods):

1) *River Test, Hampshire (Groundwater-dominated)* *(2001-2002)*
2) *River Blackwater, Hampshire (Lowland Freshet)* *(2002-2003)*
3) *River Ithon, Powys, Wales (Upland freshet)* *(2001-2002)*
4) *River Aran, Powys, Wales (Upland freshet)* *(2002-2003)*

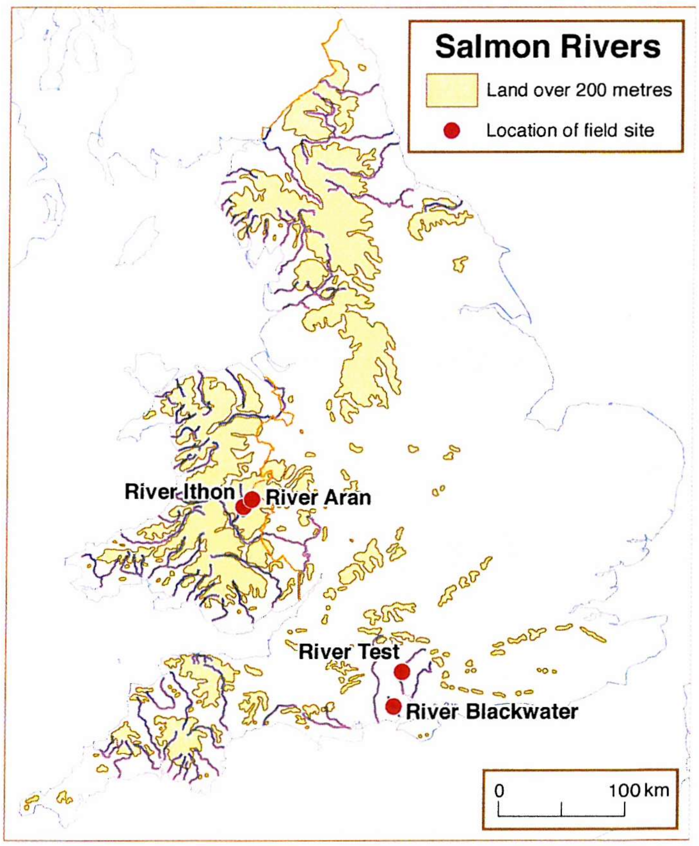


Figure 5.2 Location of field sites and summary of topographic relief.

The River Test is a groundwater-dominated chalk stream located in Hampshire (Figures 5.3, 5.4 and 5.5). Once revered as one of the 'great' salmon rivers in southern England, recent low population estimates (Environment Agency, 1997) have highlighted a population under pressure. With respect to habitat quality, the River Test represents a degraded system with a recognised sediment problem (Environment Agency, 1998). Common to many chalk rivers in southern England, agricultural and anthropogenic pressure has resulted in major physical alterations to the River Test and its catchment. In the 19th century, the introduction of water mills and fishing weirs, transformed the river from a pattern of sinuous pool/riffle channels, into sections of engineered, deepened and straightened channels (Berrie, 1992). This coupled with the removal of riparian vegetation, predominately alder carr and woodlands, for the extension of agricultural land and creation of water meadows, has resulted in a highly managed and artificial system (Berrie, 1992; ADAS, 1997). Presently, the prevailing catchment landuse is arable agriculture, although pockets of grazing are also present (Figure 5.4 (d)).

The catchment geology is 90% chalk with discrete tertiary and alluvium deposits. The dominant soil type within the catchment is brown rendzinas although pockets of paleo-argillic brown soil and argillic brown earth are present (Geological survey maps, Figure 5.4 (b) and (c)). Sections of the main channel also contain deposits of sulphuric peat soils. The flow regime is characteristic of southern chalk streams, displaying a stable hydrological regime with maximum discharges rarely exceeding 4-5 times the minimum discharge in any year (Sear and Acornley, 1999). The mean annual discharge is 11.3 $m^3 s^{-1}$ (Environment Agency Gauging Station: 42013).

The field site was located on a section of the main channel (3rd order) with a historical record of salmon spawning. The study reach is typical of spawning habitat in the River Test, which is characterised by gravel/pebble substrate and glide/run surface flow (Newson and Newson, 2000). The River Test field site allowed assessment of a system with a recognised sediment problem. Furthermore, potential inputs of organic detritus from macrophyte vegetation allowed an evaluation of the impact of organic material on the incubation environment. Finally, the stable hydrological regime of the River Test provided a reference point from which to assess the influence of surface-subsurface flow interactions.

(a)

(b)

Figure 5.3 Site photographs (River Test): (a) upstream, (b) downstream.

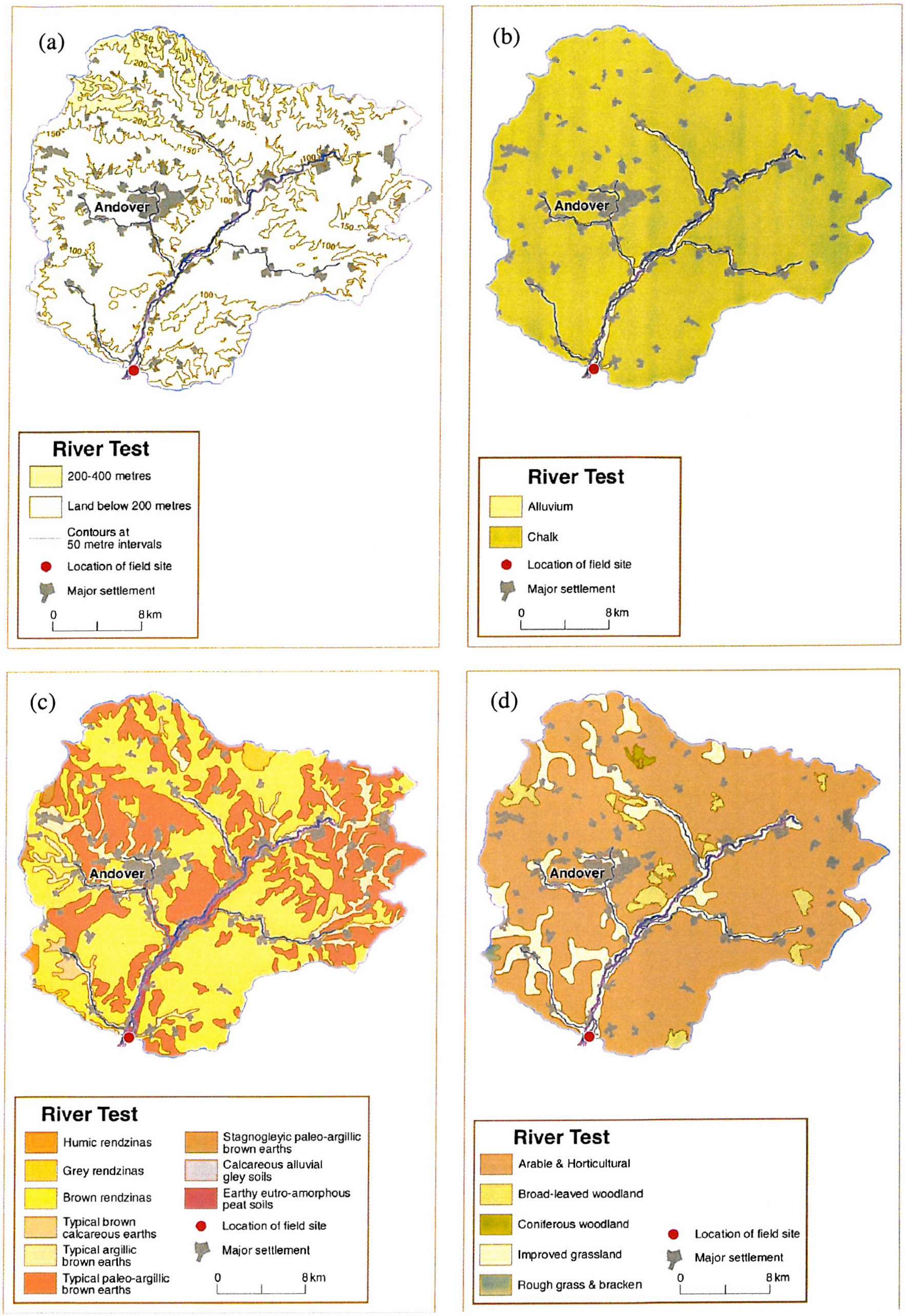


Figure 5.4 Summary of catchment characteristics (River Test): (a) relief, (b) geology, (c) soils, (d) landcover.

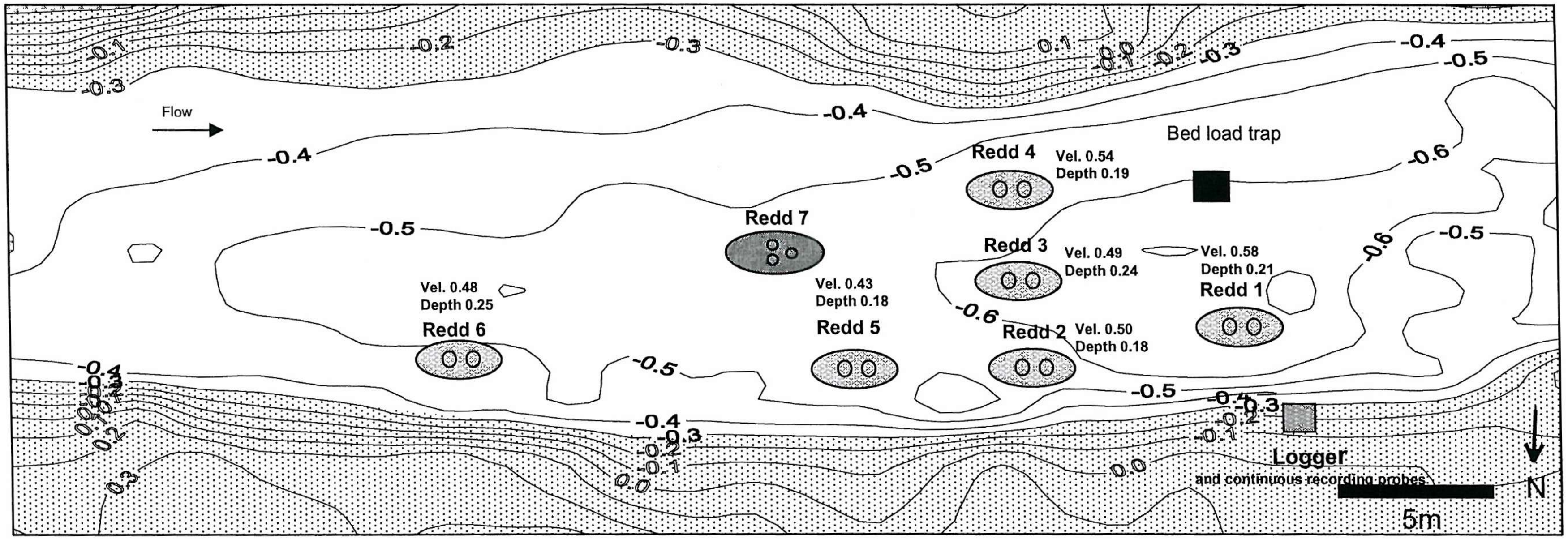


Figure 5.5 Topographic map the of River Test field site, include location of major sampling equipment. Redds 1-6 – Type 1; Redds 7 - Type III. ☐ channel, ▨ bar, ⬚ floodplain. Also shown are the average surface flow velocities (ms^{-1}) recorded at low flow (0.6 depth) and low flow water depths (m) recorded at each redd over the monitoring period.

The River Blackwater is an example of a lowland freshet stream. The Blackwater is a 2nd order tributary of the Lymington River located within the New Forest, Hampshire. The catchment flora is characterised by woodland, predominantly planted conifers, although areas of oak, birch and beech are present, and dry and wet heathland, dominated by ling, cross-leaved heath, bracken and purple moor grass (German *et al.*, 2003) (Figure 5.7 (d)). The main channel was channelised at the turn of the 20th century, and is currently in a process of readjustment. At present, the channel can be characterised as intermittent meandering with distinct pool/riffle features. Additionally, accumulations of woody debris are found within the stream, although deposits are managed. The underlying geology is characterised by of deposits of Barton sands, Barton clays and Brackleshom beds (Figure 5.7 (b)). The dominant soil type is stagno-gley, although pockets of stagno-gley podzols and stagno-gleyic argillic brown earth are also present (Geological survey maps, Figure 5.7 (c)).

The Blackwater contains both Sea and Brown trout populations. However, currently it does not contain a run of Atlantic salmon, although anecdotal evidence suggests that occasional Atlantic salmon have been observed. Although the lack of an established Atlantic salmon population was recognised as a site limitation, the spawning and incubation habitat contained all the elements associated with Atlantic salmon spawning (Section 3.1). Discussions with Environment Agency staff indicated that the absence of Atlantic salmon potentially resulted from poor nursery habitat, rather than a lack of suitable spawning locations. Therefore, in view of the semi-natural catchment and channel characteristics, the site was selected to represent a relatively unimpacted system with potentially high habitat quality.

(a)

(b)

Figure 5.6 Site photographs (River Blackwater): (a) upstream, (b) downstream.

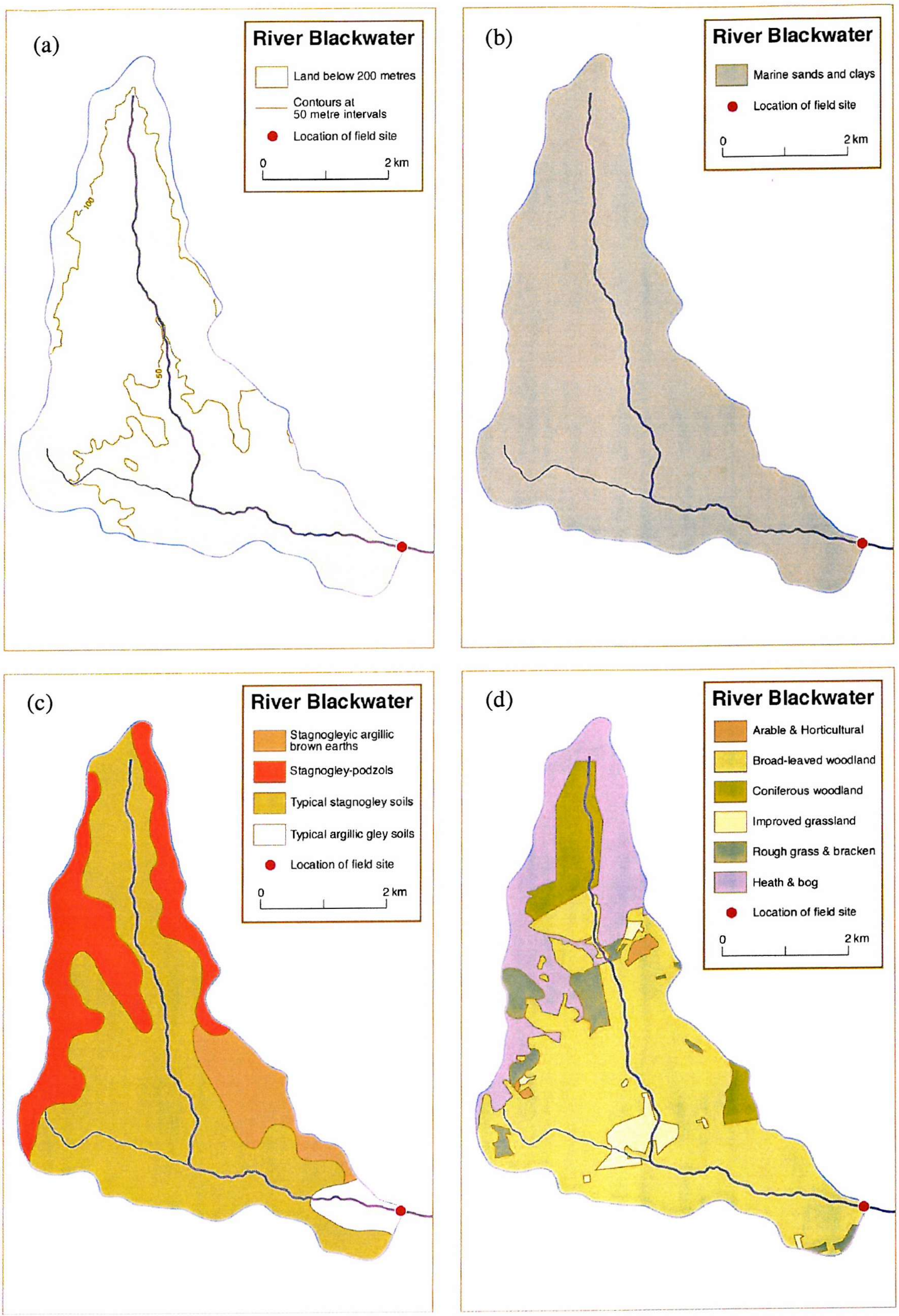


Figure 5.7 Summary of catchment characteristics (River Blackwater): (a) relief, (b) geology, (c) soils, (d) landcover.

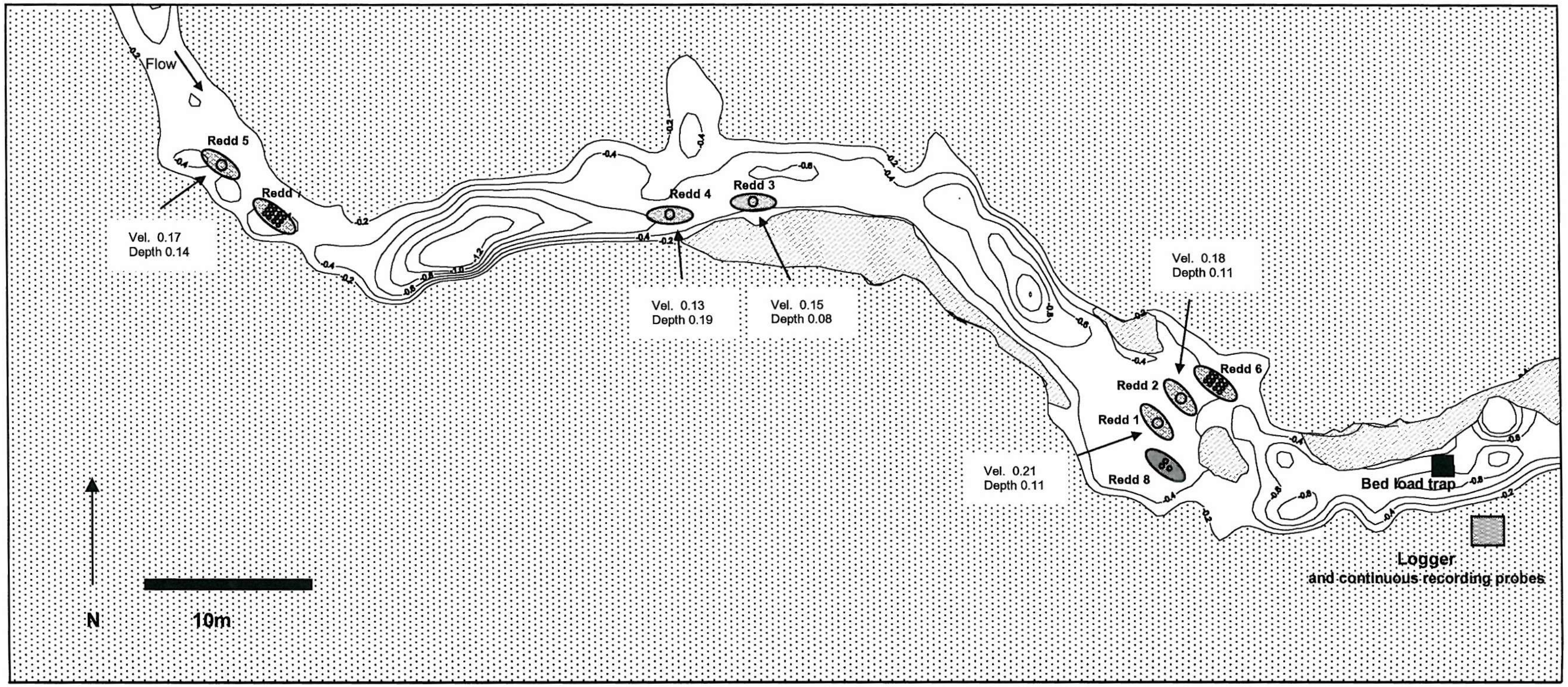


Figure 5.8 Topographic map of the River Blackwater field site, include location of major sampling equipment. Redds 1-5 – Type 1; Redds 6-7 -Type II; Redd 8- Type III. ☐ channel, ☐ bar, ☐ floodplain. Also shown are the average surface flow velocities (ms^{-1}) recorded at low flow (0.6 depth) and low flow water depths (m) recorded at each redd over the monitoring period.

The River Ithon is a 3rd order tributary of the River Wye and is an example of an upland freshet river. The dominant catchment landuse is livestock farming (Figure 5.10 (d)), and cattle and sheep were observed grazing on the fields adjacent to spawning reaches during the spawning and incubation period. With respect to habitat quality, the Ithon represents a severely degraded system. Sedimentation is recognised as a problem, and concerns regarding excess nutrient have also been raised (personal communication: Grant McMellin (Environment Agency)). The upper reaches of the catchment are underlain by Silurian Wenlock deposits comprising shales, mudstones, sandstones and limestones (Geological survey maps, Figure 5.10 (b)). In the lower catchment, the dominant soil type is cambic stagno-gley. The upper catchment is composed of a mixture of brown podzolic soils, cumbic stagno-humic gley soils, cambic stagnogley soils, brown podzolic soils, and discrete pockets of ferric stagno-podzols and brown earth (Geological survey maps, Figure 5.10 (c)). The flow regime is typical of upland streams displaying a flashy response and maximum discharges exceeding 100 times minimum flow. The mean annual discharge is 8.22 m^3s^{-1} (Environment Agency Gauging Station: 55011).

The field site was located within a heavily degraded reach with a historical record of spawning. However, it was recognised that recent evidence indicates declining spawning activity within this reach, although this may be indicative of declining populations, rather than a recent deterioration in habitat quality. Severe bank failure was present on both banks, and loss of riparian vegetation and cattle and sheep over-grazing were identified as potential causes. The River Ithon field site allowed assessment of a system with a high sediment load and potentially high flux of nutrients. Additionally, the 'flashy' hydrological response allowed an evaluation of surface flow dynamics on the subsurface environment.

(a)

(b)

Figure 5.9 Site photographs (River Ithon): (a) upstream, (b) downstream.

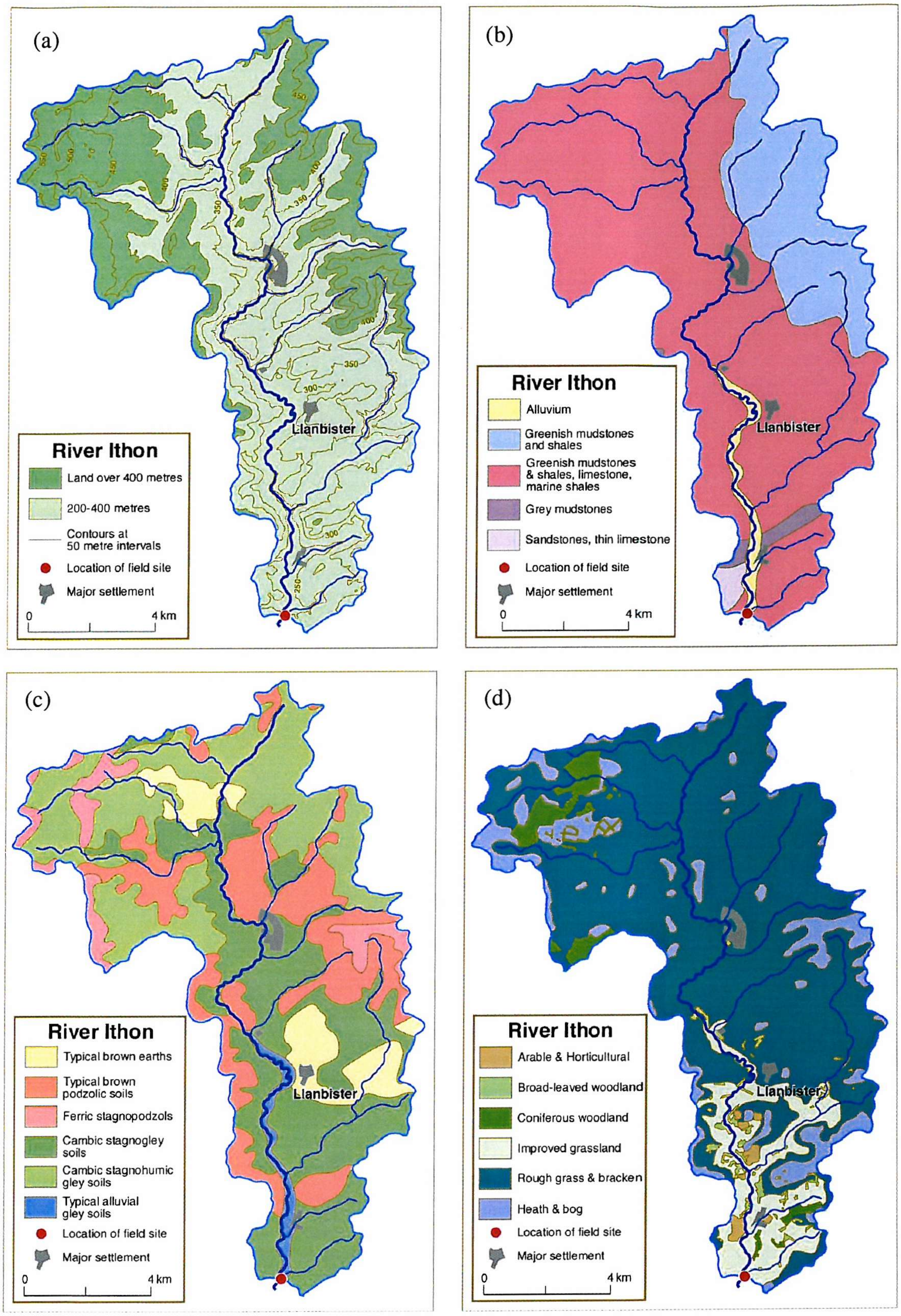


Figure 5.10 Summary of catchment characteristics (River Ithon): (a) relief, (b) geology, (c) soils, (d) landcover.

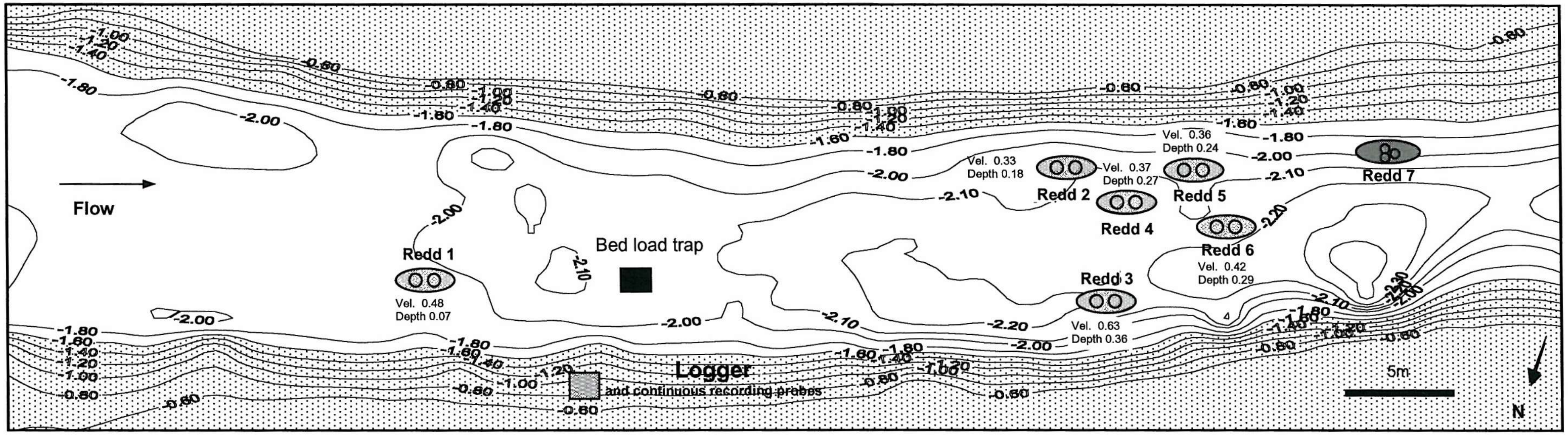
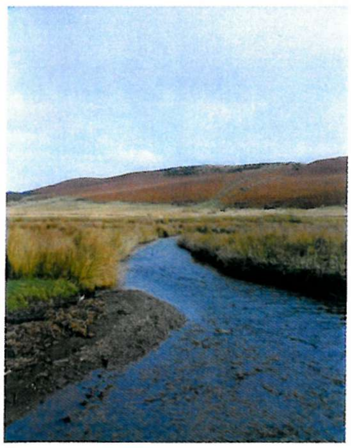


Figure 5.11 Topographic map of the River Ithon field site, include location of major sampling equipment. Redds 1-6 – Type 1; Redds 7 -Type III. ☐ channel, ☐ bar, ☐ floodplain. Also shown are the average surface flow velocities (ms^{-1}) recorded at low flow (0.6 depth) and low flow water depths (m) recorded at each redd over the monitoring period.

The River Aran is another tributary (2nd order) of the River Wye and is a further example of an upland freshet river. Landuse within the catchment is similar to the River Ithon, although agriculture is slightly less intensified and zones of heath land are located within the catchment. In view of the similarities between the catchments, many of the broad problems associated with the River Ithon are also present within the River Aran. However, population reports suggest that productivity within the Aran is higher than the Ithon. (Personal communication: Ray Dobbins (Environment Agency). The soil types and underlying geology are similar to the River Ithon, although cambic stagno-gley soils and brown earth are more common (Geological survey maps, Figure 5.13 (b) and (c)). The flow regime is also similar to the Ithon, displaying a typical flashy hydrological response.

The field site was contained within a discrete pocket of common land (Figure 5.13 (d)). Within this area (roughly 2 km^2), landcover is dominated by heath and scrubland, and vegetation comprises of improved grasses, bracken and ferns. Beyond the area of common land, the catchment comprises rough grass and bracken (sheep grazing) and heath and bog land. The River Aran field site allowed further assessment of potential problems associated with upland freshets rivers contained within heavily agricultural catchments. However, the location of the field site also allowed an assessment of incubation success within a localised area of potentially high habitat quality, embedded within a larger degraded catchment.



(a)

(b)

Figure 5.12 Site photographs (River Aran): (a) upstream, (b) downstream.

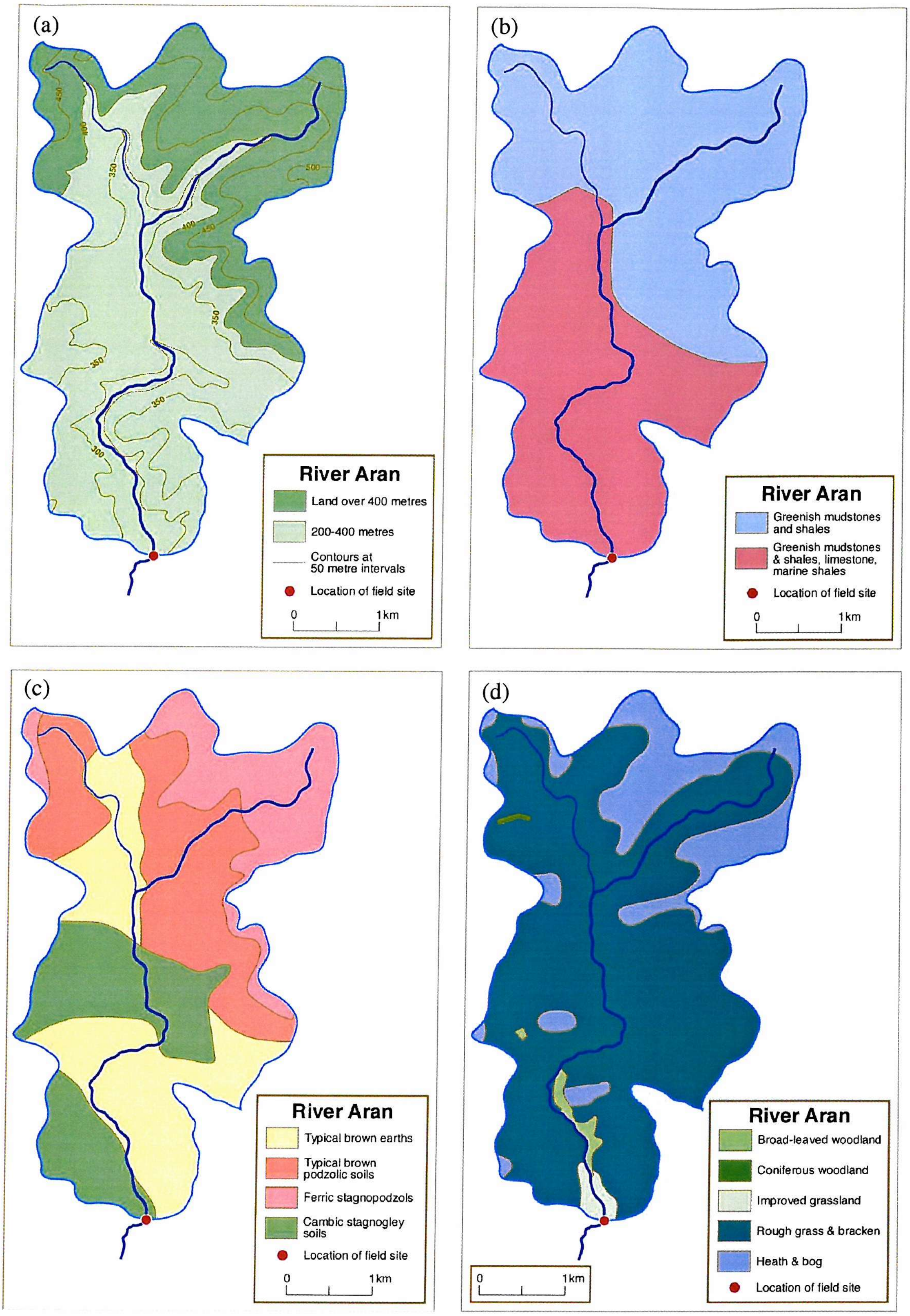


Figure 5.13 Summary of catchment characteristics (River Aran): (a) relief, (b) geology, (c) soils, (d) landcover.

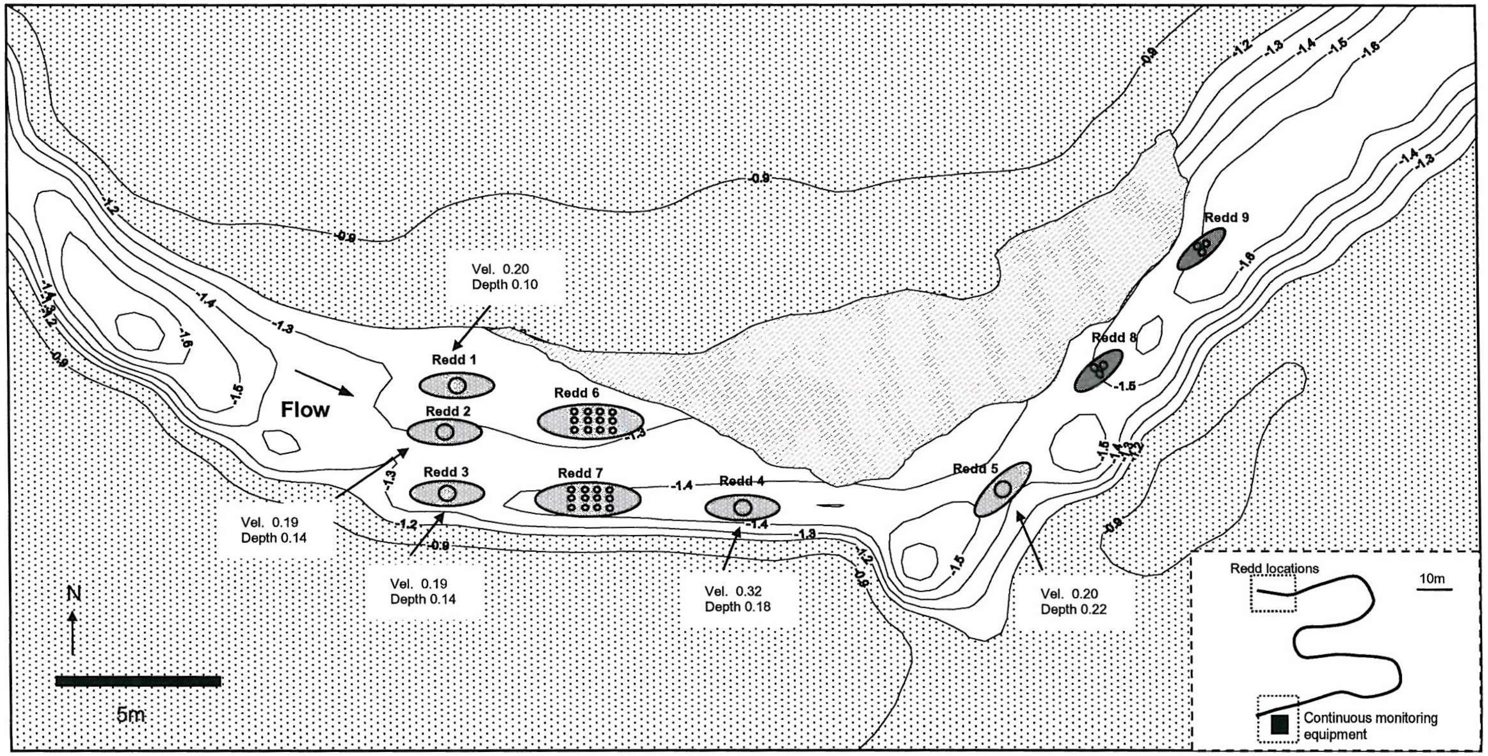


Figure 5.14 Topographic map of the River Aran field site, include location of major sampling equipment. Redds 1-5 – Type 1; Redds 6-7 -Type II; Redd 8- Type III. ☐ channel, ☐ bar, ☐ floodplain. Also shown are the average surface flow velocities (ms^{-1}) recorded at low flow (0.6 depth) and low flow water depths (m) recorded at each redd over the monitoring period. Insert shows location of continuous monitoring equipment in relation to the artificial redds.

	Test	Blackwater	Ithon	Aran
National grid reference	SU 333 298	SU 282 083	SO 105 683	SO 154 704
Altitude	25	25	230	300
Drainage area (km^2)	104	10	32	12
Stream order	3rd	2nd	3rd	2nd
Predominate valley form	Floodplain	Floodplain	Floodplain	Floodplain
Mean precipitation (1966-90)*	576	576	1086	1086
Mean temperature (1966-90)*	10.15	10.15	9.05	9.05
Annual data				
Discharge (mean)	11.02	N/A	2.63	N/A
95% exceedance	5.18	N/A	0.14	N/A
10% exceedance	17.91	N/A	6.98	N/A
Field season data				
Discharge (range) (m^3s^{-1})	3.82-5.13	0.22-7.32	1.35-129.42	0.62-3.51
Discharge (mean) (m^3s^{-1})	4.19	0.92	11.89	1.16
Flow depth (range) (m)	0.18-0.22	0.19-1.35	0.05-1.1*	0.21-0.61
Flow depth (mean) (m)	0.20	0.30	0.19	0.31
Mean channel width (m)*	12	2-5	11	5
Channel slope	0.0066	0.0068	0.0070	0.0060
Surface bed material				
D_{50} *(mm)*	28.42	14.85	45.45	23.98
D_{95} *(mm)*	55.62	36.48	62.38	54.70
Subsurface bed material				
D_{50} *(mm)*	6.33	7.69	11.89	10.41
D_{95} *(mm)*	36.95	22.88	42.25	34.3
D_g *(mm)*	6.36	4.97	4.96	6.36
% sand	25	23.87	22.53	15.9
% silt/clay	7.3	2.28	6.29	4.69

Table 5.5 Summary of site characteristics. * Met Office datasets. ** Refers to mean channel width along length of sampling reach.

5.3.2 Habitat quality

As outlined in Section 5.1, in addition to monitoring the two dominant UK Atlantic salmon bearing river types, the field sites were also selected to represent a range of levels of habitat quality and a range of physical features associated with U.K salmonid rivers. Assessments of habitat quality were based on: (i) visual assessments of features associated with good/poor habitat, for instance, observations of landuse adjacent to the sampling reach, presence of riparian vegetation, and dominant landuse with the catchment, and (ii) awareness of environmental pressures identified at the field sites (Personal communications: Environment Agency). Additionally, based on the results of a River Habitat Survey undertaken at each field site, an assessment of naturalness was undertaken. Naturalness was based on the index of habitat modification developed within the standard RHS survey (Raven *et al.,* 1996) (Table 5.6). Assimilation of this information provided a rationale framework for delineating potential habitat quality. Figure 5.14 outlines the physical features and potential habitat quality at each field site.

Level of habitat modification

High ← → Low

Potential factor influencing incubation success	**River Test**	**River Ithon**	**River Aran**	**River Blackwater**
Excess fine sediment	✔	✔	✔	
Excess organic detritus	✔			
Excessive nutrients		✔	✔	
Controlled hydrological regime	✔			
Flashy hydrological regime		✔	✔	✔
Significant Groundwater inputs	✔			

Table 5.6 Summary of important habitat features associated with selected field sites. Level of habitat modification based on the index of habitat modification (Ravenn *et al.*, 1996).

5.4 Field monitoring programme

5.4.1 Overview of methodological approach

In operational terms, the field-monitoring programme used artificial redds and site surveys to study the characteristics of the incubation environment, and factors impacting on incubation success. At each field site, a series of artificial redds were created and monitored for a variety of environmental parameters. In view of the number of parameters under consideration, ranging from sediment accumulation to oxygen concentration, it was deemed inappropriate to attempt to study all parameters in each individual redd; the principal concerns being excessive disturbance to incubation environment, although space restrictions were also a consideration. In response to these concerns, three different types of redds were constructed at each field site. Each redd was designed to meet a set of monitoring objective, which were developed around the larger project objectives (Section 4.2). All redds contained sampling equipment related to their monitoring objectives (Table 5.7, Figure 5.15).

In addition to monitoring artificial redds, detailed assessments of the surface and subsurface characteristics of each field site were undertaken (See Section 5.4 for a review of the survey undertaken to identify the presence of groundwater). Finally, information pertaining to broader physical characteristics of each field site was also acquired. This data provided allowed delineation of broader reach and catchment scale sources of factors degrading the quality of the incubation environment at each study site.

Redd type	Monitoring objectives	Sampling equipment contained in redd
Survival redd (Type I)	Assess incubation success Assess temporal trends in intragravel flow velocity Assess temporal trends in intragravel oxygen concentration Assess total sediment accumulation over the incubation period	Standpipes Sediment pots (Type A)
Sediment accumulation redd Type (II)	Assess temporal trends in rates of sediment accumulation. Investigate temporal trends in sediment accumulation	Standpipe Sediment pot (Type B)
Oxygen demand redds Type (III)	Obtain sediment samples for laboratory analysis of Sedimentary Oxygen Demands	Sediment pot (Type B)

Table 5.7 Summary of the different types of artificial redds used to monitor the incubation environment. Section 6.4 contains a description of the different types of sediment pots deployed.

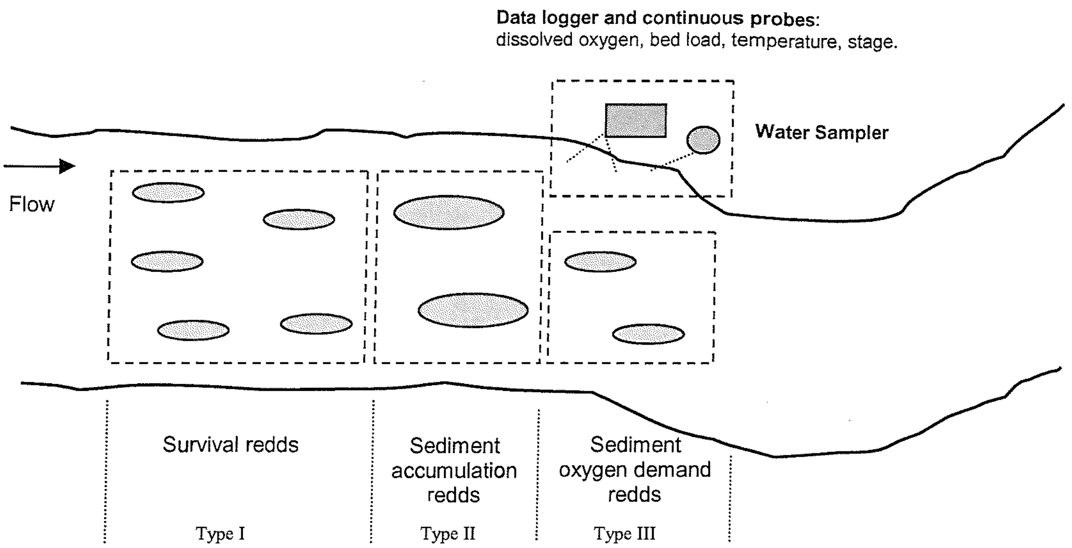


Figure 5.15 Overview of typical of field monitoring set-up adopted at field sites.

Specific sampling and methodological details are contained within the sub-sections of Chapter 6, and in Appendices 1 and 2. The following sections discuss the selection of sampling techniques and protocols.

5.4.2Artificial redds

Artificial redds were used to assess incubation success and conditions within the incubation environment. Monitoring natural redds provides a more accurate assessment of conditions encountered by incubating embryos (Chapman, 1988), however, due to difficulties obtaining permission to monitor these environments, assessments of natural redds were not possible within the remit of this project. Additionally, as the purpose of the study was assessment of survival in relation to oxygen availability, and not assessments of potential rates of survival for a given system, the adoption of artificial redds was considered an appropriate monitoring approach.

Specific advantages of using artificial redds included: (i) the ability to assess multiple factors within discrete locations, (ii) the ability to investigate spatial variability in incubation conditions across a given sampling reach and (iii) the insertion of monitoring equipment within close vicinity of the egg zone, thereby, allowing assessment of conditions directly within the zone of interest.

The principal disadvantage of using artificially created salmon redds is deciding whether a constructed redd is an adequate representation of a natural redd. To minimise discrepancies between natural and artificial redds, it was recognised that both the location and structure of the redd should mimic natural redds. Details pertaining to redd siting and construction are contained in Section 6.1.

5.4.3 Egg deployment and quantification of embryonic survival

One of the principal difficulties associated with using artificial redds to quantify incubation success is introducing eggs into the redd. Typically, one of two approaches is adopted: (i) introducing eggs during redd creation or (ii) delaying the creation of redds until eyed eggs are available. The principal benefit of using greened eggs over delaying redd creation is that it allows studies to monitor the entire incubation period. However, stripping and fertilising eggs on site is a delicate operation that requires experienced handlers. Moreover, unpredictability exits in natural survival rates, and the deployment of a 'bad' batch of eggs may compromise recorded survival rates. Delaying redd creation until eyed eggs are available removes the difficult stripping operation and allows deployment of hatchery derived eggs that have been screened for mortalities and defects. Consequently, once deployed, one may be confident that recorded mortalities are a consequence of conditions within the incubation environment. However, by delaying the creation of redds, eggs are deployed into an unrepresentative incubation environment. Furthermore, the intragravel incubation period will be reduced; consequently, recorded survival rates may not be indicative of potential survival rates for that location.

In view of the problems associated with both previously adopted techniques for deploying eggs into artificial redds, two new sampling techniques were developed that allowed deployment of eyed eggs into pre-created artificial redds (Appendix 9.2). This removed potential difficulties associated with deploying a 'bad' batch of eggs and by-passed the constraint of delaying redd construction. Potential developmental rates for each field site were assessed using a temperature-development model (Crisp, 1992).

With respect to monitoring survival, as the eggs used in each system were not native genetic stock (Section 3.1), it was important that fry did not escape. This left two choices, the application of emergence traps, or limiting the study to assessing survival to hatching. A review of previous efforts to quantify survival to emergence highlighted a number of difficulties associated with making accurate assessments of survival, for example escapement and physical disturbance to the incubation zone. With respect to escapees, emerging fry may move laterally through the bed substrate, depending on the amount of fines present in the substratum (Philips and Koski 1969). This lateral migration may result in underestimates of survival. White (1980), using a trap developed by Philips and Koski (1969), observed that 41% of the fry escaped from the trap and were caught in a net located downstream. With respect to the disturbance caused by the presence of the trap, emergence traps are large, rigid and composed of fine mesh (< 1.5mm), subsequently, their presence can modify both water dynamics and sediment deposition in and around the redd zone. Philips and Koski (1969) noted that silt had a greater tendency to settle on the gravel within the trap. If sediment increases inside the trap, the gravel permeability decreases thereby reducing survival to emergence. For this reason, Hause and Coble (1976) abandoned their experiments based on fry traps.

Field tests of an emergence trap design indicated that the physical disturbance caused by the trap seriously affect the external and internal dynamics of the incubation zone. In brief, the fine mesh required to retain alevins and fry was susceptible to clogging by fine sediments and organic material. This resulted in a zone of reduced flow within the portion of the trap protruding from the gravel surface, and a consequent increase in sediment deposition. Sedimentation within the emergence traps was on average 50% greater than recorded in the sediment pots. In view of the disturbance caused by the emergence trap, assessments of survival were abandoned.

Therefore, all survival rates reported are based on survival to hatching. With respect to the study objectives, it was concluded that the period of development of most relevance was to hatching and therefore, accurate assessments of survival to hatching were preferred over potential inaccurate assessment of survival to emergence. As outlined in section 3.2, embryonic respiratory requirements peak at hatching and decline thereafter. Furthermore, post hatching, alevins become mobile and it has been shown that they may migrate from zones of low oxygen. Therefore, with respect to oxygen availability, the critical period of development may be considered the period leading up to and including hatching. However, it was recognised that post hatching oxygen deficiencies remain a potential mechanism resulting in poor emergence success; this sampling limitation is discussed further in Section 5.6.

5.4.4 Monitoring conditions within the incubation environment

The intragravel environment of riverbeds is a notoriously difficult medium to sample. As the environment is hidden from the naked eye, all observations are based on information obtained from the extraction of samples, or the insertion of monitoring equipment. Consequently, the fundamental challenge for researchers sampling this environment is limiting the disturbance caused to the incubation environment during the insertion and removal of samples and monitoring equipment, or by objects left in-situ. Additionally, the demanding nature of the intragravel environment can influence sampling results or cause mechanical failure. Broad sampling problems associated with field investigations of incubation success include the effect of fine sediments on dissolved oxygen probes, the disturbance caused during the insertion and removal of sediment pots, the disturbance caused by sediment pots and standpipes left in-situ and the destructiveness of freeze coring techniques. Problems associated with sampling sediments are detailed in Section 5.5.1.5, this section provides an overview of potential sampling difficulties associated with monitoring properties of interstitial water.

Typically, one of two approaches to assessing interstitial water is adopted; extraction of water samples or insertion of monitoring equipment through standpipes. Water samples are generally extracted through hoses that remain within the riverbed. The extracted samples are then either processed on site, or retained for laboratory analysis. Although this technique is frequently adopted (e.g. Soulsby *et al.*, 2001, Malcolm *et al.,* 2003), for the purposes of this study, it was decided that the insertion of monitoring equipment into the incubation environment was a more appropriate approach. This decision was based on two factors: (i) as multiple redds were being monitored, the time required to successfully extract water samples (up to 90 minutes) had to be considered, and (ii) standpipes are more versatile and can be used to assess multiple parameters including oxygen concentration, temperature, intragravel flow velocity and permeability. The parameters monitored using the standpipes are outlined in Table 5.8.

Parameter	**Device**	**Units**	**Accuracy**
Dissolved Oxygen Concentration	YSI Model 250 Dissolved oxygen probe	mg l^{-1}, % sat.	± 0.3
Temperature	YSI Model 250 Dissolved oxygen probe	°C	± 0.3
Intragravel flow velocity	Conductiometric standpipe	cm h^{-1}	±18 (<200cm h^{-1})
			±97 (>200 cm h^{-})
Permeability	Pump Test	cm h^{-1}	N/A

Table 5.8 Summary of parameters and devices used to monitor the intragravel environment.

Of the intragravel parameters monitored, special attention must be given to intragravel flow velocity. With respect to quantifying intragravel flow velocity, numerous attempts to develop a reliable field technique have failed to produce an accurate or reliable field technique (Grost *et al.*, 1988). In the absence of a reliable field technique, Darcy's Law is frequently applied to the problem of determining intragravel flow velocities. However, recent evidence suggests that Darcy's Law, which was developed to describe laminar flow in a confined environment, may not provide an accurate assessment of shallow flow in riverbeds (Section 3.2). Additionally, laboratory studies have reported the influence of surface flow on the subsurface environment: a process that is not modelled by Darcy's Law (Packman and Bencala, 2000). Turbulent mixing, initiated by roughness at the bed surface, may initiate coupling of surface and subsurface flow, resulting in surface driven velocity profiles in the bed (Packman and Bencala, 2000; Mendoza and Zhou, 1992). Although turbulent coupling has only been observed at depths less than 0.1m, interactions between pressure driven and turbulent coupling have not been fully assessed.

In view of the potential problems associated with inferring intragravel flow velocities from Darcy's Law, it was decided that physical quantification of intragravel flow velocities was an important sampling objective. Among the field techniques developed to estimate intragravel flow velocity, the conductiometric standpipe method (Carling and Boole, 1986) was reported to provide data across a range of intragravel flow velocities found in salmon spawning gravels. In summary, the Carling and Boole (1986) technique is founded on the principles of Turnpenny and Williams' (1982) standpipe method for estimating intragravel flow velocities. Both techniques remotely record the rate of dilution of a saline solution within a standpipe deployed in a gravel substrate. The dilution rate, measured over a pre-determined time period, is compared with calibrated dilution curves to determine estimates of intragravel flow velocity.

Field and flume tests of the conductiometric technique indicated that although the probe performed well for velocities exceeding 200 cm h^{-1}, poor performance in gravels of low permeability and at intragravel flow velocities below 200 cm h^{-1}- conditions synonymous with poor salmonid incubation success (Cooper, 1965)- were encountered. Therefore, to improve the probes performance, the technique developed by Carling and Boole (1986) was refined and recalibrated in the flume (Appendix 1). This recalibration improved the probes performance over the range of velocities typically encountered in spawning gravels and provided a basis for a more accurate determination of oxygen flux.

5.4.5 Sediment Accumulation

Detailed assessments of sedimentary trends and characteristics were a key focus of the study. Consequently, a significant proportion of resources were allocated to implementing robust field and laboratory protocols. Key considerations included the representative of field samples (sample size and replication), limiting disturbance to the incubation zone, and the acquisition of samples that would allow an assessment of multiple aspects of sedimentary composition.

With respect to obtaining sediment samples, three approaches are commonly adopted: McNeil samplers, sediment pots and freeze coring. Sampling using the McNeil method (McNeil and Ahnell, 1964) has been shown to underestimate fine sediments (NCASI, 1986). Quantification of fine sediment levels was one of the key objectives of the monitoring programme, therefore this technique was deemed inappropriate. Consequently, a combination of sediment pots and freeze coring formed the basis of the sampling strategy. With respect to sampling for sedimentary oxygen demands, there was little information available in literature regarding sampling protocols or sources of error, therefore, it was necessary to devise a sampling protocol. For all sediment sampling, the key considerations were acquisition of representative samples, adequate replication, and limiting disturbance to the incubation environment. A detailed description of the sediment sampling techniques and protocols is outlined in Section 6.4.

With respect to the potential impact of the sediment pots on the incubation environment, all pots used mesh sizes of 5mm or greater. Therefore, the porosity of the empty pots was greater than 50%. The value exceeds the porosity of typical riverbed gravels (25-40% (Freeze and Cherry, 1979)). Consequently, the impact of the sediment pots on gravel permeability and intragravel flow velocity was assumed to be marginal. However, it was recognised that the presence of the pots may alter the internal dynamics of the incubation environment.

5.4.6 Supplementary field information

In addition to monitoring artificial redds, continuous monitoring equipment and site surveys provided additional contextual information. The information gathered from these sources was also used to identify potential reach and catchment scale sources of factors degrading the quality of the incubation environment. Table 5.9 summarises the continuous monitoring equipment installed at each field site. Supplementary information pertaining to key continuous monitoring protocols and methods are contained at appropriate junctures in Chapter 6.

Variable	Equipment	Sampling frequency	Accuracy
Suspended solids	ISCO™ water sampler	24 hour	N/A
Turbidity	Partech™ IR40C turbidity probe	15 min	± 1%
Stream dissolved oxygen	Environment Agency multi-parameter water quality station (YSI 6920)	15 min	± 2%
Stream temperature	Environment Agency multi-parameter water quality station (YSI 6920)	15 min	± 0.2 °C
Stream pH	Environment Agency multi-parameter water quality station (YSI 6920)	15 min	±0.2 units
Stream conductivity	Environment Agency multi-parameter water quality station (YSI 6920)	15 min	± 0.5 ohms
Stage	Pressure transducer	15 min	± 0.1%
Discharge	Environment Agency Gauging station	15 min (where available)	N/A
Stream and intragravel water temperature (depths 0.1, 0.2, 0.3 and 0.4 m)	Thermister column	15 min	± 0.2 °C
Intragravel dissolved oxygen concentration (depth 0.25m)[1]	Greenspan™ D100 oxygen sensor	15 min	± 0.2ppm
Bedload	Logging bed load trap	15 min	± 0.61
Surface flow velocity	Braystoke BFM 002	Weekly and bi-weekly	0.001 ms^{-1}
Data Logger	Delta T Devices™ DL2	15 min	N/A

Table 5.9 Summary of supplementary data and associated sampling equipment.

Detailed topographic surveys of the channel and riparian margins at each field site were carried out using a Geodimeter™ System 600. Additionally a River Habitat Survey (RHS) was carried out at each field site. The RHS was developed to describe and evaluate physical habitat at national, catchment and lesser scales in England, Scotland, Wales and Northern Ireland. The system is based on standard field survey method with full accreditation controls[2]. A computer database can then be used to provide a comparative analysis of habitat quality. This approach has been used to support rationales for systematically selecting sites for rehabilitation at a catchment scale. Within this project, the RHS provided basic site characterisation data and afforded a simple means of assessing the extent of habitat modification at each field site.

[1] Sediment interfering with the continuously recording intragravel oxygen probe resulted in the abandonment of this parameter.
[2] All surveys were carried out by an accredited RHS assessor.

5.5 Laboratory studies

The laboratory studies provided information pertaining to factors influencing oxygen availability that could not be adequately assessed in the field. Two laboratory-based studies were undertaken: (i) a laboratory investigation of embryonic oxygen consumption and the impact of clay particles on the exchange of oxygen across the egg chorion, and (ii) a flume investigation into the influence of discharge on intragravel flow paths and flow velocities. A brief précis of these studies is provided; specific sampling details are contained in Sections 6.2 and 6.3.

5.5.2.1 Impact of clay particles on oxygen consumption

One of the principal factors influencing incubation success is the accumulation of fine sediments within the incubation environment. However, investigation into the impact of fine sediments on incubation success has typically focused on determining empirical relationships between incubation success and bulk properties of the gravel substrate (Section 1.2). In contrast, the focus of this study was assessment of the impact of clay particles on the exchange of oxygen across the egg chorion.

Rates of oxygen consumption were determined for batches of eggs incubating in free water. Clay particles were then introduced to the incubation environment and rates of consumption were assessed. Comparisons of oxygen consumption by eggs incubating in free water and by eggs coated in a thin film of clay material, allowed an assessment of the impact of clay particles on oxygen consumption.

5.5.2.2 Investigation of discharge on intragravel flows and velocities

As discussed in Section 3.2, a number of studies have highlighted the potential significance of surface flow conditions on the exchange of water with the riverbed. As discussed by Soulsby *et al.* (2002), increased discharges result in increased penetration depth of surface water within the riverbed. Likewise, flume studies of turbulent exchange have suggested that surface velocity can influence intragravel flow velocities in the upper gravel layers. Furthermore, a number of studies have discussed increased intragravel flow under high flow conditions (Section 3.2), however these statements are generally not validated by field data or theoretical analysis. In view of these observations an assessment of the significance of surface flow conditions on intragravel flow paths and velocities was undertaken.

Field analysis of this process provided difficult. Determination of intragravel flow velocities under low flow conditions was obtainable, however, under higher discharges, access to the field sites was considered too dangerous. Consequently, the range of discharges under which surface-subsurface exchanges could be monitored was restricted, and analysis of the influence of surface flow proved difficult to quantify.

Therefore, a simple flume experiment was designed which would allow analysis of the influence of discharge on intragravel flow. In summary, a 25 m hydraulic flume was used to assess the influence of discharge on intragravel flow velocity. The flume was filled with a mixture of fine sand and gravel to a depth of 0.4 m. The interaction of surface and subsurface flow was assessed across three distinct morphological features: flat bed, riffle and salmon redd. Multiple standpipes inserted in each section provided access points for the conductiometric standpipe, which was used to estimate intragravel flow velocities. Intragravel flow was assessed under a series of discharges.

5.6 Assessment of groundwater inputs at the field sites

As discussed in Section 3.2, groundwater inputs have been shown to influence the availability of oxygen to incubating embryos. Within the remit of this project, a full-scale assessment of the influence of groundwater, for instance using hydrochemical indicators to define spatially and temporally variable inputs was unattainable. However, in view of the potential significance of groundwater inputs, an assessment of the potential influence of groundwater at each field site was undertaken. Delineation of the presence of upwelling groundwater at each field site was achieved by investigating subsurface flow paths, thermal regimes and hydrochemical parameters. It should be noted that time and resource constraints did not allow a complete assessment of groundwater inputs at the River Ithon. However, during field site set up, the presence of a subsurface layer of clay at roughly 40cm depth was recorded at multiple locations across the study site. The presence of an extensive clay layer would suggest that upwelling groundwater would be of minor significance at this field site. This assessment is validated by the thermal profile recorded at the field site (Section 5.4.3).

5.6.1 Hydrochemical analysis

Hydrochemical indicators can be used to infer the presence of groundwater (Maddock *et al.*, 1995). Typically, groundwater has a chemical signature that is distinct from surface water. Assessment of the chemical character of subsurface water can be used to infer the presence of groundwater within the hyporheic zone. Among the potential hydrochemical markers, conductivity has been shown to be a good determinant that can be used to identify the presence of groundwater (Soulsby *et al.*, 1999). Furthermore, conductivity can be measured directly in the field with relatively inexpensive equipment.

As groundwater moves through subsurface storage mediums, it will normally dissolve material from the underlying geology, consequently, the concentration of dissolved solids will increase resulting in higher conductivities than in surface waters (Price, 1995). Therefore, assessments of conductivity at depth into the gravel substratum provide an indication of the presence of groundwater inputs.

During the 2002-2003 the conductivity of surface water was compared with the conductivity of subsurface water at typical egg burial depths. All measurements were made with a Siemans™ conductivity probe. Subsurface measurements were taken from within the standpipes located at each redd. To ensure that surface water did not intrude into the standpipes, a standpipe adaptor was attached to each standpipe prior to sampling (Section 6.1). Studies have shown that upwelling is more pronounced during low flow conditions (Soulsby *et al.*, 2001; Malcolm *et al.*, 2003), therefore, all measurements were taken at low flow. At all sampling locations, the conductivity of subsurface water did not deviate from surface water conductivity (Table 5.10), suggesting that upwelling groundwater was not present at the egg incubation depth.

Date	**07/01/2003**					**25/03/2003**				
Location	Redd 1	Redd 2	Redd 3	Redd 4	Redd 5	Redd 1	Redd 2	Redd 3	Redd 4	Redd 5
Surface	2.1	2.1	2.1	2.1	2.1	2	2	2	2	2
Subsurface	2.4	2.3	2.2	2.1	2.2	2.1	2	2.3	2	2.2

(a)

Date	**06/01/2003**					**21/03/2003**				
Location	Redd 1	Redd 2	Redd 3	Redd 4	Redd 5	Redd 1	Redd 2	Redd 3	Redd 4	Redd 5
Surface	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Subsurface	1.7	1.6	1.5	1.5	1.7	1.7	1.65	1.5	1.5	1.6

(b)

Table 5.10 Surface and subsurface (0.25m) conductivities (ohms $\times 10^{-4}$); (a) River Aran, (b) River Blackwater.

5.6.2 Hydraulic head

The subsurface environment of riverbeds is composed of multiple interacting flow paths of variable, direction, depth and length (Section 3.2). Delineation of intragravel flow path characteristics can be used to assess the potential presence of upwelling groundwater. Intragravel flow paths can be characterised by assessing variations in intragravel hydraulic pressure. Hydraulic pressure, referred to as hydraulic head, is influenced by surface topography, surface flow and groundwater inputs (Section 3.2). Typically, at points of upwelling groundwater, positive hydraulic pressure will be recorded, and at points of downwelling negative hydraulic pressure will be recorded. Piezometers are a commonly adopted tool for assessing intragravel hydraulic pressures. Figure 5.16 provides a description of the piezometers used to assess hydraulic head. The difference in water level between the mini-piezometer and the riverbed provided an indication of the vertical direction of flow. When the water level in the mini-piezometer was higher than the river stage, water was considered to be upwelling. Conversely, when the water level within the mini-piezometer was lower than the river stage water was defined as downwelling (Lee and Cherry, 1978; Baxter *et al.*, 2003).

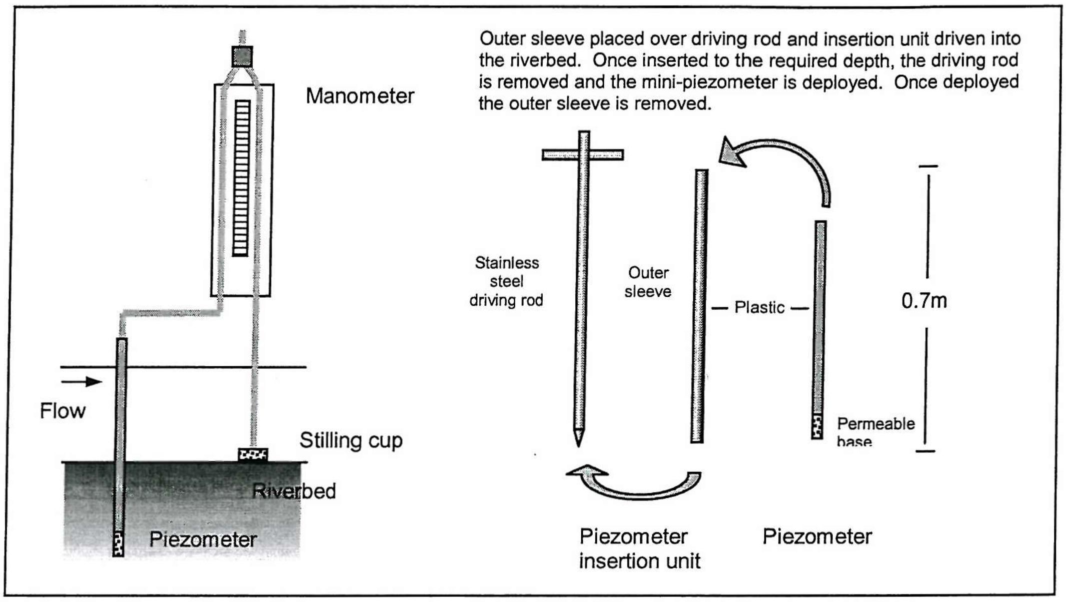


Figure 5.16 Schematic of sampling protocol for measuring hydraulic head. Includes description of min-piezometers and insertion unit.

At the River Aran and River Blackwater, detailed surveys of subsurface hydraulic pressure were undertaken (Figure 5.15). Due to monetary and time constraints, it was not possible to deploy networks of permanent piezometers at each field. Consequently, point measurements of hydraulic head were made at each site at low flow. To provide an indication of conditions at egg incubation depths, all measurements were taken between 0.2 and 0.3 mm depth (relative to bed topography). All sampling points were surveyed using a Geodimeter™ System 600. Generally, sampling was concentrated around the monitoring zone, although, where it was felt that additional data would aid characterisation of subsurface flow paths, supplementary measurements were taken at upstream and downstream locations.

At the monitoring locations (artificial redds), downwelling was the dominant flow direction. This would be expected as redds were typically sited at points of accelerating flow or on the crest of riffles. If significant groundwater inputs were present, one would expect to record positive hydraulic pressures. Therefore, it was surmised that, based on hydraulic head data, groundwater upwelling was not a dominant process at these study sites. However, groundwater inputs can be influenced by climatic conditions and fluctuations in aquifer level (Winter *et al.*, 1998). Therefore, although providing an indication of the dominant subsurface flow paths, as temporal variability was not assessed, it is possible that temporally variable groundwater inputs were missed.

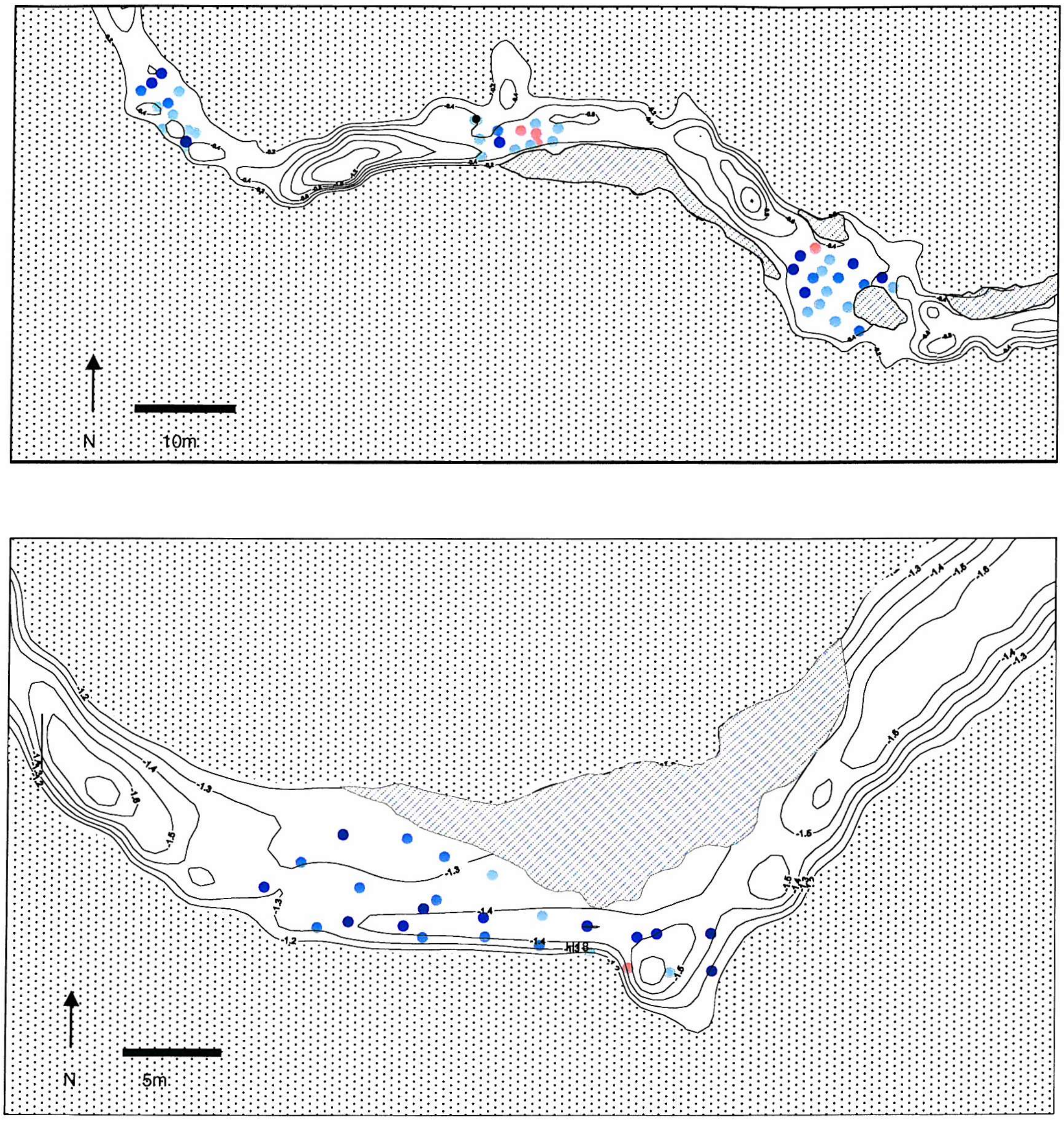


Figure 5.17 Summary of trends in hydraulic head at the (a) River Blackwater and (b) River Aran. Coloured dots represent direction (blue downwelling, red upwelling) and magnitude (mm) of hydraulic head: ● >40, ● 30-40, ● 20-30, ● 10-20, ● 0-10, ● 0-10

Channel, Bar, Floodplain.

At the River Test, resource constraints did not permit a detailed assessment of hydraulic head. However, during routine monitoring, significant peat and clay deposits had been recorded under the sampling reach. It was felt that these relatively impermeable deposits would limit the potential presence of significant groundwater upwelling at the study site. To test this conjecture an assessment of hydraulic head at each redd locations was undertaken. It should be noted that this assessment was undertaken in 2003, whereas, the monitoring programme was completed in 2002. However, as the presence of groundwater inputs is dependent on subsurface parameters that are unlikely to have changed in the interim period, assessing groundwater inputs in 2003 provided a good indication of potential inputs during the 2002 sampling period. At all redd locations, downwelling was the dominant flow path, suggesting that groundwater inputs were not significant at this site.

5.6.3 Thermal profiles

Thermal profiling can be used to identify potential groundwater inputs (Maddock *et al.,* 1995). Typically, the temperature of surface water is similar to air temperature, although temperatures fluctuate over a narrow range and exhibit a lagged response. In contrast, groundwater temperatures are mediated by the thermal character of the subsurface storage medium, and typically remain in the range 8°C to 10°C (Walling and Webb, 1992). Therefore, in winter groundwater is typically warmer than surface water, whereas, in summer groundwater is generally cooler than surface water. Studying the temperature variations between surface water and groundwater provides a basis for delineating the presence of groundwater.

Upwelling groundwater will typically remain at a constant temperature with little or no response to diurnal fluctuations. The depth of the mixing zone between groundwater and surface water is dependant on local conditions such as permeability, bed roughness, bed morphology and substrate size, and larger scale influences such as precipitation events, geology and landscape topography (White *et al.,* 1987). Generally, surface water temperatures can influence hyporheic temperature patterns to depths of more than 50cm (Maddock *et al.*, 1995). Figure 5.18 outlines typical thermal profiles associated with surface groundwater interactions across a riffle feature.

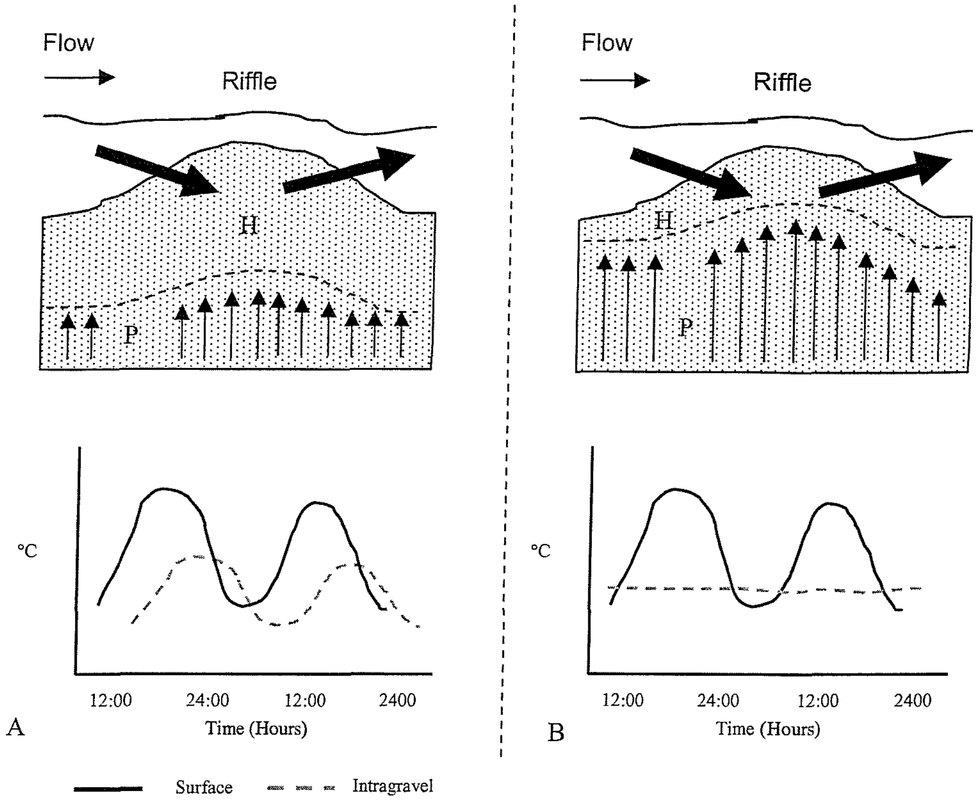


Figure 5.18 Intragravel flow paths and corresponding thermal profiles (after Shepard *et. al.*, 1986).

In situation A, streamwater enters the riverbed at the interface between the pool and the riffle and remerges at the downstream tail of the riffle. Temperature patterns within the streambed display two distinct characteristics: (i) A time lag is present between maximums and minimums of surface water temperature and those of interstitial water, and (ii) intragravel water temperature displays less variation than surface water (Maddock *et al.*, 1995). In situation B, surface water follows a similar flowpath, however, the zone of mixing between groundwater and surface water is closer to the bed surface, and groundwater emerges from the riverbed at the low pressure point at the rear of the riffle. Intragravel water temperatures show no diurnal variation and mirror the temperature characteristics of the groundwater source.

Thermister columns, composed of steel metal probes housing a series of five thermisters at 0.1m intervals, were deployed at each field site (Acornley, 1999). The first thermister was located above the riverbed and the remaining thermister were located below the bed surface. Each thermister column was connected to Delta T™ data logger and temperature was recorded at 15-minute intervals. At the end of the monitoring period, the data was filtered to select for periods of low flow, and mean diurnal temperature fluctuations were analysed. Periods of low flow were selected based on evidence that surface-subsurface exchange is lower during low flow conditions, therefore, the influence of upwelling groundwater is potentially more pronounced than during periods of higher flow (Soulsby *et al.*, 2001, Malcolm *et al.*, 2003).

At all sampling sites, the temperature response in the upper gravel layer (0.1, 0.2m depth) closely follows surface water temperatures, however at 0.3 and 0.4m, a distinct decline in temperature response is recorded (Figure 5.19). This buffered response is most evident at the River Ithon and River Blackwater. The decline in temperature response with depth may indicate the presence of groundwater. However, as groundwater temperatures can vary dependent on the residence time within the substratum, it is difficult to assess the typical attenuation of maximum and minimum diurnal temperatures associated with groundwater inputs. Furthermore, the attenuation of maximum and minimum temperatures at 0.3 and 0.4m depth into the riverbed may also be indicative of long residence (long flow path and slow intragravel flow velocity) hyporheic water; the temperature of which will be buffered by the overlying gravels.

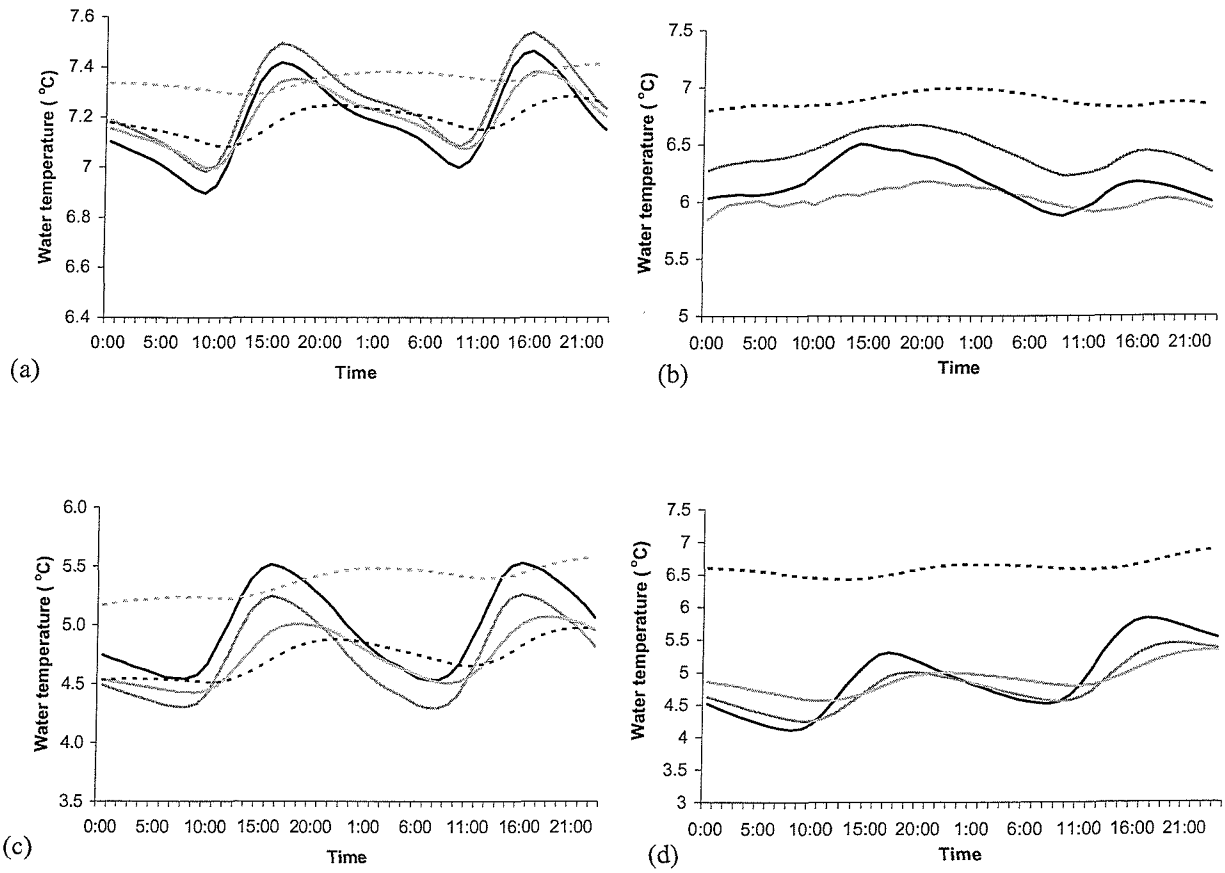
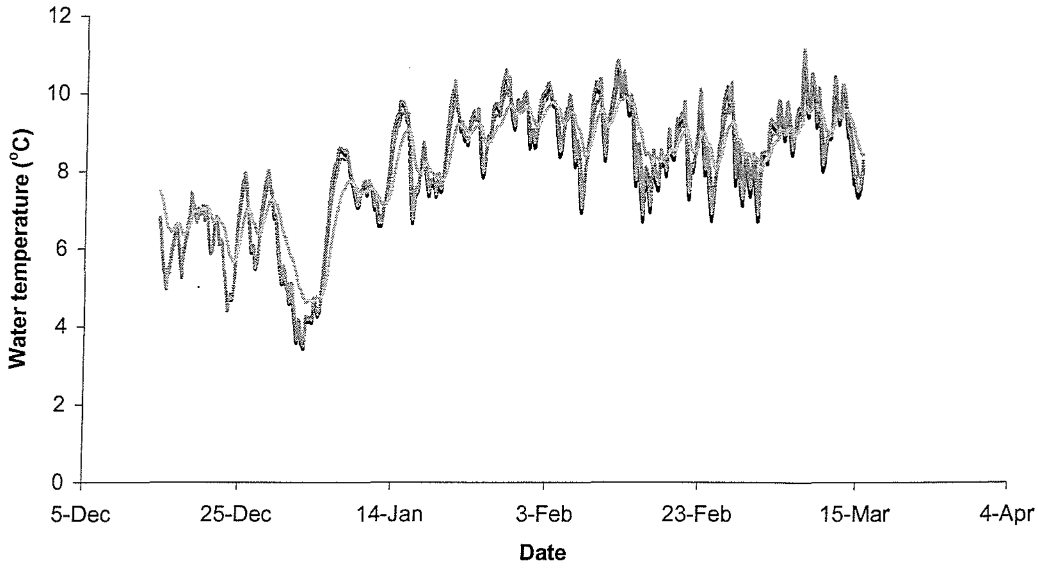


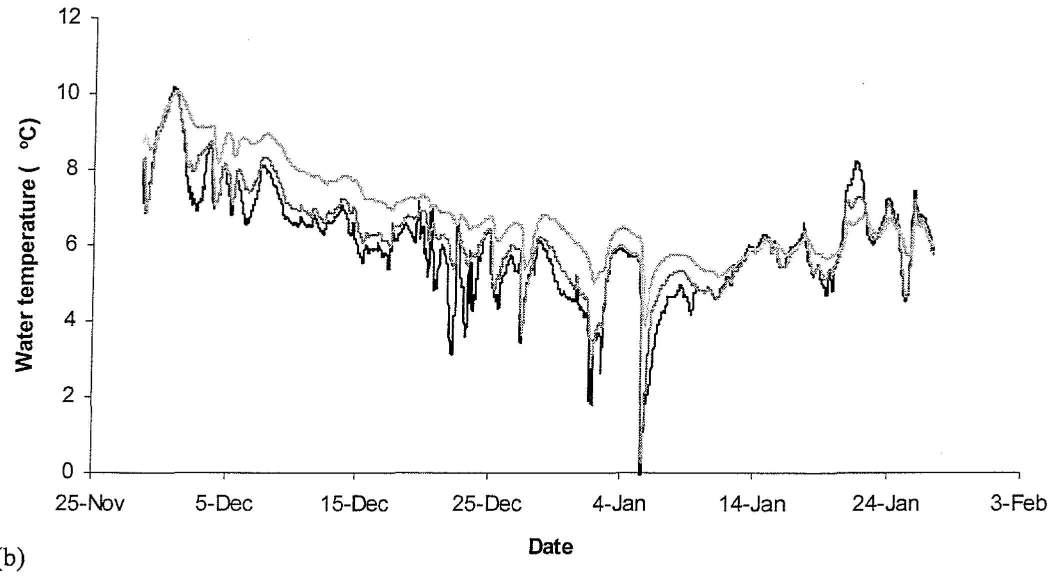
Figure 5.19 Diurnal temperature fluctuations at field-sites. (a) River Test, (b) River Ithon, (c) River Aran, (d) River Blackwater.— Surface;— 0.1m; — 0.2m;····· 0.3m; ····· 0.4m.

To assist delineation between the two potential mechanisms influencing subsurface water temperatures, the complete thermal time trends obtained over the monitoring period were analysed to assess longer-term trends in temperature response within the riverbed (Figure 5.20). It was hypothesised that if upwelling groundwater was influencing subsurface water temperatures, one would expect to observe considerable buffering of longer term changes in surface water temperatures. As shown in Figure 5.20, although evidence of some buffering of longer term changes in surface temperature is evident, particularly at surface water temperatures below 4°C and at 0.4m depth, in broad terms, subsurface water temperatures display an association with surface water temperature at all locations and depths.

Based on the data obtained from the thermister columns, it is difficult to discount a potential groundwater input at the River Ithon and River Blackwater sampling locations. However, based on the evidence provided from the hydrochemical and hydraulic head studies, it is probable that groundwater upwelling did not comprise a significant portion of the water sampled at egg burial depths at each study site. Furthermore, it should be noted that the thermal trends were based on a single measurement point. Therefore, it is possible that thermal trends were influenced by discrete groundwater inputs, potentially associated with seepage from the riverbank or localised areas of permeable substratum.

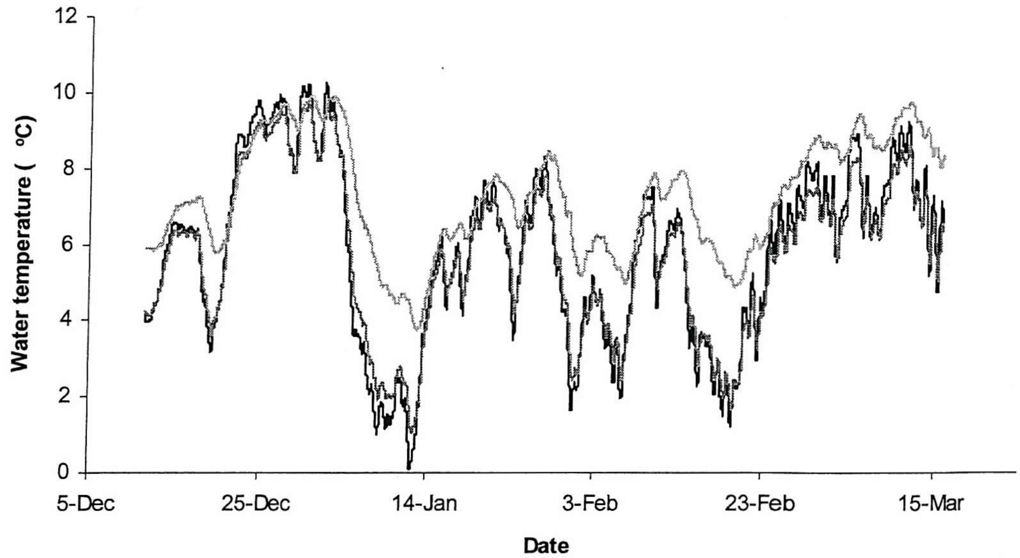


(a)

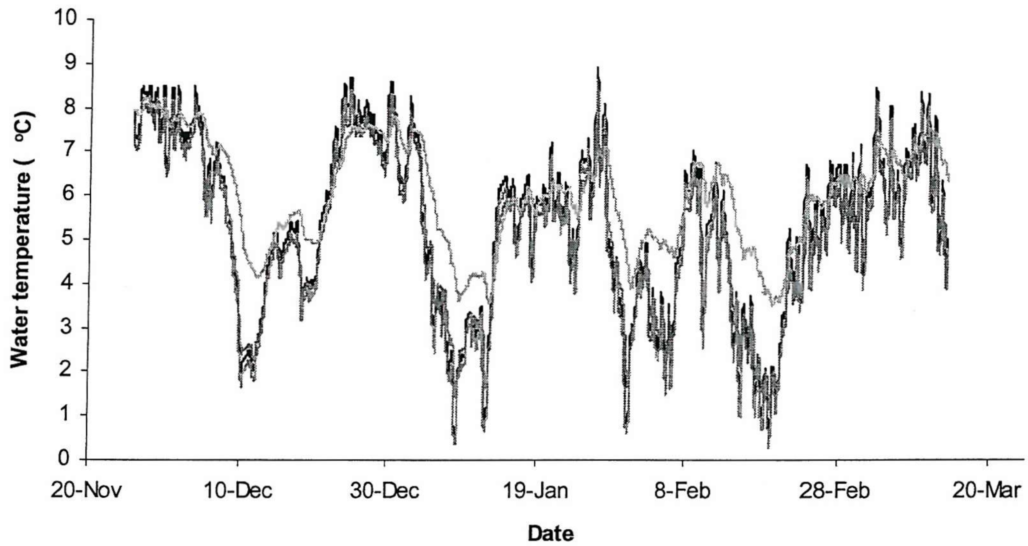


(b)

Figure 5.20 Thermal profiles of surface water and at four depths into the riverbed: (a) River Test, (b) River Ithon. ——— Surface ——— 0.2m ——— 0.4m.



(c)



(d)

Figure 5.20(cont) Thermal profiles of surface water and at four depths into the riverbed: (c) RiverAran, (d) River Balckwater. ——— Surface ——— 0.2m ——— 0.4m.

5.7 Operational limitations of the monitoring strategy

Artificial redds

Low population size status at each study site necessitated the use of artificial redds. It was recognised that although efforts were made to accurately mimic important characteristics of natural redds, it is possible that natural redds contain features that were not adequately represented by the artificially constructed redds. Consequently, it was conceded that all survival rates, although providing an indication of potential survival at the field sites, should be more accurately described as measures of survival within the environments created at the field sites. Similarly, the presence of monitoring equipment within the redd may have influenced conditions within the incubation environment. However, as the purpose of the study was to quantify survival in relation to incubation conditions, these factors were deemed inconsequential within the context of the study objectives.

Embryonic survival

In the early stages of project development, it was decided that assessments of survival would be limited to assessment of survival to hatching. Consequently, survival from hatching to emergence was not assessed. This decision was based on two observations drawn form previous investigations into incubation survival (Section 2.2): (i) poor reliability of estimates of survival to emergence and (ii) reduced possibility of oxygen deficiency related mortalities post hatching. With respect to estimates of survival to emergence, it has been shown that the ability of emerging fry to move laterally through the bed substrate can influence recorded rates of survival (Philips and Koski 1969). White (1980), using an emergence trap developed by Philips and Koski (1969), observed that 41% of the fry escaped from the trap and were caught in a net located downstream. Additionally, the disturbance caused by the presence of an emergence trap has been shown to influence recorded rates of survival. Emergence traps are typically large, rigid and composed of fine mesh (< 1.5mm), subsequently, their presence can modify both water dynamics and sediment deposition in and around the redd zone. Philips and Koski (1969) noted that silt had a greater tendency to settle on the gravel within the trap. If sediment increases inside the trap, the gravel permeability decreases, thereby reducing survival to emergence. For this reason, Hause and Coble (1976) abandoned their experiments based on emergence traps.

With respect to post hatching oxygen deficiency related mortalities, observations of respiratory requirements indicate that peak metabolism occurs during hatching and that post hatching, oxygen consumption declines (Rombough, 1988). Furthermore, alevins are mobile and can migrate towards areas of higher oxygen availability. Based on these observations, it was hypothesised that potential oxygen deficiency related mortalities were reduced post hatching.

Consequently, it was decided that robust assessments of survival to hatching were preferable to poor assessments of survival to emergence. Furthermore, it was conjectured that assessments of survival to hatching provided a guide to the total number of oxygen deficiency related pre-emergent mortalities. However, as comparisons were not undertaken to validate this assumption, all survival rates are reported as survival to hatching.

Oxygen related mortalities

The project is limited to delineating oxygen related mortalities. It is recognised that additional factors may also influence survival within the incubation zone. Of particular relevance is the accumulation of metabolic waste and inhibited emergence from the incubation zone. The accumulation of metabolic waste (ammonia) excreted by incubating embryos has been identified as a factor potentially influencing survival (Burkhalter and Kaya, 1977; McCabe *et al.,* 1985), however, with the resources available for this project, it was not possible to assess ammonia concentrations in the incubation environment. Consequently, it was not possible to delineate between mortalities resulting from the toxic impact of ammonia accumulation and those resulting from oxygen deficiencies.

With regard to impeded emergence from salmon spawning gravels, it is recognised that this may be an important additional factor degrading the quality of salmon spawning gravels. However, beyond recognising this factor and suggesting a requirement for further research in this area, it was beyond the scope of this study to assess this factor. This issue is discussed further in Section 6.4.

Intragravel flow velocity

Intragravel flow velocities were monitored using a conductiometric standpipe technique (Appendix 1). Although the technique was refined and recalibrated for the purposes of the study, the limitations of the probe must be recognised. Of particular relevance are the lower limit of the probes response and the probes level of accuracy, which were defined as 1 cm h^{-1} and 18 cm h^{-1} (velocities < 200cm h^{-1}) respectively.

Sub-lethal impacts of oxygen availability

A number of studies have discussed the impact of restricted oxygen availability on embryonic growth rates and potential post hatching fitness (Mason, 1969; Pucket and Dill, 1985; Malcolm *et al.*, 2003). Assessments of the length and weight of recovered embryos was not undertaken. Therefore, it was not possible to assess sub-critical impacts of oxygen availability on embryonic fitness and potential post emergence survival.

Groundwater

Although the potential importance of groundwater inputs have been highlighted, it was beyond the scope of this study to thoroughly investigate trends in groundwater upwelling and its potential impact on embryonic survival. However, during the monitoring programme, efforts were made to assess the presence of groundwater upwelling at the study site, and based on these observations and the work of other researchers, the presence of groundwater upwelling at the field sites was investigated (Section 5.4).

Fine sediment loads

Within the project constraints, an assessment of suspended sediment loads at each site was undertaken. Although providing datasets upon which to develop some coarse rating relationships, the data was not of a sufficient frequency to provide robust estimates of suspended sediment loads. Furthermore, bed load, which can comprise a significant proportion of the sediment available for deposition, was not quantitatively assessed. Finally, detailed analysis of the particle size of materials available for infiltration was not undertaken. Consequently, with respect to assessing variations in the availability of sediment for infiltration into spawning and incubation gravels, the project is limited to broad assessments of suspended sediment loads at each field site.

As described in Section 2.2, the principal purpose of the thesis was the investigation of factors and processes influencing the availability of oxygen within the incubation environment. Therefore, with respect to fine sediments, the thesis focuses on the impact of fine sediment accumulation on oxygen availability within the incubation environment. Analyses of temporal and spatial trends in infiltration rates, and assessments of the relationship between sediment availability and infiltration rates, can be found in the literature (Einstein, 1968; Frostick *et al.*, 1984; Carling and McCahon, 1987; Lisle, 1989; Carling, 1992; Sear, 1993).

Chapter 6. Scientific findings

Chapter 6 details the results of the monitoring programme. Five sections are presented: (i) a field-based assessment of oxygen supply to incubating Atlantic salmon embryos, (ii) an assessment of the impact of clay particles on cutaneous exchange of oxygen across the egg chorion, (iii) flume observations of the influence of surface flow on subsurface flow patterns and intragravel flow velocity, (iv) an assessment of the impact of fine sediment accumulation on intragravel oxygen fluxes and salmonid incubation success and (v) an assessment of the application of mass transport theory as a measure of habitat quality and potential incubation success.

6.1 An assessment of oxygen flux through artificial salmon redds created in natural spawning gravels

The following section reports the findings of the field-based assessment of oxygen supply to incubating Atlantic salmon embryos. Results from the 2001-2002 and 2002-2003 monitoring periods are presented.

6.1.1 Introduction

The development of a robust and reliable method of defining the quality of salmon spawning gravels remains an important objective in fishery research and river management (Chapman, 1988; Bjorn and Reiser, 1997; Reiser, 1998; Wu, 2000). Commonly, salmonid spawning and incubation habitat quality is assessed from predetermined relationships between physical features of the incubation environment and incubation success. Proposed determinants of survival include measures of the sedimentary structure of the riverbed and quantification of intragravel oxygen concentrations (Table 1.1 and 1.2). However, these determinants of survival are based on empirical relationships, and do not assess the primary processes influencing incubation success. During the embryonic stages of development, four principal factors influence potential survival to hatching: insufficient oxygen availability, poor water quality, physical disturbance of the incubation environment, and the accumulation of metabolic waste (Meehan 1997). Although investigation into the relative impact of these factors in different river systems is limited, available information suggests that insufficient oxygen availability is the dominant factor limiting incubation success in many rivers (Harvey, 1928, Krough, 1941; Hayes *et al.*, 1951; Philip and Campbell, 1963; Turnpenny and Williams, 1980; Hartmann, 1988; Maret *et al.*, 1993; Rubin and Gilmsater, 1996; Ingendahl, 2001; Malcolm *et al.*, 2003).

Oxygen availability is defined by the relationship between respiratory requirements and oxygen flux through the incubation zone. Oxygen consumption by incubating embryos is driven by diffuse solute exchange across the egg membrane. The concentration gradient required to support diffuse oxygen exchange is maintained by the bulk movement of oxygen through the riverbed. The flux of oxygen through spawning gravels is controlled by a complex interaction of intragravel and extragravel factors (Figure 3.2.7). In summary, fine sediments deposited in the riverbed block interstitial pore spaces and inhibit the passage of oxygenated water through the incubation zone (Chapman, 1988, Bjorn and Resier 1997). Oxygen demands, which develop when oxygen-consuming material accumulates in the riverbed, remove oxygen from interstitial water, thereby lowering intragravel oxygen concentrations (Whitman and Clark, 1982; Chevalier and Carson, 1984; Otakar *et al.*, 1992). Groundwater, which seeps into the riverbed from subsurface storage zones, imparts a spatially and temporally variable influence over intragravel oxygen concentrations (Sheriden, 1962; Soulsby *et al.*, 2000, 2001; Malcom *et al.*, 2002,). Finally, pressure and turbulent driven surface-subsurface exchange processes influence the depth of penetration and flux of surface water into and through the riverbed (Vaux, 1968; Savant *et al.*, 1987; Shimizu *et al.*, 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Harvey and Bencala, 1993). The interaction and relative impact of these factors varies between systems dependent on localised channel features and broader catchment characteristics (Section 3.2). Consequently, the precise factors, or suite of factors, influencing the flux of oxygen through spawning gravels may vary between river systems.

In view of the complex interaction of factors influencing conditions within the incubation zone, a number of concerns regarding the application of current metrics of survival can be identified. Assessments of habitat quality based on the sedimentary structure of the riverbed, which include percent fines, Fredle index and permeability (McNeil and Ahnell, 1964; Koski, 1966; Hall and Lantz, 1969; Bjorn, 1969; Phillips, 1975; Koski, 1975; McCuddin, 1977; Platts, 1979;

Shirazi *et al.*, 1981; Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Cederholm *et al.*, 1981; NCASI, 1981; Tappel and Bjorn, 1983, 1989; Tagart, 1976, 1984; McCrimmon Gots, 1986; Chapman, 1988; Young *et al.*,1991; Kondou *et al*, 2001), do not assess the impact of sedimentary oxygen demands, the influx of groundwater or variable surface-subsurface exchange. Consequently, the ability of these determinants to accurately assess incubation success may be influenced by the presence of additional factors affecting oxygen availability. Similarly, assessments of habitat quality based on oxygen concentration alone (Philip and Campbell, 1963; Turnpenny and Williams, 1980; Hartmann, 1988; Maret, *et al.*, 1993; Rubin and Gilmsater, 1996; Ingendahl, 2001) may not identify zones where incubation success is impeded by rates of oxygen supply insufficient to support respiratory requirements, for instance as a result of low intragravel flow velocities or combinations of lowered oxygen concentrations and lowered intragravel flow velocity (Coble, 1961; Cooper, 1965; Bjorn and Reiser 1997).

In light of the limitations associated with current metrics of survival, there is a requirement for more comprehensive assessments of oxygen availability and incubation success. This section details the results of the field-based assessment of oxygen fluxes through salmon spawning gravels. The investigation is divided into two primary components; first, an analysis of temporal and spatial (both intra and inter site) variations in intragravel oxygen concentrations and flow velocities, and second, an analysis of metrics of survival based on measures of oxygen availability.

6.1.2Methods[3]

6.1.2.1Artificial redds and quantification of incubation success

Artificial redds (Type 1) were used to assess intragravel incubation conditions and rates of survival to hatching. Six redds were created within zones of recorded spawning at the River Test and River Ithon field sites, and five redds were created at the River Blackwater and River Aran field sites. Redds were constructed at spawning times that reflected natural spawning preferences in each systems. Similarly, consultation with experienced Environment Agency staff (personal communication: Ray Dobbins, Alan Price, Mark Fidebottom) ensured that all redds were constructed in areas of recognised spawning activity. As the River Blackwater does not support an Atlantic salmon population, redds were located in zones that were representative of typical salmon spawning preferences (Section 3.1). The topographic features of the sampling reaches and location of artificial redds are outlined in Figures 5.11-5.15.

In response to concerns regarding the application of artificial redds to study processes operating within natural redds (Chapman 1988), important morphological and sedimentological features of natural redds were replicated (Section 3.1). The cleansing action of the hen salmon was mimicked using flexing motions of a spade, and larger particles, referred to as centrum particles in natural redds (Chapman 1988), were allowed to accumulate in the bottom of the excavated pit. Egg pockets were infilled by digging additional holes directly upstream and allowing ejected gravel to wash into the previously created hole. All sampling equipment was inserted into redds during construction. The dimensions of the artificial redds were loosely modelled on the relationships developed by Crisp and Carling (1989) and were based on an average female fish length of 0.7m (Personal communication: Ray Dobbins, Mark Fidebottom, Environment Agency).

As described in Section 4.4, the information presented in this section formed part of a larger integrated assessment of factors influencing incubation success, consequently, in addition to the sampling equipment associated with this study, the redds also contained equipment pertaining to supplementary monitoring objectives. At the River Test and River Ithon, each redd contained two sediment pots (Type A), and a standpipe. At the River Aran and River Blackwater, each redd contained a single sediment pot (Type B) and a standpipe (Figure 6.1.1). The two-sediment-pot-set-up was used to assess potential differences in oxygen

[3]Data from all four field-sites are presented. For detailed site descriptions, the reader is referred to Section 5.3.

availability and survival along the length of the redd. However, based on the results of the 2001-2002 monitoring season, there was no statistical difference in survival between front and rear sampling locations (two sample t-test 95% confidence limit). Therefore, for the second field season (2002-2003), a single pot replaced the two-pot-set-up.

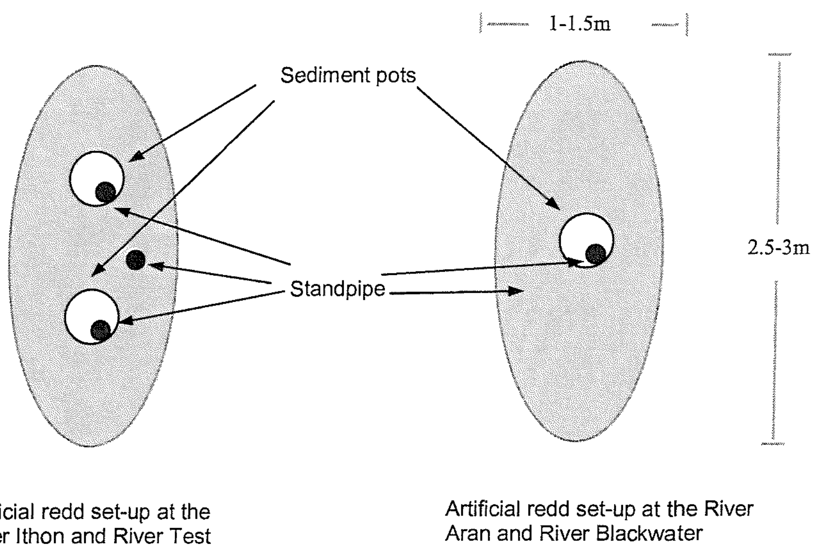


Figure 6.1.1 Plan view of the location of sampling equipment.

An Environment Agency hatchery (Kielder Hatchery) provided eyed eggs for insertion into the artificial redds at typical eyeing times for each river. Although the potential importance of population adaptations were recognised, population pressures in each system negated the potential deployment of eggs sourced from local populations. Furthermore, as the purpose of the study was to investigate the processes and factors impacting on incubation success, and not quantification of potential survival rates in specific systems, the use of eggs sourced from an external population was deemed appropriate to the project objectives.

At each field-site, continuously logging (15 min) thermister columns connected to Delta-T™ data loggers, provided hourly intragravel water temperatures at typical incubation depths (0.2m-0.3m) (Acronley,1999). This information was used to estimate potential embryonic development rates within the artificial redds. Rates of embryonic development were estimated from Crisp's (1992) daily incremental temperature/development model. At theoretical eyeing times, batches of newly eyed eggs were transported to the field sites for deployment. To allow deployment of the eggs into the redds with minimal disturbance to the incubation zone, two new techniques that allowed insertion of eyed eggs into pre-cut gravels were applied (Appendix 2 provides a detailed description of the egg insertion techniques). In summary, an egg deployment unit was contained within the sediment pots deployed within the artificial redds. When eyed eggs were available for deployment, the deployment unit was used to insert the eyed eggs into the sediment pots. The potential interference of the sediment pots on the incubation environment was considered. However, as the purpose of the study was delineation of survival in relation to oxygen supply and oxygen supply through the sediment pot was assessed, any interference from the sediment pots was accounted for in the analysis. In addition to deploying eggs within sediment pots, at the River Blackwater and River Aran, eggs were also deployed directly into the redd gravels. Eggs were deployed adjacent to the sediment pot using the procedure outline in Appendix 2. All eggs were deployed within Harris baskets (diameter 45mm, height 70mm) composed of 4mm plastic mesh, and were arranged in three layers: top, middle and bottom. The mesh size adopted ensured that eggs could not be washed out during deployment. Additionally, adopting a large mesh size reduced potential disturbance to the natural flow of water through the incubation zone. All Harris baskets were inserted to a depth of 0.3m; thus, eggs were incubated across a depth range of 0.25-0.30m.

Natural variations in the survival rates of deployed eggs were determined from control batches retained and monitored at Environment Agency hatcheries local to each field site. Additionally, control batches were also deployed in freshly cut gravels at each site. These batches allowed determination of the influence of any undetected pollutants in each river system. All Harris baskets were removed from gravel directly post hatching. Hatching times were predicted using the same temperature/development model applied to determine the timing of eyeing (Crisp, 1992). Weekly assessments of the development of embryos within the control batches deployed at each river provided an additional estimation of hatching times. After it was determined that 100% hatching had occurred, all Harris baskets were recovered by removing the sediment pots or carefully excavating the redds. Rates of survival in each layer were recorded. Additionally, to provide estimates of the timing of mortality, rudimentary visual assessments of stage of embryonic development and physical condition of the eggs were also recorded. Based on these assessments, embryos were divided into three classes: healthy, deceased during or close to hatching, and deceased in advance of hatching. Unfortunately, resource restrictions did not allow a size analyses to be performed on the healthy alevins. Therefore, the potential effect of hypoxia on egg development was not assessed. Additionally, it should be noted that while efforts were made to excavate redds post hatching, in some instances a proportion (<15%) of the healthy embryos had not hatched or were in the process of hatching. These embryos were recorded as healthy, however, as they had not hatched, it is possible that minor over estimates of embryonic survival to hatching are reported.

6.1.2.2 Monitoring dissolved oxygen and intragravel flow velocity

Standpipes (Figure 6.1.2) provided access points for monitoring the intragravel incubation environment. Standpipes were composed of 100 mm long sections of drilled stainless steel, sheathed in a section of retractable 260 mm long aluminium tube. The aluminium tube had two positions, (i) a sampling position where the tube is lifted 50 mm, allowing water to flow laterally through the drilled tube, and (ii) a non-sampling position where the aluminium tube is pushed to the base of the standpipe; thereby, protecting the standpipe from the intrusion of fine sediments. When not in use, the tubes were sealed with a cylindrical piece of foam and a rubber bung, further restricting the influx of fine sediments that may potentially interfere with monitoring equipment or obstruct access. To create a stable monitoring environment, an adaptor, which extended beyond the water surface, was attached to each standpipe prior to monitoring. Each redd contained two standpipes. The first was located within the sediment pots and the second was deployed directly into cut gravels. At the River Test and Ithon field sites, the standpipes were located in two positions within each redd: front and rear. At the River Blackwater and Aran field sites the standpipes were located adjacent to each other. It should be noted that at the River Test and Ithon, as all eggs were deposited within sediment pots, data from standpipes located in the sediments pots is presented. At the River Blackwater and River Aran, eggs were deposited into sediment pots and directly into cut gravels, therefore, data from standpipes located in the sediment pots and directly in the cut gravels are presented.

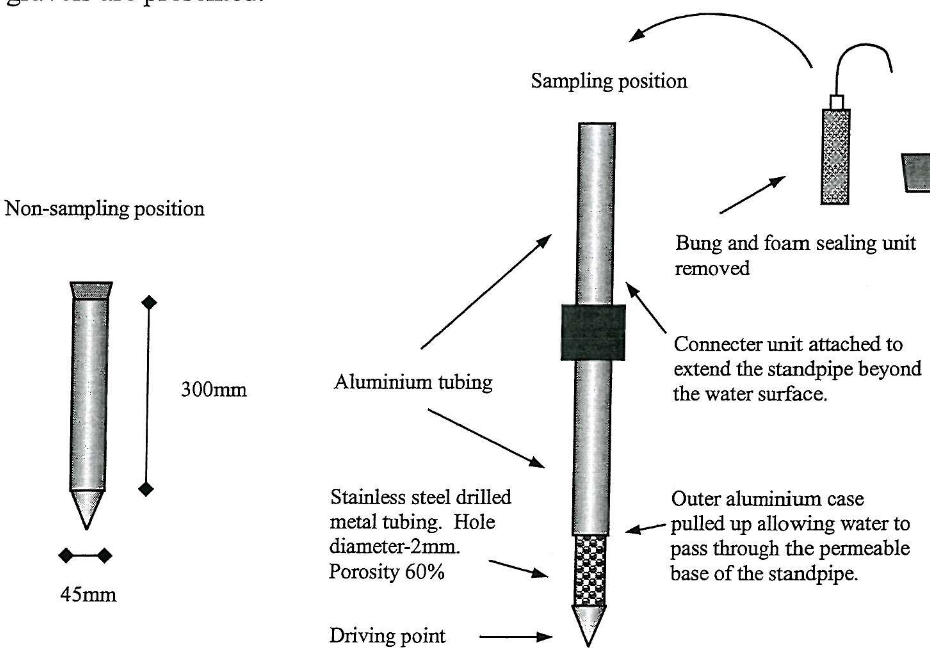


Figure 6.1.2 Overview of standpipe design and sampling protocol. Note: standpipes located in the sediments were of the same design minus the driving point.

Dissolved oxygen concentrations (mg l^{-1}) and intragravel water temperature (°C) were determined using a YSI ™ 250 oxygen probe. Intragravel flow velocities were estimated using a recalibrated conductiometric standpipe technique developed by Carling and Boole (1987) (See Appendix 1 for a detailed description of the conductiometric technique and recalibration procedure). In summary, the conductiometric standpipe technique assesses intragravel flow velocities by recording the rate of dilution of a saline solution. Post-sampling comparison of the exponent of the exponential decay curve with calibrated dilution curves, allows estimation of intragravel flow velocities. The lower limit of the probes response is 1 cm h^{-1}, and velocities below the probes threshold of response are reported as 1 cm h^{-1}. At velocities less than 200 cm h^{-1}, the probes 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 97 cm h^{-1} (Appendix 1). Intragravel flow velocities and oxygen concentrations were recorded at weekly intervals in the River Test and River Ithon, and at bi-weekly intervals in the River Aran and River Blackwater. It should be noted that although sampling was conducted within the egg pocket, and within close vicinity of deployed eggs, conditions sampled are representative of conditions within the sampling area, and may not be representative of conditions directly within the incubation zone. Therefore, all results are reported as a guide to conditions within the incubation zone (Figure 6.1.3).

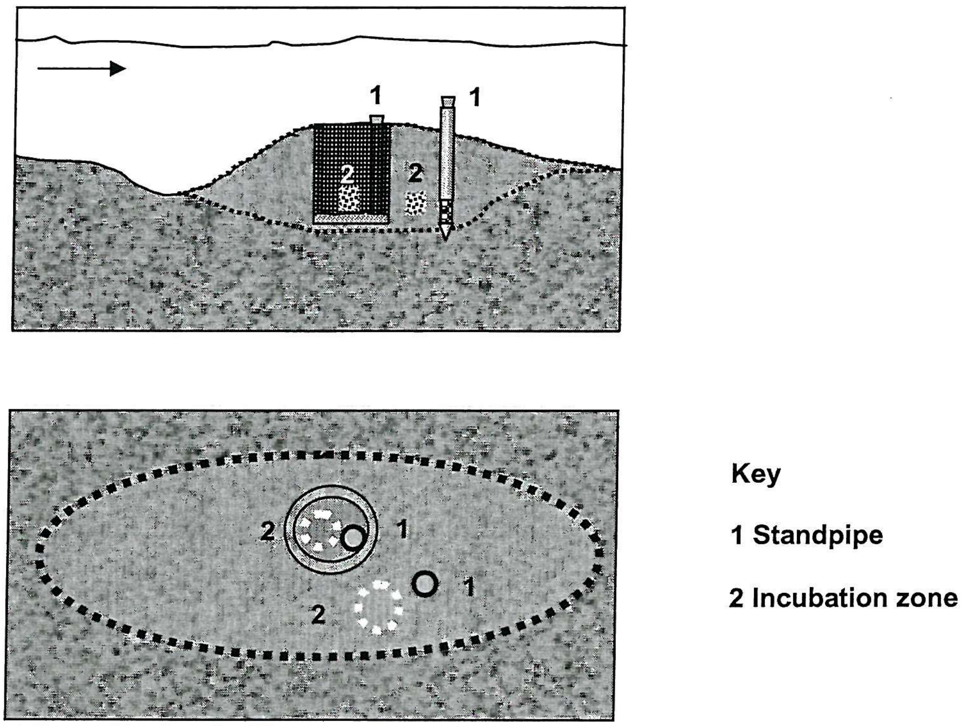


Figure 6.1.3 Graphical representation of the position of sampling equipment.

6.1.3 Results and analysis

6.1.3.1 Embryonic survival

Control batches retained in the streams (two per site) and at the hatcheries recorded survival rates comparable with expected hatchery survival rates (> 95% survival), indicating that survival within the artificial redds was not offset by high rates of natural mortality or adversely affected by poor surface water quality. All sites recorded differences in survival between the redds (Table 6.1.1). Minimum survival was zero at all sites. Maximum survival at the River Test, Blackwater, Ithon and Aran was 35%, 100%, 97% and 91% respectively. Mean survival was 22% at the River Ithon, 8.7% at the River Test, 71% at the River Blackwater and 28% at the River Aran.

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

Table 6.1.1 Rates of survival recorded within artificial redds. Data omissions result from problems encountered during sampling. As a consequence of the high rates of survival recorded for the control batches 96-100%, there was no requirement to compensate the field data derived survival rates.

Based on the stage of embryonic development and the condition of expired eggs, the probable timing of mortality was assessed. Deceased eggs in the River Test were either in the latter stages of development, or in the process of hatching, suggesting that mortalities had occurred directly prior or during hatching. At the River Blackwater, mortalities at redd 5 were in a severe state of decay and mortalities were estimated to have occurred a number of days prior to removal. Deceased eggs at all other locations did not show any signs of decay and mortalities were assessed to have occurred close to hatching. In the River Ithon, the condition of deceased eggs was more variable. At locations redd 1 (front and rear), redd 2 (rear), redd 4 (front) and redd 5 (front) eggs were in a severe state of decomposition, suggesting that mortalities had occurred a number of days prior to hatching. The condition of deceased eggs at the remaining redds suggested that mortalities had occurred during or close to hatching. Deceased eggs recovered in the River Aran were in the latter stages of development and showed little evidence of decomposition, suggesting that mortalities had occurred close to hatching. At the Rivers Ithon, Aran and Blackwater, over 90% of the Alevins recovered were healthy. However, at the River Test this figure was only 60%.

6.1.3.2 Dissolved oxygen concentrations and intragravel flow velocities

At the River Ithon, prolonged periods of high flow in February and March restricted access to the field site, resulting in interruptions to recovered data sets; at all other field sites, complete data sets were recovered. Figures 6.1.4 shows the dissolved oxygen concentrations recorded over the sampling period at each field site. Generally, dissolved oxygen concentrations declined over the incubation period from a maximum directly post redd creation, although localised fluctuations were recorded. Typically, minimum oxygen concentrations were recorded at hatching, although in the River Ithon and River Aran, minimum concentrations at a number of locations were recorded a number of weeks prior to hatching (Ithon: February 16th and March 12th; Aran: March 18th).

Figure 6.1.4 also shows the intragravel flow velocities, as estimated by the conductiometric probe, at each sampling location and field site. Generally, intragravel flow velocities declined over the incubation period from a maximum directly post redd creation to a minimum at hatching. It should be noted that at a number of locations, intragravel flow velocities were below the lower threshold of the conductiometric probe (1 cm h $^{-1}$). Consequently, although velocities are reported as 1cm h $^{-1}$, actual velocities may have dropped below 1cm h $^{-1}$. Additionally, consideration should be given to the probes level of accuracy (Appendix 1).

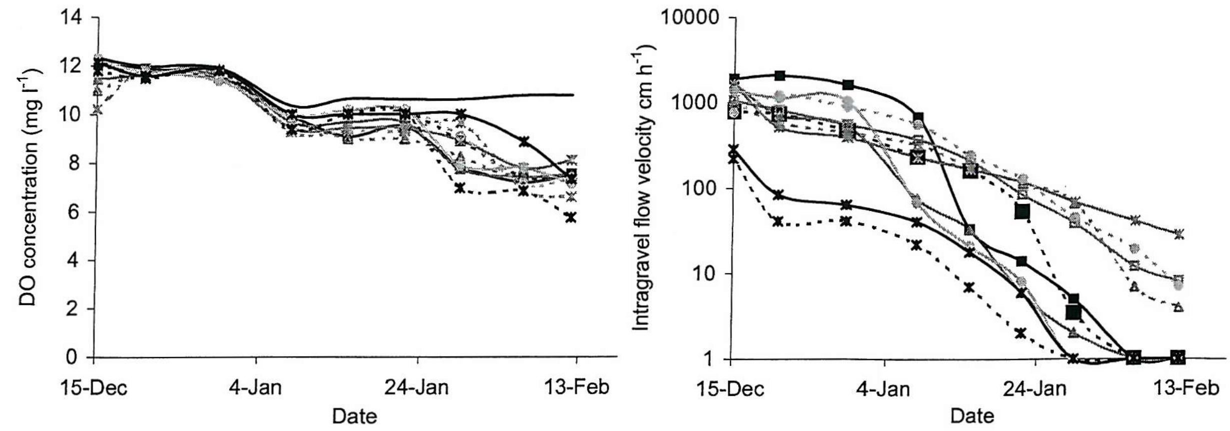


Figure 6.1.4 (a) Dissolved oxygen (DO) concentrations and intragravel flow velocities recorded over the incubation period (River Test).

R1 (front) R2 (front) R3 (front) R3 (rear) R4 (front)
R4 (rear) R5 (front) R5 (rear) R6 (front) R6 (rear)

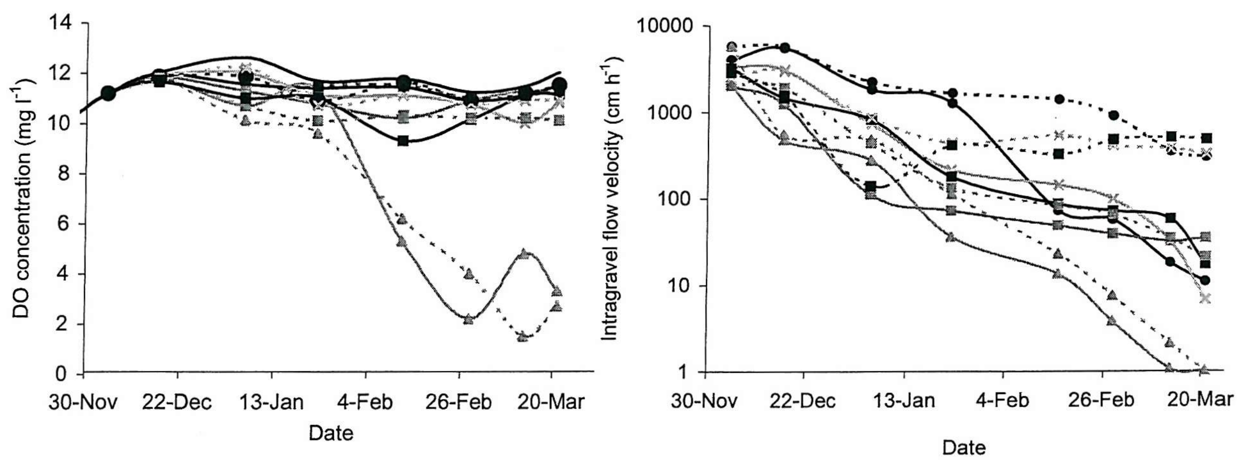


Figure 6.1.4 (b) Dissolved oxygen (DO) concentrations and intragravel flow velocities recorded over the incubation period (River Blackwater).

R1 (right) R1 (left) R2 (right) R2 (left) R3 (right) R3 (left)
R4 (right R4(left) R5 (right) R5 (left)

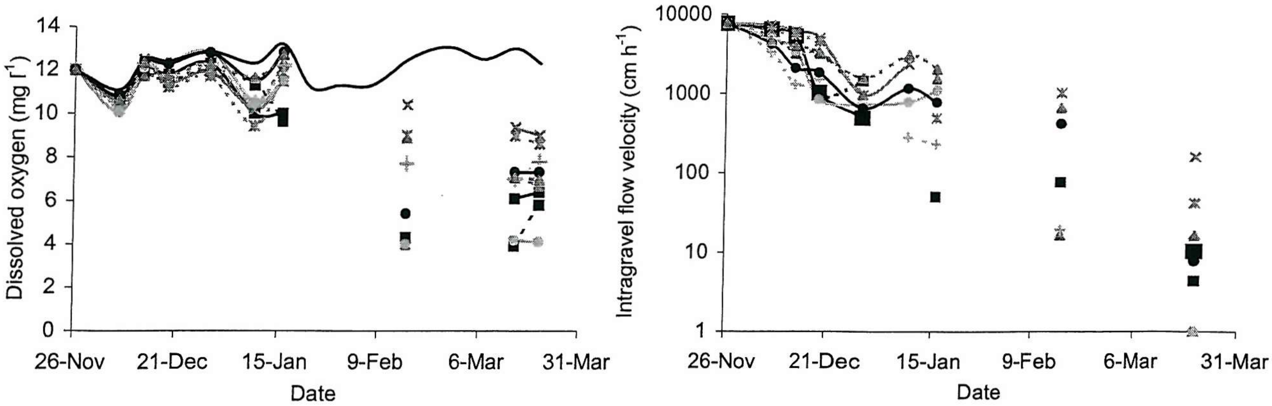


Figure 6.1.4 (c) Dissolved oxygen (DO) concentrations and intragravel flow velocities recorded over the incubation period (River Ithon).

R1 (front) R1 (rear) R2 (rear) R3 (front) R3 (rear)
R4 (front) R4 (rear) R5 (front) R6 (rear)

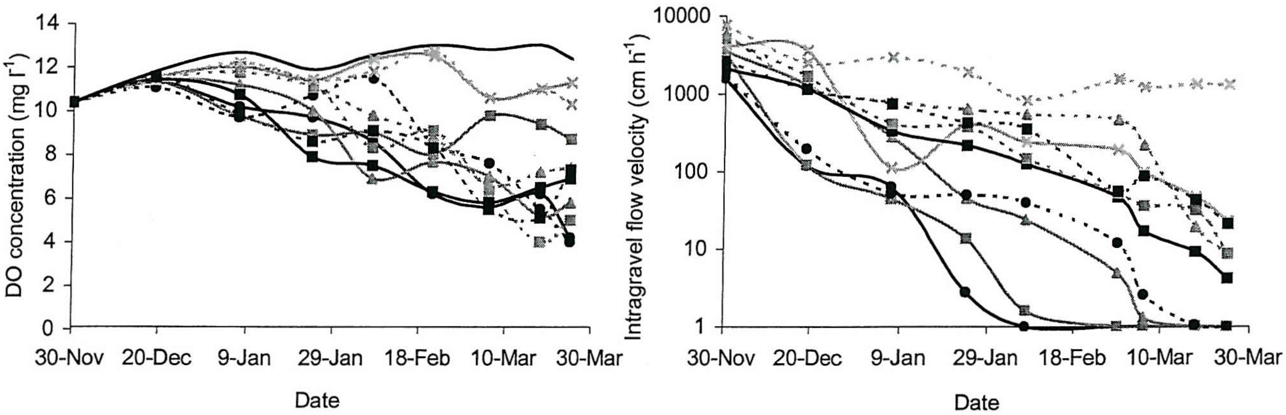


Figure 6.1.4 (d) Dissolved oxygen (DO) concentration and intragravel flow velocities recorded over the incubation period (River Aran).

R1 (right) R1 (left) R2 (right) R2 (left) R3 (right) R3 (left)
R4 (right R4(left) R5 (right) R5 (left)

Intra-site spatial variability in dissolved oxygen and intragravel flow is summarised in Table 6.1.2. As indicated by values of standard deviation, the River Test displayed the lowest spatial variability in intragravel conditions. The highest spatial variability was recorded at the River Blackwater, however, this trend is influenced by an outlying data point (Redd 3). The River Ithon and River Aran recorded similar spatial variability to the River Blackwater.

In addition to intra site variations in intragravel conditions, intra redd variations were also recorded. Although intragravel flow velocities and oxygen concentrations were spatially averaged over a vertical distance of 50mm, evidence of vertical variations in intragravel incubation conditions was provided by observations of survival within the Harris baskets. Survival was typically restricted to the top layer of eggs within each Harris basket and the results of a two-sample t-test (5% confidence limit) indicated a significant difference in survival between top and lower egg layers. The supposition that oxygen availability declines with depth is supported by studies of oxygen concentration and intragravel flow velocity within riverbeds (Whitman and Clark, 1982; Malard and Hervant, 1999; Soulsby *et al.*, 2001; Malcolm *et al*, 2003). In additional to vertical variations in incubation conditions, differences in survival and intragravel oxygen availability were recorded between egg deployment locations within individual redds (Table 6.1.1, Figure 6.1.4).

	River Test n=10	River Blackwater n=9	River Ithon n=10	River Aran n=10
		Standard deviations at hatching		
Intragravel Dissolved oxygen concentration (mg l^{-1})	0.6	3.4	1.5	2.4
Intragravel flow velocity (cm h^{-1})	8	177	52	392
Survival to hatching (%)	12.1	38.4	30.5	28.3
		Maximum standard deviations		
Intragravel Dissolved oxygen concentration (mg l^{-1})	0.9	3.4	2.55	2.4
Intragravel flow velocity (cm h^{-1})	585	1485	1714	1946
		Mean standard deviation		
Intragravel Dissolved oxygen concentration (mg l^{-1})	0.5	1.7	0.9	1.5
Intragravel flow velocity (cm h^{-1})	228	702	824	713

Table 6.1.2 Analysis of spatial variability of intragravel conditions at the study sites. Standard deviation based on variations between sampling locations at each sampling date.

In addition to assessing oxygen concentration and intragravel flow independently, oxygen fluxes (mg O_2 egg $^{-1}$) through the incubation zone were calculated from the product of discharge and oxygen concentration of water perfusing incubating embryos:

$$O_2(flux) = C_o\ (v \times a_{egg}) \qquad (6.1.1)$$

Where C_o is the intragravel oxygen concentration within the egg pocket, v is intragravel flow velocity, estimated with the conductiometric standpipe (cm h $^{-1}$) and a_{egg} is the cross section area of an Atlantic salmon egg (cm^2) based on an egg radius of 0.3 cm. Generally, temporal trends in oxygen flux were similar to those of intragravel flow and dissolved oxygen concentration; with maximum fluxes recorded at redd creation and minimum fluxes recorded at hatching. Similarly, intra-site spatial variability followed similar patterns to those discussed for dissolved oxygen and intragravel flow velocity (Table 6.1.3).

	River Test	River Blackwater	River Ithon	River Aran
		Oxygen flux (mg 0_2 egg h^{-1})		
Maximum (Redd creation)	26.6	72.2	98	85.9
Minimum (Hatching)	0.006	0.0029	0.004	0.004
Standard deviation (Mean)	2.82	8.92	11.57	8.7

Table 6.1.3 Analysis of temporal and spatial variability in oxygen flux. All standard deviation based on variation betweens sampling locations at each sampling date.

6.1.3.4 Relationships between survival and oxygen availability

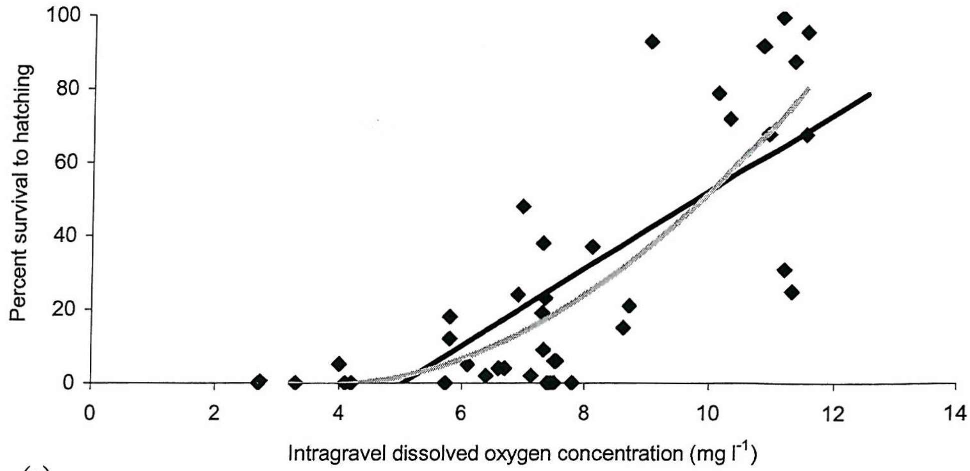
An assessment of the ability of measures of oxygen availability to delineate survival to hatching was performed. This analysis was divided into two stages. First, the data from each field site was collated to allow an analysis of broad trends between oxygen availability and survival. Second, to promote understanding of the process and mechanism influencing survival at the different field sites, a site-specific analysis of the strength of the relationships between oxygen availability and survival was performed.

The results of the analysis of the collated information are presented in Figure 6.1.5, and summaries of the regression equations are presented in Table 6.1.4. With respect to dissolved oxygen concentration, two regression relationships were fitted to describe the relationship with survival: a linear model and a polynomial model. The polynomial regression model provides a slightly better descriptor of relationship between oxygen concentration and survival than the linear model. This is particularly evident at oxygen concentrations below 8 mg l^{-1}, where similar survival is recorded across a range of oxygen concentrations. This trend may be indicative of the importance of intragravel flow as a mechanism to support oxygen availability and survival at lowered oxygen concentrations.

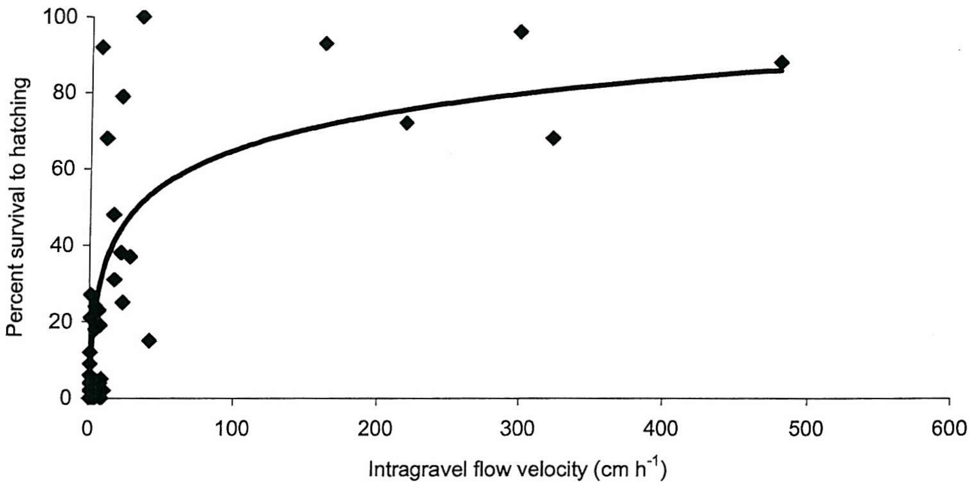
With respect to intragravel flow velocity and oxygen flux, trends in embryonic consumption suited the application of logarithmic functions (Figures 6.1.5 (b) and (c)). Incubating embryos have an upper oxygen consumption threshold; therefore, it is rational to conceive that rates of oxygen supply that support consumption above this threshold will not improve the potential survival of incubating embryos. In general, all the relationships tested performed reasonably as measures of incubation success, although, statistically, oxygen flux was the best determinant of incubation success oxygen.

Regression model applied to describe relationship between oxygen availability and survival	**Equation**	r^2	**Equation number**
linear relationship with oxygen concentration	$y = 10.62\,x - 53.65$	0.58	6.1.2
)Polynomial relationship with oxygen concentration	$y = 1.33\,x^2 - 9.78x + 17.4$	0.64	6.1.3
logarithmic relationship with intragravel flow velocity	$y = 13.383 \ln(x) + 3.31$	0.59	6.1.4
logarithmic relationship with oxygen flux	$y = 12.88 \ln(x) + 67.27$	0.65	6.1.5

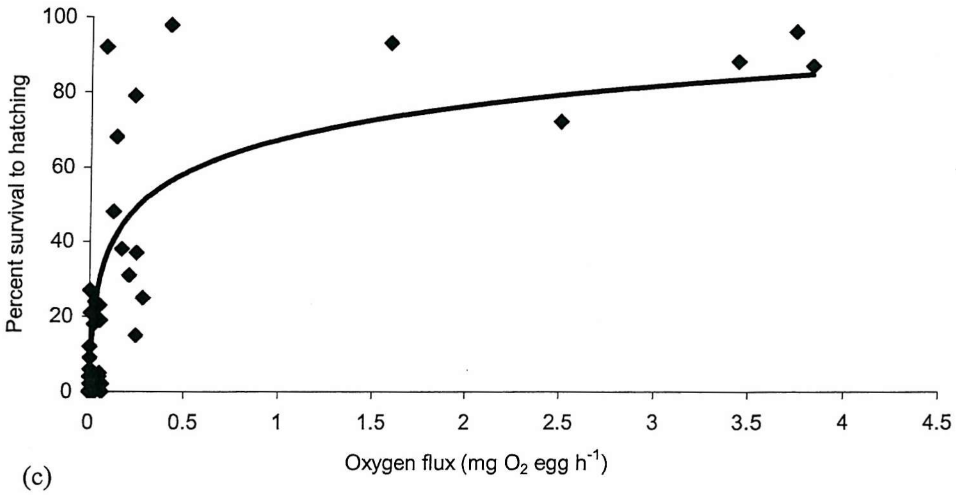
Table 6.1.4 Regression models relating embryonic survival to oxygen availability, where y = survival to hatching and x = oxygen concentration (Equation 6.1.2 and 6.1.3), x = intragravel flow velocity (Equation 6.1.4) and x = oxygen flux (Equation 6.1.5).



(a)



(b)



(c)

Figure 6.1.5 Relationship between survival to hatching and measures of oxygen availability.
(a) ▬ equation 6.1.2, ▬ equation 6.1.3; (b) ▬ equation 6.1.4; (c) ▬ equation 6.1.5.

To assess site specificity, the strength of the relationships between oxygen availability and survival were determined for each field site. A Pearson correlation analysis was performed to assess the statistical strength of any relationships between oxygen concentration, intragravel flow, oxygen flux and survival (Table 6.1.5). The results of the analysis indicated that at the River Test, Ithon and Aran field sites, oxygen supply was the best determinant of survival (significant at the 5% confidence limit). This was followed by intragravel flow velocity, which was also statistically significant at these field sites. Oxygen concentration at these field sites was the poorest predictor of survival. Conversely, at the River Blackwater, oxygen flux and intragravel flow were poorer determinants of survival than oxygen concentration, which was statistically significant at the 5% confidence limit.

Variable	River Test	River Blackwater	River Ithon	River Aran
Final oxygen concentration	0.53	0.82•	0.3	0.55
Minimum oxygen concentration	0.37	0.49	0.61	0.57
Final Intragravel flow Velocity	0.84•	0.5	0.84•	0.85•
Final Oxygen Flux	0.80•	0.56	0.89•	0.82

Table 6.1.5 Correlation coefficients (Pearson Analysis). • Significant at the 5% confidence limit.

6.1.4- Discussion

6.1.4.1 Spatial and temporal variability in intragravel conditions

With respect to temporal variations, all redd displayed a decline in conditions over the incubation period. Typically, intragravel flow velocities were highest at redd creation, which is concurrent with the increased gravel permeability that resulted from the ejection of fine sediments during the redd creation process. Thereafter, flow velocities declined, probably in response to the infiltration of fine sediments (Section 6.4). Similarly, oxygen concentrations were also at a maximum at redd creation, before declining over the incubation period, potentially associated with fine sediment infilling and the probable oxygen demand induced by deposited materials (Section 6.4).

Generally, the freshet site displayed greater spatial variability in intragravel conditions between redds. The homogeneity in intragravel conditions recorded within the incubation zones of redds created within the River Test potentially results from the stable hydrological regime and limited geomorphic variability associated with lowland chalk streams (Sear *et al.*, 1999). In contrast, the variable hydrology and distinct morphological features associated with the freshet systems may have resulted in more complex flow patterns and greater spatial variability in intragravel incubation conditions. In addition to intra site variations in intragravel conditions, intra redd variations were also recorded. It is probable that small differences in gravel and sediment structure within the riverbed, resulted in a complex intragravel environment in which oxygen availability varied within a small spatial field.

6.1.4.2 Relationship between survival and oxygen availability

The field study has highlighted the importance of considering both oxygen concentration and intragravel flow velocity as mechanisms influencing respiratory deficiency related embryonic mortalities. As highlighted in Figure 6.1.5 (a), embryonic survival displayed large variations across similar oxygen concentrations, including concentrations approaching oxygen saturation (11.5 mg l^{-1}). Similarly, although 5 mg l^{-1} is recognised as representative of the critical oxygen concentration threshold, in this study, at oxygen concentrations below 9 mg l^{-1} the upper threshold of survival was 50%. These trends are indicative of the coincident effect of oxygen concentration and intragravel flow on oxygen availability. The strong relationship between oxygen flux and embryonic survival supports the analysis.

With respect to defining the relative influence of oxygen concentration and intragravel flow velocity on survival, the mechanisms controlling embryonic respiration dictate that the importance of intragravel flow increases at lower oxygen concentrations, similarly, at reduced intragravel flow velocities, higher oxygen concentrations will be required to support respiratory oxygen demands. However, within this broad trend, the data presented in this study suggests that at these study sites, intragravel flow becomes an important control over survival at velocities less than 50 cm h^{-1} (Figure 6.1.5 (b)). With respect to oxygen concentration, the data indicates that negligible survival was recorded at oxygen concentrations below 5 mg l^{-1}. This equates well with previously defined critical oxygen concentrations that lie within a range of 2 to 5mg l^{-1} (Shumway *et al.*, 1964; Davis 1975), and suggests that at these values, oxygen concentration is the principal factor influencing survival.

The assessment of the relationship between oxygen availability and embryonic survival indicated that measures of oxygen concentration, intragravel flow velocity and oxygen flux can be used to delineate potential rates of embryonic survival. However, site specific inspections of these relationships indicated variability in the strength of these relationships between the study sites. Although this site specificity may be partly explained by the impact of reduced data points on the strength of the statistically analysis, it may also be indicative of variations in the specific cause of oxygen related mortalities at the field sites. Furthermore, although the relationships developed are statistically valid, the effective use of statistical correlations requires knowledge of the processes linking variables under investigation and awareness of additional pressures affecting the variables under consideration. With respect to factors influencing incubation success, the successful interpretation of statistical correlations requires appreciation of the importance of temporally variable conditions within the incubation zone, threshold responses and the interaction of additional pressures on survival. The results of the field-monitoring programme indicated that threshold responses may have influenced embryonic mortalities, for instance, at a number of locations, oxygen concentrations within the range considered critical to survival (2-5mg l^{-1}) were recorded (Shumway *et al.*, 1964; Davis 1975). In response to these observations, a deductive analysis of incubation success is described.

At the River Test, oxygen concentrations remained above critical levels for the duration of the incubation period, therefore, mortalities were not assessed to have occurred as a result of critical oxygen concentrations in the macro-environment. Rather, insufficient oxygen availability, resulting from a combination of reduced oxygen concentration and low intragravel flow velocity is proposed as the probable cause of mortalities over the incubation period. This reduction in oxygen supply would have reduced the oxygen concentration of water contained in the boundary layer, thereby, creating an oxygen deficit at the egg surface. As a large proportion of deceased eggs were recovered in the process of hatching, it is also possible that oxygen availability only exceeded demand as a consequence of the increased respiratory activity associated with breaking free from the egg capsule (Hamor and Garside 1978).

In addition to oxygen availability, the accumulation of metabolic waste within the egg pocket is a further factor that must be considered. Ammonia, which is by product of respiration, is toxic to incubating embryos (Burkhalter and Kaya, 1977). At present information regarding critical ammonia concentrations and required flushing velocities is limited. However, in view of the low intragravel flow velocities recorded at a number of locations at the River Test field site, ammonia accumulation must be considered as a potential factor influencing survival.

At the River Blackwater oxygen concentration was a statistically superior determinate of survival than oxygen flux. However, analysis of the Blackwater data set indicates that with the exception of redd 3, oxygen concentrations remained above levels considered harmful to incubation success. Consequently, the strength of the correlation between survival and dissolved oxygen concentration may be a statistically anomaly that is unjustified on the basis of knowledge regarding oxygen related mortalities and conditions within the incubation environment. Similarly, the poor relationship between oxygen supply and survival may be a consequence of the high rates of survival and lack of variability (with exception of one data outlier) in intragravel conditions, which may have reduced the potential effectiveness of the correlation analysis. The high survival rates recorded at the River Blackwater were primarily a consequence of the high oxygen concentrations, however, consideration must also be given to the intragravel flow velocities. With the exception of redd 3, estimates of intragravel flow velocity were above 10cm h^{-1}at all sampling locations. As highlighted by the results presented for the River Test, without an adequate through flow of water, the oxygen demand imposed by incubating embryos would have reduced the oxygen concentration in the microenvironment surrounding the egg capsules and resulted in an oxygen deficit at the egg surface. It has been shown that at 100% oxygen saturation, under zero velocity conditions, the diffuse supply of oxygen to an incubating embryo can only sustain respiration temporarily (Chevalier and Carson, 1984).

Oxygen concentration was a poor determinant of survival at the River Ithon and River Aran, however, analysis of the field data suggests that mortalities at a number of locations at each field site may have resulted from periods of sub-critical oxygen concentrations. Although intragravel monitoring data at the River Ithon is incomplete, an assessment of general trends can be undertaken. The oxygen concentration data indicates that directly prior to egg deployment (16th February), oxygen concentrations at locations redd 1 (front and rear), redd 2 (rear), redd 4 (front) and redd 5 (front) were below, or approaching, levels considered critical to incubation success (2-5mg l^{-1}) (Shumway *et al.*, 1964; Davis 1975). Furthermore, one week prior to hatching, oxygen concentrations at these locations remained lower than at other locations (Figure 6.1.4 (c)). If these intragravel oxygen concentrations are characteristic of conditions over this period, it is probable that eggs within these locations endured either prolonged or intermittent exposure to dissolved oxygen concentrations within the range reported as critical to survival (Shumway *et al.*, 1964; Davis 1975).

Based on the condition of deceased eggs, mortalities at these locations were assessed to have occurred in advance of hatching, suggesting that exposure to critical oxygen concentrations was the probable cause of mortalities. Oxygen concentrations recorded at the other locations in the River Ithon remained above critical levels for the incubation period, however, high rates of mortality were observed, suggesting that insufficient oxygen supply, resulting from a combination of reduced oxygen concentrations and intragravel flow velocities, was the more probable cause of mortalities at these locations. Oxygen concentrations at a number of locations at the River Aran field site were also below levels considered critical to survival. However, these low concentrations were recorded towards the end of the incubation period, therefore it is difficult to distinguish between mortalities resulting from critical oxygen concentrations and those resulting from low oxygen supply rates.

Table 6.1.6 summarises the potential causes of embryonic mortality at each field site. The factors influencing survival varied between the study sites, with intragravel flow velocity influencing survival at the two systems recording the lowest rates of survival (River Test and River Ithon).

Cause	River Test	River Blackwater	River Ithon	River Aran
Sub-critical oxygen concentration		✓	✓	✓
Low intragravel flow velocity	✓		✓	
Low oxygen flux	✓		✓	✓

Table 6.1.6 Summary of potential causes of mortalities at each field site.

6.4.3 *Potential causes of oxygen limiting conditions*

Based on the data presented, an analysis of the potential causes of oxygen limiting conditions is presented. The purpose of this analysis is to highlight the application of information pertaining to oxygen availability to identify potential environmental pressures. The following sections provide a detailed analysis of factors potentially influencing oxygen availability at the field sites.

With respect to potential causes of oxygen limiting conditions within the incubation environment, investigations into processes operating within riverbeds indicate that the flux of oxygen through spawning gravels is dependent on a complex interaction of surface and subsurface factors (Section 3.2). In summary, sediment accumulation within the riverbed blocks interstitial pore spaces and inhibits the passage of oxygenated water (Chapman, 1988; Bjorn and Reiser, 1991). Sedimentary oxygen demands, associated with the presence of oxygen consuming materials, remove oxygen from interstitial water, thereby lowering intragravel oxygen concentrations (Chevalier and Carson, 1984; Otakar *et al.*, 1992; Rutherford et al., 1993). Similarly, inputs of low oxygen content groundwater may lower intragravel oxygen concentrations (Sheridan, 1962, Soulsby *et al.,* 2001; Malcolm, 2003). Finally, evidence suggests that during periods of low flow, exchange of surface water with the riverbed is reduced, resulting in lower intragravel flow velocities and greater inputs of groundwater (Soulsby *et al.,* 2001, Malcolm *et al.*, 2003).

The data presented in this section suggests that the factors influencing oxygen availability within the study sites were distinct. At the River Test, factors influencing intragravel flow, for instance sediment accumulation or low surface-subsurface exchange, are suggested as the dominant limiting factors within this system. In the River Blackwater, mortalities were generally restricted to one location at which dissolved oxygen concentrations and intragravel flow velocities were severely depleted. The cause of depleted oxygen at this location is difficult to assess, however, gravel deposition over the redd was observed. In effect, this increased the egg burial depth from 0.25 m to 0.40m. It is possible that this resulted in reduced exchange of surface water with the incubation zone and allowed low oxygen content groundwater to influence oxygen concentrations with in the incubation zone. At the River Ithon and Aran, low oxygen concentrations and intragravel flow velocities were recorded. A potential rationalisation of the River Ithon and Aran data is that excess sedimentation coupled with high sediment oxygen demands within the riverbed, resulted in the depletion of oxygen from the intragravel water. .

6.1.5 Summary

Oxygen fluxes through salmon spawning gravels were quantified within the artificial redds at field sites within four U.K. river systems. Intra and inter site variations in rates of oxygen supply were observed. With respect to causes of mortalities, oxygen supply was shown to be a strong determinant of survival at all field sites. However, the application of statistical relationships to define incubation success provided was criticised. Therefore, to improve delineation of potential causes of mortality, the statistical analysis was synthesised with a deductive analysis of survival that was based on knowledge of the processes controlling respiration. Based on this analysis, the causes of oxygen deficiency related mortalities were shown to vary within and between the study sites. At the study sites, mortalities were assessed to have resulted from periods of either lethal oxygen concentrations, intragravel flow velocities insufficient to remove metabolic waste, or combinations of oxygen concentration and intragravel flow that did not support respiratory requirements.

6.2 Impact of clay particles on cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs

This section discusses the results of a laboratory based assessment of the respiratory requirements of Atlantic salmon eggs at hatching and the impact of clay particles on oxygen consumption.

6.2.1 Introduction

The oxygen available to incubating salmonid eggs is contained within a thin film of water at the egg surface; termed the boundary layer. Embryonic oxygen consumption requires a concentration gradient between the internal egg environment and the boundary layer. If oxygen concentration in the boundary layer declines, the concentration gradient is reduced, potentially resulting in restricted consumption, growth deficiencies and mortalities (Silver *et al.*, 1963; Shumway *et al.*, 1964; Cooper 1965; Garside 1966; Mason 1969) (Section 3.2.2). Oxygen availability within the boundary layer is dependent on the supply of oxygen from the macroenvironment. Oxygen is transferred to the boundary layer from the surrounding macro-environment primarily by diffusion, although natural convection and advection have also been proposed as additional mechanisms (Daykin 1968; O'Brien 1978; Rombough 1988). The passage of oxygen through the macroenvironment is driven primarily by advection (Daykin 1968; Wicket, 1975). Consequently, factors influencing oxygen fluxes through the macroenvironment directly impact on the availability of oxygen to incubating embryos.

One of the principal factors influencing the passage of oxygen through salmonid spawning gravels is the presence of excessive levels of fine sediments. In brief, fine sediments block interstitial pore spaces and inhibit the passage of oxygenated water through the riverbed. A number of studies have developed simple empirical relationships linking recorded rates of survival to emergence, with measures of the physical structure of spawning gravels. Typically, these studies have focused on defining either bulk properties of the gravel substrate or quantifying levels of fine sediment below an arbitrary size threshold (McNeil and Ahnell, 1964; Koski, 1966, 1975; Phillips, 1975; McCuddin, 1977; Platts, 1979; Shirazi and Seim, 1981; Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Tappel and Bjorn, 1983, 1989; Tagart, 1976, 1984; McCrimmon and Gots, 1986; Chapman, 1988; Young *et al.*, 1991). Although providing evidence of a link between the presence of sediment and embryonic survival, these studies do not quantify the direct impact of sediment on oxygen consumption or availability.

The principle source of fine sediments (<0.5mm) in rivers is the erosion of soil from the catchment land surface (Walling 1995). Clay particles and fine silts represent the most mobile size classes, providing a direct connection between land management practices and the spawning environment.

The purpose of this study was (i) determination of rates of embryonic consumption by Atlantic salmon embryos at hatching and (ii) analysis of the impact of clay particles on oxygen consumption. It was hypothesised that the presence of clay particles at the egg surface could influence oxygen consumption by two processes. First, clay particles are readily infiltrated into interstitial pore spaces (Frostick *et al.*, 1984; Sear 1993), the resultant accumulation within the egg incubation zone could reduce gravel permeability and inhibit the flux of oxygenated water to the egg surface. Second, clay particles are of similar or smaller diameter than the micro-pores in the egg chorion. Therefore, clay particles may potentially obstruct these respiratory canals inhibiting oxygen consumption.

6.2.2 Apparatus and methodology

Salmon egg respiration rates were measured within an incubation chamber composed of a Digital Model 10 Respirometer in conjunction with a 50ml Perspex electrode cell (Rank Brothers Ltd.). Dissolved oxygen concentrations were continuously recorded using a dual channel Model BD112 chart recorder. A magnetic stirrer ensured compete mixing within the incubation chamber and reduced the potential for zones of oxygen depletion to develop around respiring eggs. Temperature control was maintained via a Grant LTC6-40 cooled thermo-circulator (Figure 6.2.1). All tests were carried out on hatchery reared Atlantic salmon embryos and borehole water at 100% dissolved oxygen saturation was used as the incubation medium. Consumption rates were determined for eggs in the final stages of embryonic development. Assessing consumption at hatching provided an estimation of maximum rates of oxygen uptake and, therefore, maximum oxygen requirements. Embryonic development was assessed using an empirical temperature-development model (Crisp, 1992). Based on the model predictions, estimations of oxygen consumption were carried out on eggs beyond 95% development to hatching. Visual assessments of the eggs indicated that hatching was occurring within the experimental egg batch, verifying that the eggs were in the final stage of embryonic development.

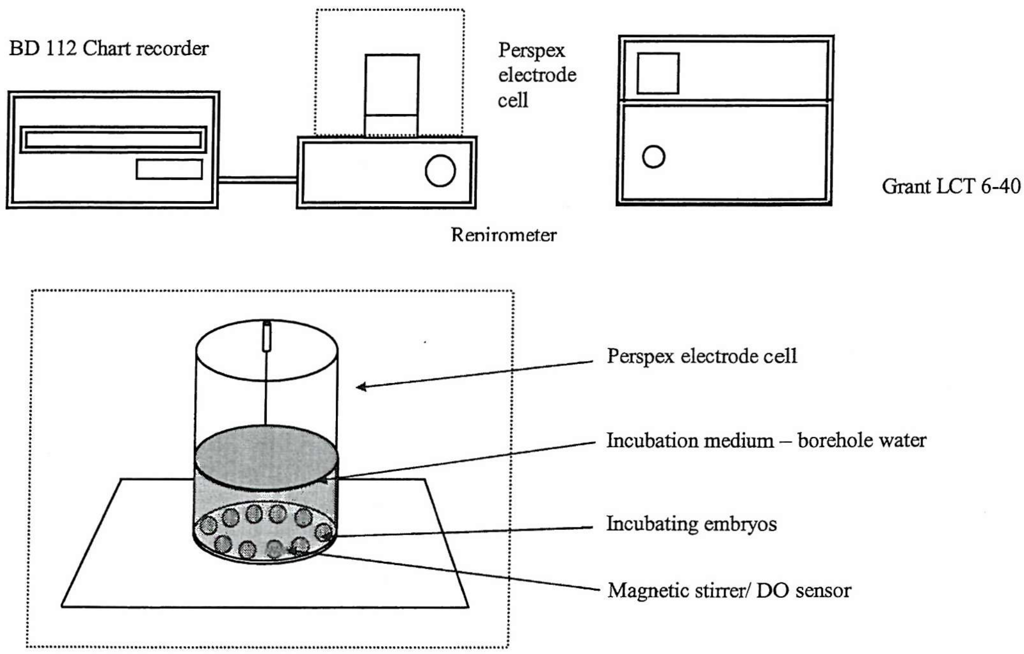


Figure 6.2.1 Overview of monitoring set-up.

Rates of oxygen consumption were assessed at 5°C. A water temperature of 5°C was selected to allow comparisons with previously reported consumption rates. Furthermore, 5°C is representative of UK river temperatures over the hatching period. Prior to assessment of oxygen consumption, eggs were measured and weighed. The average egg weight and diameter was 152 mg and 62 mm, respectively. All consumption rates were based on batches of ten eggs and were assessed over 30 minutes. The data output from the sampling equipment was in the form of continuous time trend plots of the decline in oxygen (% saturation) within the incubation chamber. The data was adjusted to hourly rates of embryonic consumption by converting recorded consumption rates to mg l^{-1} and dividing through by the number of eggs. The oxygen demand of the ambient water was also assessed and subtracted from the final consumption values. Finally, the oxygen demand of the clay material was assessed and found to be negligible. In total, oxygen consumption was assessed for six batches of eggs.

Once consumption rates were determined for eggs incubating in particle-free water, 0.3 g of inert clay sediment (Figure 6.2.2) was introduced to the incubation chamber. The action of the stirrer forced the clay material away from the oxygen probe membrane, removing any potential interference with the oxygen probe, and promoting particles to settle evenly over the embryos. The sediment formed an even film of sediment, <1mm in thickness, across the egg surface. Visual estimation of the surface coverage of sediment indicated that only small areas of egg surfaces (<20%) remained free from sediment. Once rates of consumption were determined for 0.3g, a further 0.2 g of sediment was introduced to incubation chamber. This additional sediment promoted complete egg coverage and increased the thickness of the sedimentary film to roughly 1mm. Rates of consumption were once again monitored. In total, four runs were carried out assessing the impact of clay particles on oxygen consumption.

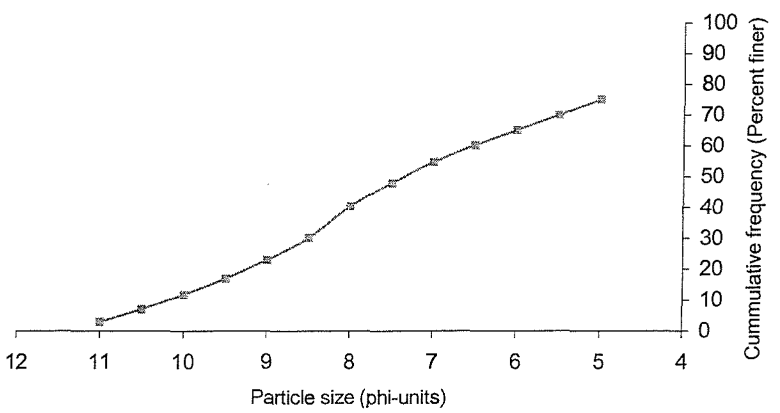


Figure 6.2.2 Particle size distribution of clay material. Based on coulter analysis of number of particles at ½ phi intervals.

6.2.3 Results and discussion

Calculated rates of embryonic oxygen consumption at hatching are shown in Table 1. Consumption rates ranged from 0.00282 mg O_2 egg^{-1} h^{-} to 0.0038 mg O_2 egg^{-1} h^{-1} and the mean consumption value was 0.00329 mg O_2 egg^{-1} h^{-1}. Generally, consumption rates recorded between batches were similar (standard deviation 0.0004). The small discrepancies recorded are indicative of marginally different stages of development, variations in consumption between different sized embryos and natural variability in consumption between embryos (Alderdice *et al.*, 1958; Silver *et al.*, 1963; Shumway *et al.*, 1964). Furthermore, in batches four and five, hatching occurred during the experiment, potentially resulting in slightly elevated consumption levels associated with breaking free from the egg capsule (Hamor and Garside, 1979).

Egg batch	1	2	3	4	5	6
O_2 consumption (mg 0_2 egg^{-1} h^{-1})	0.0028	0.0031	0.0024	0.0038	0.0036	0.0036

Table 6.2.1 Hourly oxygen consumption rates for batches of ten eggs incubated at 5°C. Consumption per egg based on hourly average of 10 eggs.

Table 6.2.2 highlights previously reported values of oxygen consumption. From Table 6.2.2, it is apparent that differences exist between reported rates of oxygen consumption. Broadly, the consumption values recorded in this study are in agreement with values recorded by Hayes (1951), Lindroth (1942), Alderdice *et al.* (1958) and Einum and Fleming (2003). The slight variations are potentially explained by small differences in stage of embryonic development and variations in egg size, which are not comprehensively detailed in the literature. For instance, the lower consumption rates reported by Einum and Fleming (2003) were on eggs defined as 'well eyed' and, therefore, may have been at an earlier stage of development than the eggs used in this study.

In contrast, the consumption rates recorded in this study are approximately an order of magnitude lower than those reported by Hamor and Garside (1979). Hamor and Garside (1979) were aware of the disparity between their results and those of previous studies, and provided a potential explanation for this discrepancy. Early assessments of oxygen consumption rates were carried out in closed systems in which the oxygen concentration of the ambient water declined over time as oxygen was consumed by incubating embryos. Hamor and Garside (1979) suggested that this decline in concentration may have reduced the oxygen available to incubating embryos, resulting in reduced consumption. Hamor and Garside (1979) circumvented this problem by incubating eggs in an open system in which the water was continually re-aerated.

Although a closed system was used in this study, reductions in oxygen concentration at the egg surface were avoided by adopting short run times and installing a magnetic stirrer within the incubation chamber. Maximum run times were 30 minutes. This resulted in ambient oxygen concentrations within the incubation chamber remaining above 10 mg l^{-1}. The magnetic stirrer promoted mixing within the incubation chamber, thus avoiding the development of zones of oxygen depletion at the egg surface. Similarly, although Einum and Fleming (2003) evaluated rates of oxygen consumption in a closed system, their incubation chambers were rotated every 8 hours, thereby avoiding the development of oxygen gradients. It is suggested that further investigation is required to assess the variations in reported rates of embryonic oxygen consumption.

Species	**Temperature (°C)**	**Stage of development**	**Relative developmental stage**	**Oxygen consumption (mg 0_2 egg^{-1} h^{-1})**	**Reference**
Chum salmon	10	Day 12	0.24	0.0009	Alderdice *et al.* (1958)
	10	Day 27	0.52	0.0022	
	10	Day 46	0.77	0.0053	
Atlantic salmon	5.5	'Domed'	0.5*	0.0014	Lindroth (1942) cited in Fry (1957)
	5	'Prior to hatch'	0.9*	0.0039	
	17	'Hatching'	0.99*	0.0067	
	10	'Eyed'	0.5*	0.0010	Hayes (1951)
	10	'Hatching'	0.99*	0.0048	
	10	Day 1	0.02**	0.0013	Hamor and Garside (1979) (From graphical data)
	10	Day 10	0.22**	0.042	
	10	Day 20	0.44**	0.025	
	10	Day 30	0.66**	0.02	
	10	Day 40	0.88**	0.042	
	10	Day 45	0.99**	0.048	
	5	Day 5	0.06**	0.007	
	5	Day 40	0.47**	0.0141	
	5	Day 60	0.71**	0.0141	
	5	Day 85	0.99**	0.031	
	4.8	'well eyed'	0.5-0.9*	0.0012	Einum and Fleming (2003)

Table 6.2.2 Comparative data set of embryonic oxygen consumption. *Relative development estimated from development description provided in the reference. ** Relative development estimated from graphical data provided in the reference.

The introduction of clay particles and the development of a thin film of sediment across the egg surface reduced the consumption of oxygen from the surrounding ambient environment (Figure 6.2.3). The addition of 0.3 g of fine clay material reduced consumption to between 0.00129 mg O_2 egg^{-1} h and 0.00139 mg O_2 egg^{-1} h. This equates to an average reduction in consumption of 0.00195 or 41%. The addition of an extra 0.2 g of sediment further reduced oxygen consumption, and recorded consumption ranged from 0.0007 to 0.00002 mg O_2 egg^{-1} h. This equates to a total drop in consumption of 96% compared to particle-free water. The differences in consumption recorded between the addition of 0.3 g and 0.5 g of sediment are conjectured to result from differences in sediment coverage and thickness across the egg surface. The addition of 3 g of sediment left a small portion of the egg surface free from sediment, which may have allowed the egg to continue consuming oxygen at a slightly greater rate than under conditions of complete surface coverage.

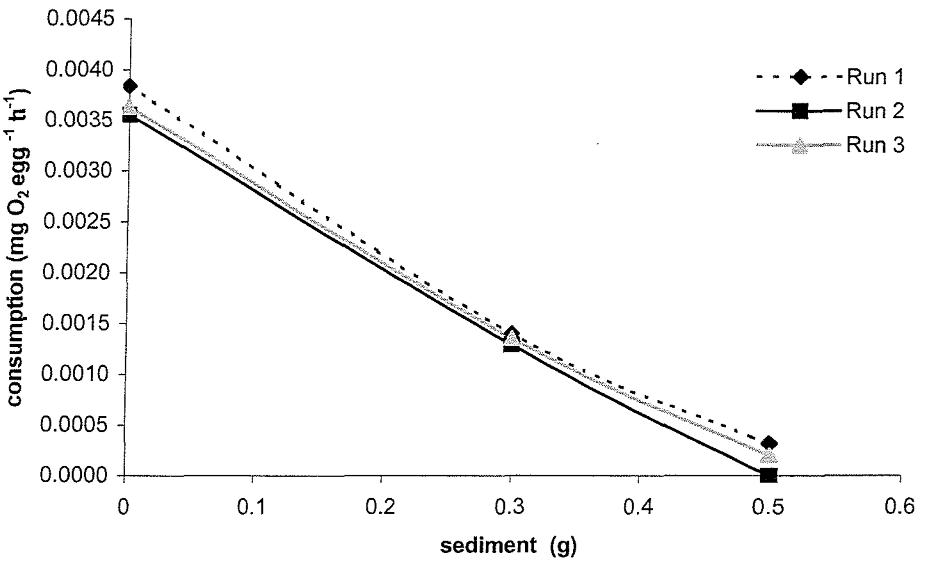


Figure 6.2.3 Impact of clay particles on oxygen consumption.

Two explanations for the recorded drop in consumption are proposed. First, the clay particles created a zone of reduced oxygen supply around the eggs. The presence of the clay film created a zone of low permeability (k = 10^{-8} to $10^{-9}ms^{-1}$) around the incubating eggs. It is probable that this low-permeability clay layer would have restricted advective driven oxygen supply. Similarly, although clay is highly porous medium, the low permeability and high tortuosity of the pore geometry, would have reduced the rate of oxygen diffusion to, and across, the boundary layer surrounding the eggs. Fick's First Law, which describes the diffusion of a substance through a given cross section of unit time, can be used to assess the potential supply of oxygen through the clay layer. Fick's First Law is expressed as:

$$F = -D\frac{dC}{dx} \quad (6.2.1)$$

where F, which is the mass flux, is the unit of solute per unit area time (M $L^{-2}T^{-1}$); D is the diffusion coefficient (L^2T^{-1}); C is the solute concentration (M L^{-3}); and dC/dx is the concentration gradient over a distance x. In porous material, the elongated flow paths, which result from the presence of particles, and the influence of adsorption onto solids will reduce the diffusion coefficient relative to diffusion through particle free water. The apparent diffusion coefficient (D^*) for non-adsorbed material in porous substances is represented by:

$$D^* = \omega D \quad (6.2.2)$$

where ω is an empirical coefficient that compensates for the solid phase of the porous media on diffusion. Laboratory studies of the diffusion of non-absorbed ions in porous materials commonly report ω values of between 0.5 and 0.01. The diffusion coefficient of oxygen through a salmonid egg membrane has been estimated to be of the order 1×10^{-6} cm^2 s^{-1} (Daykin, 1965). This compares with the diffusion coefficient of water, which is of the order 1×10^{-5} cm^2 s^{-1}. Given that clay has a ω of 0.01 (Yanful, 1994), the diffusion coefficient of the clay film is estimated to be 1×10^{-7} cm^2 s^{-1}. This is less than the diffusion coefficient of the egg membrane, therefore, it is probable that cutaneous exchange of oxygen across the egg chorion was impaired by the presence of the clay film.

It is suggested therefore, that the clay film reduced advective and diffuse exchange of oxygen from the macro-environment to the egg boundary layer. The acute drop in consumption recorded in the presence of the clay film, potentially indicates that the rate of oxygen supply to the boundary layer was lower than the rate of consumption by the incubating embryos, resulting in an insufficient oxygen gradient to support respiration.

The second conjecture regarding the impact of clay particles on oxygen consumption concerns the physical blocking of pore canals in the egg chorion. The chorion, or cell wall, is composed of tough ichthulokeratin perforated by mirco-pore canals that permit oxygen to diffuse through the eggs tough outer shell. Micrographs of the egg surface suggest that the total area of canals is roughly one tenth the total egg surface area, and that the pore canals are between 0.5 and 1.5 microns in diameter (Bell *et al.,* 1968) (Figure 6.2.4). It is suggested that fine particles can physically obstruct these pore canals and restrict the transport of oxygen across the cell membrane. A comparison of the size of pore canals with the size of clay particles introduced to the incubation chamber (Figure 6.2.2), indicates that the clay material potentially contained particles which were less than or equal to the size of the pore canals. It is possible, therefore, that clay particles block or penetrate the pore canals, thereby restricting the passage of oxygen across the egg membrane. Unfortunately, the monitoring apparatus used in this study did not allow delineation between the two processes potentially restricting consumption.

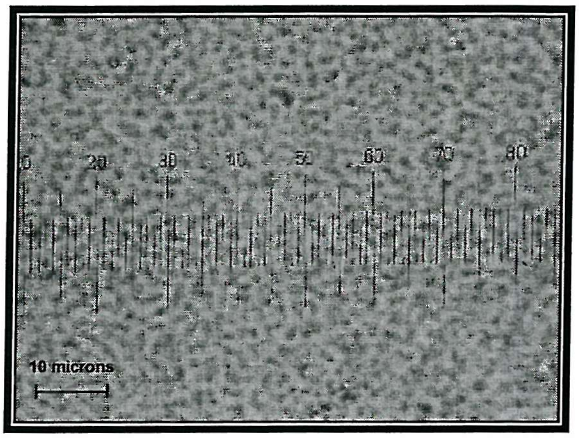


Figure 6.2.4. Micrograph of egg surface. Dark areas indicate pore canal. One unit on the scale represents 1 micron.

Typical values for the percentage of clay (by weight) within U.K. spawning gravels are available from the literature (Carling and Reader, 1982; Milan *et al.*, 2000). Generally, levels attain values in the range of 0.1-6% (mean 0.7%) at depths of 0-0.15m and 0.1-8.0% (mean 1.2%) at depths below 0.15m. Importantly, clay particles are mobile even at low discharge (Sear, 1993), and may penetrate deep into the interstices of freshly cut gravels (Frostick *et al.*, 1985). Consequently, there may be a propensity for clay sized materials to accumulate within the base of salmon redds during the weeks directly post redd creation, thereby, inducing environmental conditions that may impede oxygen consumption by one or both of the mechanisms discussed above.

6.2.4 Summary

It is concluded that relatively small accumulations of clay-sized materials can severely restrict the passage of oxygen to and/or across the chorion of incubating salmonid eggs. It is therefore proposed that when assessing incubation habitat quality or developing metrics of survival, increased consideration is given to the detrimental impacts of clay-sized particles. With respect to future research, it is suggested the application of microelectrode oxygen probes may provide a means to detail the oxygen characteristics of the microenvironment surrounding incubating embryos, thereby allowing delineation of the precise mechanism by which fine materials inhibit consumption.

6.3 Investigation into the influence of surface flow on subsurface flow patterns and intragravel flow velocities

The following section details the results of a flume investigation into the influence of surface flow conditions on intragravel flow paths and velocities. Field data supporting the flume observations is presented, and implications for salmonid incubation success are discussed.

6.3.1 Introduction

The interaction of surface and subsurface water at the riverbed interface is recognised as an important process influencing biogeochemical exchanges between surface water and the hyporheic zone (Packman and Bencala, 2000). Furthermore, the flux of oxygenated water through spawning gravels is an important factor influencing incubation success of salmon embryos and alevins (Bjorn and Reiser, 1997) (Section 6.1). Current awareness of processes controlling the exchange and passage of water with riverbeds suggests that the rate of exchange, and subsequent flow through the streambed, is controlled by two mechanisms: pressure driven exchange and turbulent momentum exchange (Section 3.2 provides a detailed description of exchange processes). To summarise, topographic features or changes in bed permeability induce pressure fields at the bed surface that drive flow into and through the bed (Vaux, 1968; Savant *et al.*, 1987; Harvey and Bencala, 1993). Turbulent momentum exchange induces a slip velocity at the bed surface that promotes a velocity gradient within the riverbed (Shimizu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Packman and Bencala, 2000).

Based on the influence of surface flow, flow within the gravel substratum of a riverbed may be defined as dependent or independent of surface flow. The independent portion is driven solely by pressure gradients and bed permeability and can be described by Darcian principles. The dependent portion of stream flow is influenced by turbulent mixing and momentum exchange and is non-Darcian. The penetration depth of non-Darcian flow has been quantified for homogenous porous medium over a flat bed, and has been shown to be within the range 0.05 to 0.1 m. (Shimizu *et al.,* 1990; Packman and Bencala, 2000). However, to date the interaction of turbulent momentum driven and pressure driven exchange has not been assessed. Similarly, the influence of bed entrainment on the exchange of surface water with the riverbed has not been investigated. It is probable that bed entrainment, and the consequent transient lowering of the bed surface, will result in increased penetration depths of surface water into the riverbed.

The purpose of this study was to investigate the influence of surface flow on subsurface flow patterns. Applying mini-peizometers and dilution techniques, hydraulic head and intragravel flow velocities were assessed across a sinusoidal wave bedform and across a flatbed under varying discharges. Data recovered from the field sites was then analysed to investigate exchange processes in the natural river environment, including the influence of gravel entrainment.

6.3.2 Methods

6.3.2.1Flume study

A re-circulating hydraulic flume was used to investigate the influence of discharge on subsurface flow (Figure 6.3.1). The flume had a working length of 21.4m, a width of 1.37m and a depth of 0.61m. The flume was equipped with three electrically driven centrifugal pumps, with individual pump capacities of 0.09, 0.15 and 0.23 m^3 s^{-1}, providing a maximum flow capacity of 0.47m^3 s^{-1}. Two annular flow meters attached to the inlet pipes monitored the discharge, measuring to within 0.001m^3 s^{-1}. The slope of the flume was set to 0.12°. Flow was assessed through two morphological features: flat bed and sinusoidal wave (Figure 6.3.2). The sampling zones were composed of a well-sorted mixture of sand, grit and gravel. The depth of gravel ranged from 0.5 m across the crest of the dune and 0.4m across the flat bed. In the non-sampling zones, the bed was composed of an unsorted mixture of sand and gravel.

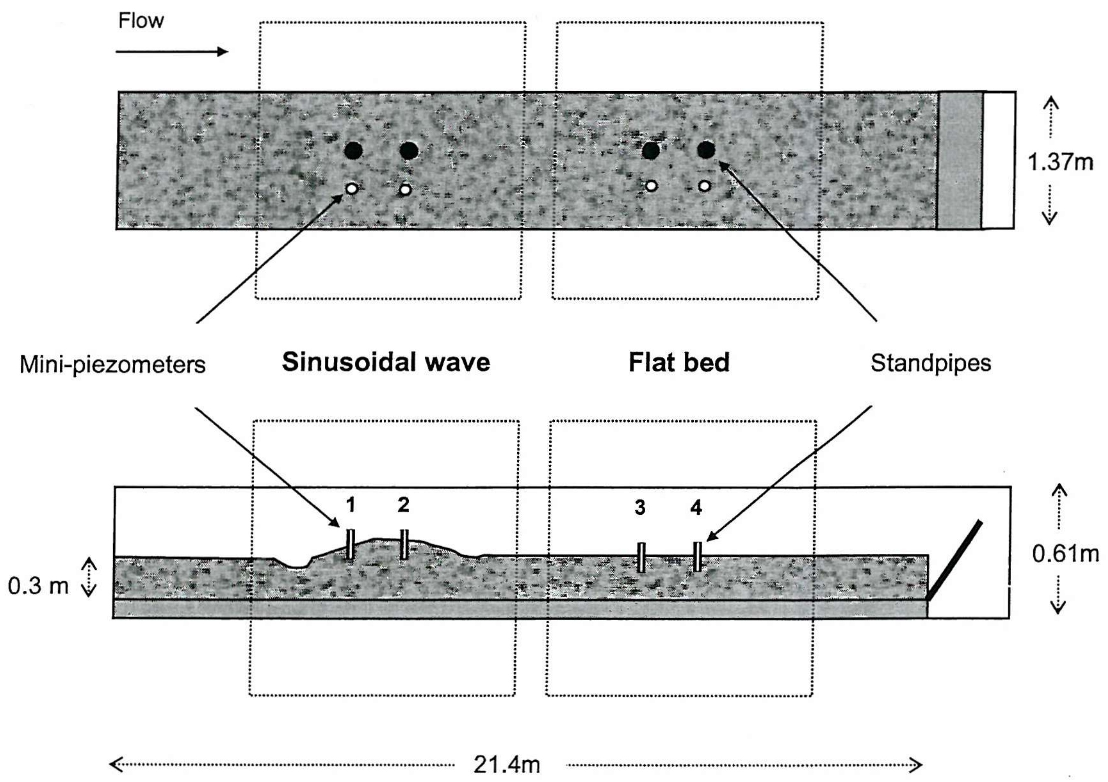


Figure 6.3.1 Simplified diagram of flume set-up (not to scale).

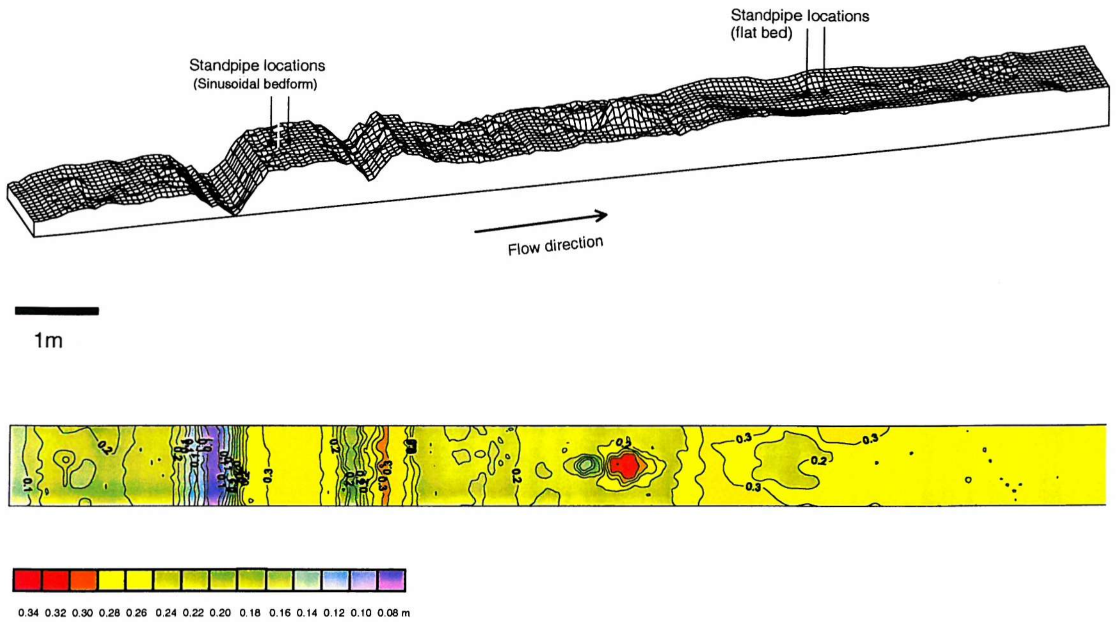


Figure 6.3.2 Topographic summary of gravelbed (flume).

Two standpipes located in each sampling section provided access points for monitoring the intragravel environment. The standpipes were of the same design outlined in Section 6.1 and were inserted to a depth of 25 cm to represent typical egg burial depths. Intragravel flow velocity was assessed using the recalibrated conductiometric standpipe technique, as detailed in Appendix 1. After the final run, gravel permeability was assessed at each sampling location using the standard pump test method. As the standpipes were of similar dimensions to those used by Carling and Boole (1986), all permeabilities were converted from pumping rate (Q) to Darcian permeabilities (K) by applying an equation developed by Carling and Boole (1986):

$$\ln K = 7.7416 - 0.5804[\ln (4.61 - \ln Q) - \ln (\ln Q)] \quad (5.3.1)$$

The intragravel movement of fine sediments has been reported (Sear, 1993). Therefore, there was concern that under high discharges and consequent high intragravel flow velocities, the subsurface movement of fine sediments may influence gravel permeability and intragravel flow velocities. To assess whether intragravel movement of fine sediments was influencing permeability and intragravel flow, the experiment was repeated running from high to low discharges and the intragravel flow and permeability results were compared.

To assess trends in hydraulic head across the sampling features, two mini-piezometers were deployed in upstream and downstream locations within each sampling section (Baxter *et al.*, 2003). For a description of the piezometers, the reader is referred to Section 5.4. To allow accurate determination of changes in hydraulic head, each piezometer was connected to a manometer and the difference in hydraulic head between the surface and subsurface environment were recorded. Portable mini-piezometers were also inserted into the standpipes to allow additional assessments of hydraulic head across each sampling feature. Intragravel flow velocity and hydraulic head were assessed at five discharges: 0.01, 0.02, 0.04, 0.08 and 0.1 $m^3 s^{-1}$. Three replicates were carried out at each location for each discharge. In total 38 measurements were taken over the range of discharges.

Darcy's law was applied to estimate the average Darcian intragravel flow velocities across the sampling features:

$$v = -K\frac{\Delta h}{\Delta l} \qquad (6.3.1)$$

where v is apparent velocity (ms^{-1}), $-K$ is the hydraulic conductivity (also referred to as permeability) and Δh is the difference in hydraulic head over the distance Δl. Volumetric displacement analysis was performed on gravel sub-samples to determine porosity. All discharges were then multiplied by porosity to estimate intragravel flow velocities.

6.3.2.2 Field study

The field study, which was integrated within the larger monitoring programme (Section 5.5), comprised of an assessment of surface flow conditions during the motoring period and an analysis of temporal differences between surface and intragravel water temperatures. At the River Ithon, an Environment Agency Gauging Station (55011) supplied discharge data. At the remaining field sites, stage discharge curves were developed for three of the study reaches using standard handbook estimation based on the Manning's roughness formula (Table 6.3.1). A relationship was developed between the stage measured at the pressure transducer, and the cross-section area (A), Hydraulic radius (R), and Slope (S) measured at 0.1m increments. Mannings n was determined on the following basis:

1) Wherever possible values were back-calculated from the measured discharge/Area/Slope (e.g. two values from the Test at intermediate stage flows).

2) Other locally derived values from study rivers (e.g. low flows for a similar reach of the Test were available, together with higher flows based on work of Acornley (unpublished); n values were available for another reach of New Forest stream (Highland Water – Booker, 2001) from low-bankfull discharges.

3) Where no such data was available and as a check against the measured values, Cowans (1956) method of estimating n was applied to estimate bankfull n roughness values. Low flow roughness values were estimated based on the grainsize distribution of the bed sediments using Stricklers (1923) approach ($n = 0.0151D_{50}^{1/6}$). The changes in n between these values were then interpolated (e.g. Aran). Discharge data was available from a gauging station located immediately upstream of the study reach for the Ithon.

Site	**Discharge (m^3s^{-1})**	r^2
Test	$Q = 36.347S^2+7.0574S+1.5075$	0.987
Blackwater	$Q = 6.0025S-0.900$	0.963
Ithon	Measured at EA Gauging Station	
Arran	$Q = 6.9961S^2+1.5432S-0.0348$	0.998

S = stage (m), Q = discharge (m^3s^{-1})

Table 6.3.1 Rating equations for discharge and suspended sediment concentration

As detailed in Section 5.4, water temperatures can used to identify the presence of groundwater within the riverbed. Applying the same principles, it was hypothesised that temperature could also be used to determine the temporally variable exchange of surface water with the riverbed. Thermister columns connected to Delta-T™ data loggers were located in sections of concave (riffle) bed morphology. Figure 6.3.3 shows the longitudinal profiles of sampling reaches into which the thermister columns were deployed. The profiles are based on cross sections through the topographic survey maps (Section 5.3). The linear regression models fitted to the data points define pool and riffle features. Water temperatures were recorded at 15 minute intervals at five depths: surface water and at 0.1m, 0.2m, 0.3m and 0.4m into the riverbed (Acornley, 1999) (Figure 6.3.4). Temporal trends in the difference in water temperature between surface water and water at a depth of 0.4m into the riverbed were then compared with discharge over the same period. Under low flow conditions, a natural temperature gradient, resulting from the buffering effect of the overlying gravels, or from inputs of high temperature groundwater, should be observed (Malcolm, *et al.*, 2003; Maddock, *et al.*, 1996). If increased exchange occurs under high flow events, a synchronous reduction in this natural temperature gradient should be observed (Malcolm et al., 2003).

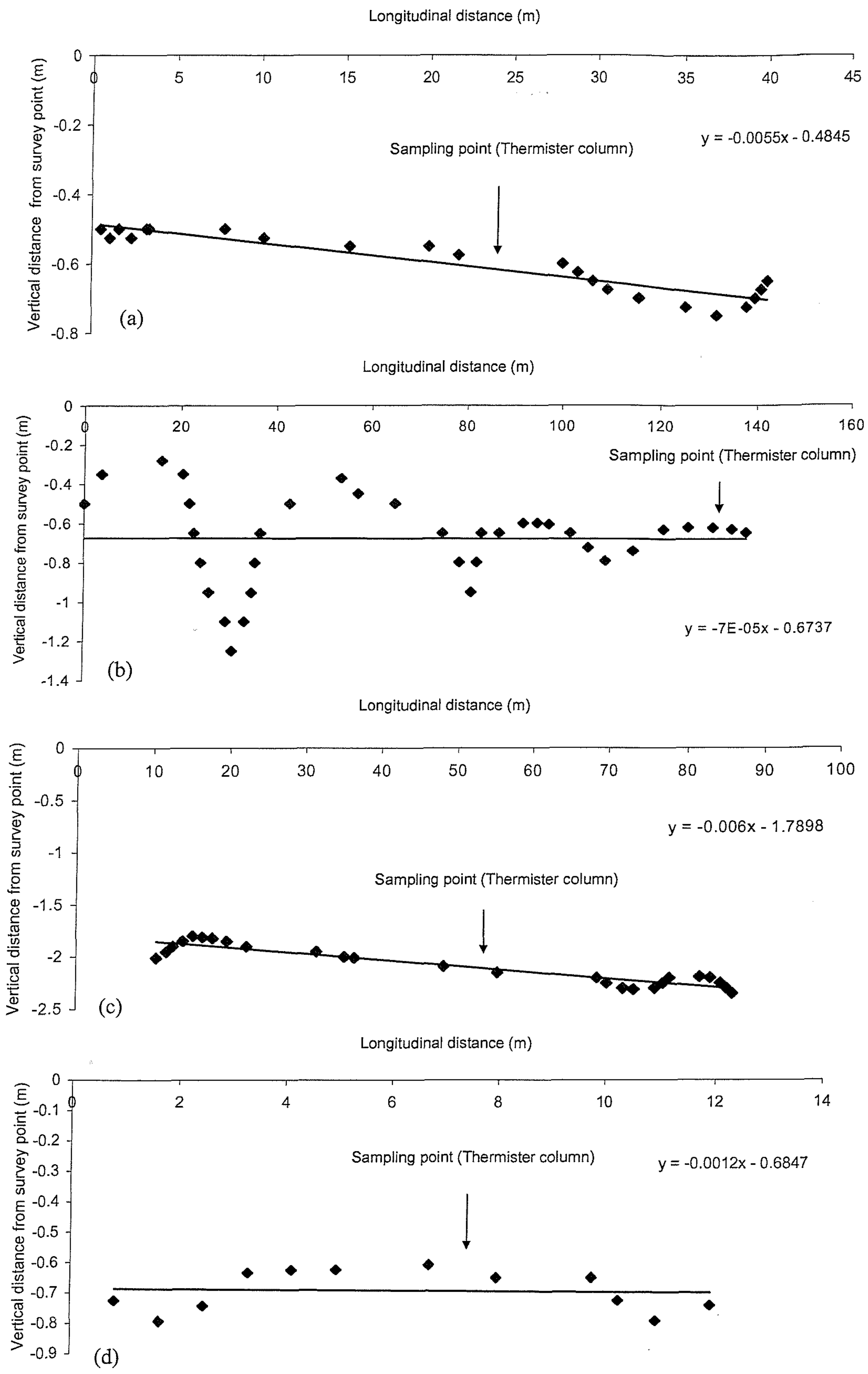


Figure 6.3.4 Longitudinal profiles of sampling reaches in which the thermister columns were located. Profiles created from cross sections through the topographic survey maps. Linear regression models were used to define pool and riffle features. Areas above the line represent riffles, and areas below the lines represent pools. (a) River Test, (b) River Blackwater, (c) River Ithon, (d) River Aran.

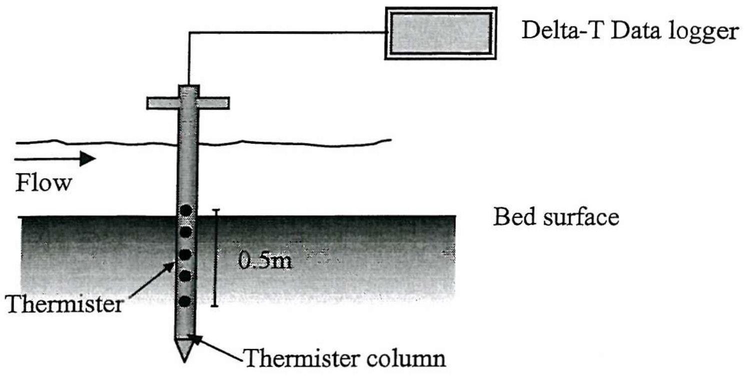


Figure 6.3.5 Monitoring set up for quantifying temperature gradient between surface water and 0.4m depth into the riverbed.

Finally, bed load pit traps were installed at each field site (Figure 6.3.6). The bed load traps, which were also connected to the Delta-T loggers, used pressure sensors to record the movement of riverbed gravels (Sear *et al.*, 2000). When riverbed gravels are entrained, they are deposited into the bedload trap. The load cell, which is pre-calibrated for weight, records the amount of material that accumulates in the trap over time. Integration of the surface flow data with the bedload data allows delineation of gravel entrainment thresholds. The entrainment thresholds are defined by locating the discharges that result in a rapid increase in the rate of infilling of the bedload trap (*Sear et al.*, 2000).

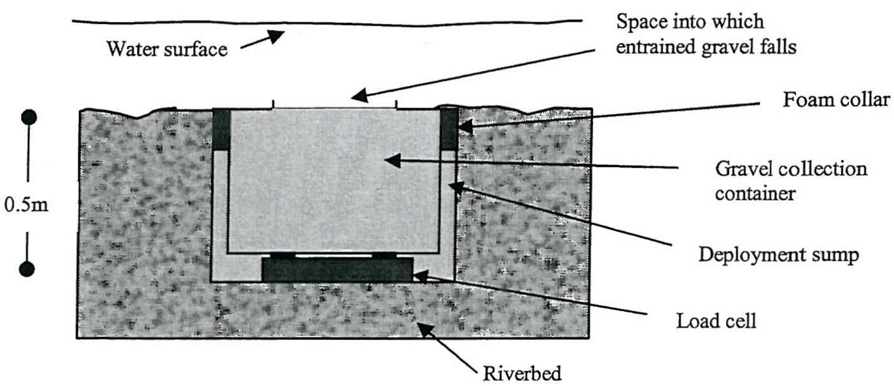


Figure 6.3.6 Schematic of bedload trap deployed at the field sites.

6.3.3 Results and analysis

6.3.1 Intragravel flow paths

At each sampling location, surface flow conditions influenced hydraulic head (Table 6.3.2). To summarise, across the sinusoidal wave bedform, at low flow (0.01 $m^3 s^{-1}$) upwelling was recorded at locations 1 and 2. At a discharge of 0.02 $m^3 s^{-1}$, hydraulic head at the upstream face of the waveform (location 1) switched from upwelling to downwelling. On the downstream face of the bedfrom (location 2) increased upwelling was recorded. At increasing discharges thereafter, increased downwelling was recorded at location 1 and slight increases in upwelling were recorded at location 2. The observations from the mini-piezometers are in agreement with observations of the difference in hydraulic head recorded between the standpipes located in the across the sinusoidal bedform (Table 6.3.3). Less variation in hydraulic head was recorded across the flatbed. Generally, the mini-piezometers recorded slight downwelling through the flatbed. At increasing discharges, a slight increase in downwelling was recorded at location 4. A similar response was observed within the standpipes. Based on the hydraulic gradients recorded between the sampling locations, Figure 6.3.7 summarises the effect of discharge on hydraulic head.

Discharge ($m^3 s^{-1}$)	Riffle L1	Riffle L2	Flatbed L3	Flatbed L4
0.01	2	7	-2	-1
0.02	-1	7	-2	-1
0.04	-2	10	0	-2
0.08	-4	10	0	-3
0.1	-5	12	0	-4

Table 6.3.2 Difference in hydraulic head (mm) between surface and 0.25m depth into gravel medium. All hydraulic head measurements in mm.

Discharge ($m^3 s^{-1}$)	Riffle ΔL1-L2[1]	Flatbed ΔL3-L4[1]	Riffle ΔL1-L2[2]	Flatbed ΔL3-L4[2]
0.01	5	1	5	1
0.02	8	1	8	1
0.04	14	-2	11	-1
0.08	16	-3	13	-2
0.1	17	-4	15	-3

Table 6.3.3 Difference in hydraulic head between sampling locations. [1]Based on permanent mini-piezometers. [2]Based on mobile min- piezometers placed in standpipes.

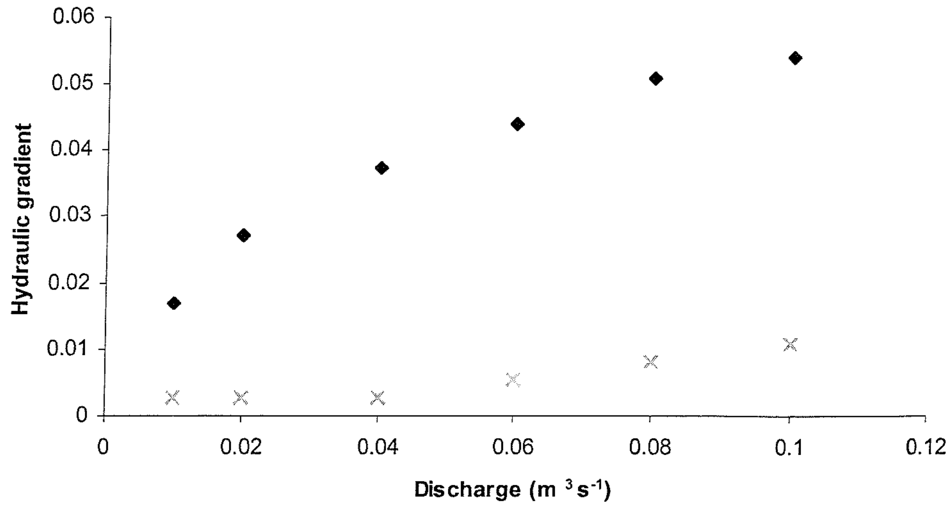


Figure 6.3.7 Variation in hydraulic gradient across the flat bed and sinusoidal wave under varying discharges. ◆ Hydraulic gradient across sinusoidal wave (L1-L2), ✕ Hydraulic gradient across flatbed (L3-L4).

6.3.3.2 Intragravel flow velocity

Increases in intragravel flow with discharge were recorded at all sampling locations. The greatest increase was recorded at sampling location 1 (upstream face of the sinusoidal wave form). Also plotted on Figure 6.3.8 is the relative change in velocity estimated using Darcy's law. Across the sinusoidal waveform, the large changes in hydraulic gradient with discharge resulted in consequent increases in intragravel flow velocities estimated from Darcian principles. The smaller changes in hydraulic head with discharge across the flatbed resulted in smaller increases in velocity estimates using Darcy's Law.

Finally, also shown on Figure 6.3.8 is the mean velocity (conductiometric standpipe) estimated between the two standpipes in each sampling zone. Comparison of this spatially averaged data with the spatially averaged Darcian velocities allowed an assessment of the potential magnitude of non-Darcian driven flow. Across the sinusoidal wave, the velocities estimated applying Darcy's Law were roughly three times lower than those estimated using the conductiometric standpipes. Across the flatbed the Darcian velocities were roughly six times lower than those estimated with the conductiometric standpipe.

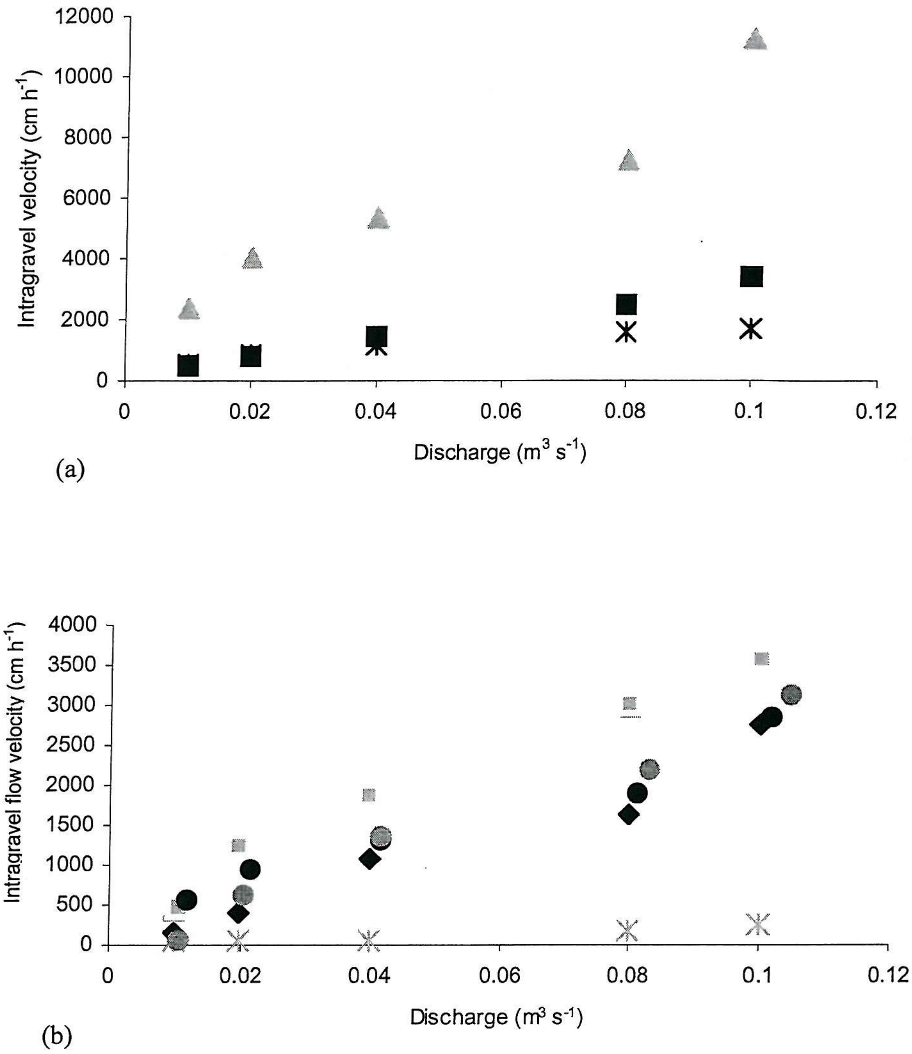


Figure 6.3.8 Variations in intragravel flow velocity recorded across the (a) sinusoidal bedform and (b) flatbed. Also shown are the velocities between the sampling locations estimated from Darcy's Law.

▲ Velocity (L1) ■ Velocity (L2) ■ Velocity (L3) ◆ Velocity (L1) ● Average velocity (L1-L2)
● Average velocity (L3-L4) ✱ Darcian velocity (L1-L2) ✳ Darcian velocity (L3-L4)

6.3.3 Field observations

Figure 6.3.9 outlines the hydrological regimes at each field site over the monitoring period[5]. The River Test maintains a stable hydrological regime over the incubation period. Consequently, one would expect limited temporal variability in pressure and turbulent driven coupling of surface and subsurface water. Consequently, conditions within the incubation zone will be influenced primarily by the influx of materials over the incubation period. At the freshet field sites, flashier hydrologic responses were recorded over the incubation period. Based on the flume observations of increased downwelling and intragravel flow velocities during high flow events, one would expect increased coupling of surface and subsurface flow during the high flow events at these field sites, resulting in temporal fluctuations in intragravel conditions that may not be observed from monitoring solely at low flow.

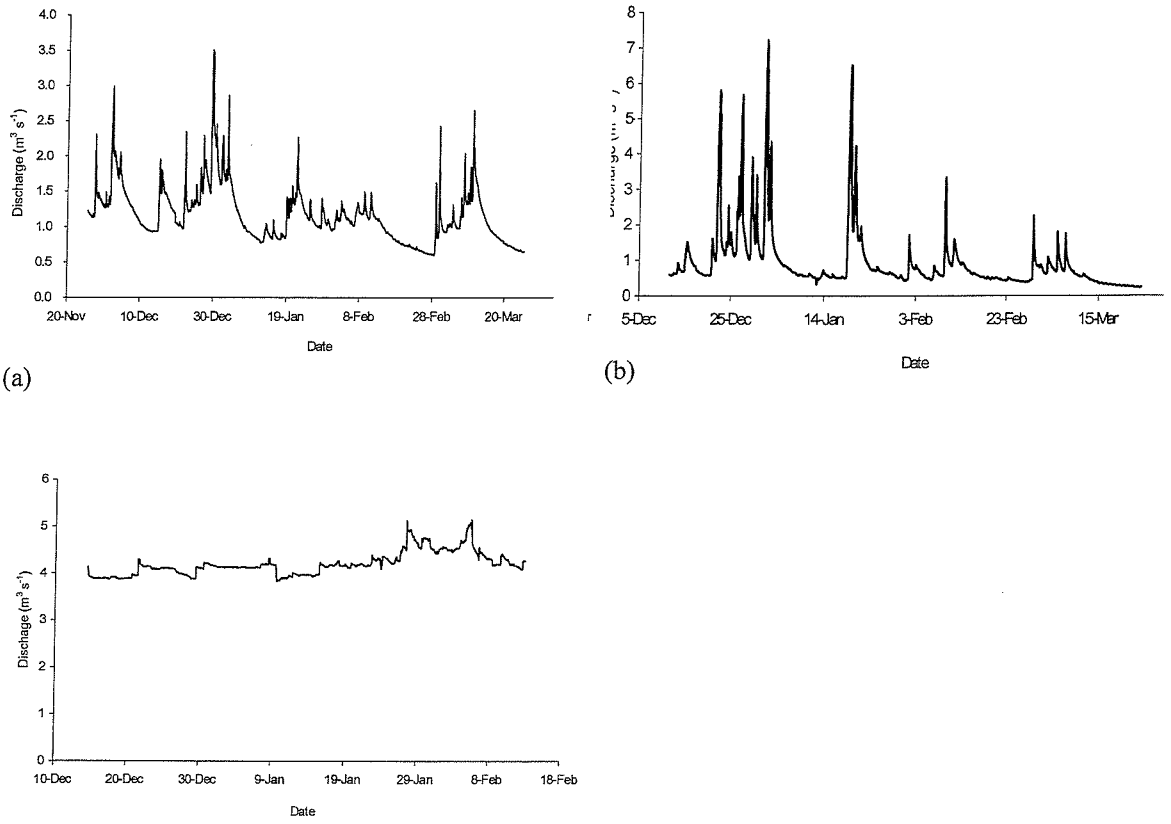


Figure 6.3.9 Discharges ($m^3\ s^{-1}$) recorded over monitoring period. (a) River Blackwater, (b) River Aran, (c) River Test.

[5]The temperature logging equipment was damaged at the River Ithon, consequently, the data set has been omitted from the analysis

Figure 6.3.10 outlines temporal variations in the difference in temperature between surface water and water at 0.4m depth into the riverbed. Also displayed is the discharge recorded at each field site. As highlighted in Figure 6.3.7, during high flow events at the River Aran and Blackwater, there is a concurrent decrease in the difference in temperature between surface water and water at a depth of 0.4m into the riverbed, potentially suggesting increased exchange and deeper penetration of surface water into the riverbed during these periods. The high frequency fluctuations in temperature gradient between surface and subsurface flow that exist within the broader temperature pattern described above, potentially result from temperature lag effects and the buffering capacity of the overlying gravels (Malcolm, *et al.*, 2002; Maddock, *et al.*, 1996). Temperature lag effects may also explain the reductions in temperature gradient recorded in the absence of changes in surface flow conditions. Rapid charges in surface water temperature that match the lagged temperature adjustment within the riverbed, may result in an artificial reduction in temperature gradient that reflects a coincident, but unconnected, change in surface and subsurface water temperatures.

The River Test, which has a stable hydrologic response characteristic of groundwater-dominated systems, displays little variation in the difference in temperature between the surface and 0.4m depth into the riverbed beyond those resulting from the temperature lag induced by the buffering effect of the overlying gravels (Figure 6.3.10).

To investigate the flow thresholds required to induce increased exchange of surface water with the riverbed, variations in the magnitude of the difference in temperature between the surface water and water at 0.4m depth were assessed at different flow ranges (Figure 6.3.11). As negative and positive temperature differentials were recorded, only the absolute temperature differential was assessed. As detailed in Figure 6.3.11, below the 50% exceedance flow at each field site, the difference in temperature between the surface water and water at 0.4m depth into the river bed is fairly constant. However, above the 50% exceedance flow, the difference in temperature between surface water and water at 0.4m depth reduces, suggesting displacement of either longer residence, thermally buffered hyporheic water, or groundwater.

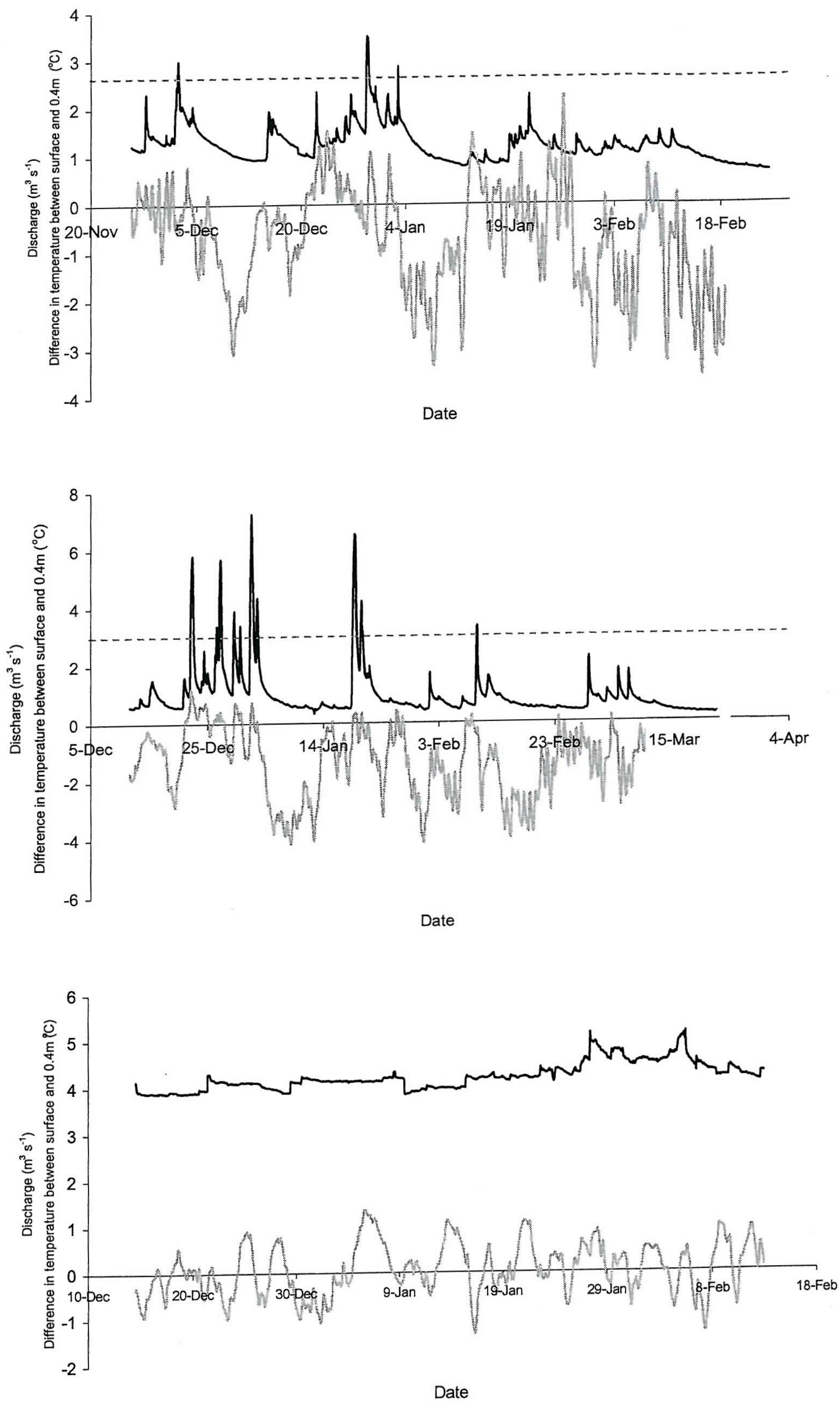


Figure 6.3.10 Temporal variations in thermal gradient between surface water and water at a depth of 0.4m into the riverbed. (a) River Aran, (b) River Blackwater, (c) River Test. Discharge —— ; Temperature difference —— ; Bed entrainment threshold - - - .

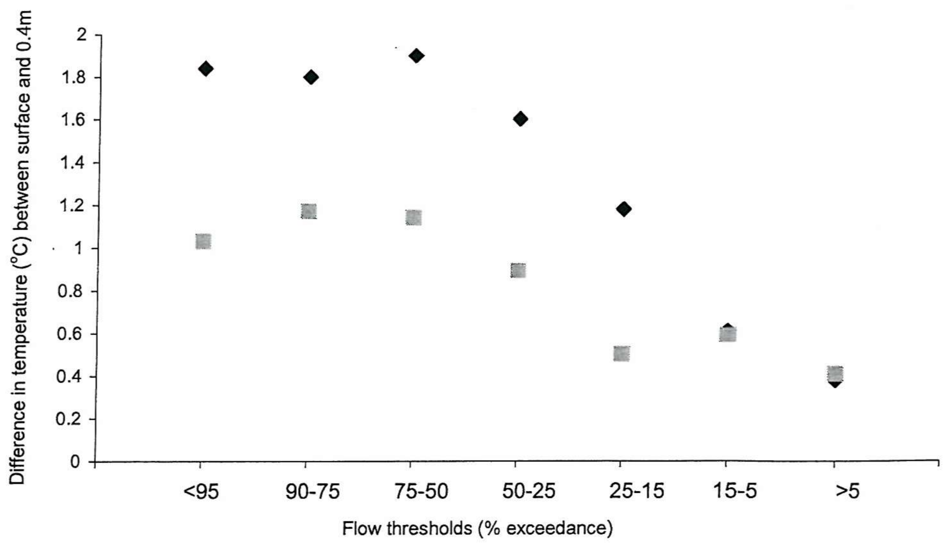


Figure 6.3.11 Influence of discharge on the absolute temperature differential between surface waster and water at 0.4m depth. ◆ River Blackwater, ■ River Aran.

Finally, to assess the influence of bed mobility on surface-subsurface exchange, the gravel entrainment thresholds estimated from the bedload traps were calculated and compared with the temporal fluctuations in temperature gradient between surface and subsurface water[6] (Figure 6.3.10). It was conjectured that gravel entrainment would lower the effective bed surface height, and result in deeper penetration of surface water into the riverbed. At the River Aran, the gravel entrainment threshold was briefly exceeded on two occasions over the study period. However, although synonymous with periods of reduced thermal gradient, there was insufficient data to perform a statistical analysis to distinguish between the effect of gravel entrainment and the influence of increased surface-subsurface exchange during the concurrent period of high flow. At the River Blackwater, bed entrainment thresholds were exceeded more frequently than at the River Aran. Once again, these entrainment periods were generally synonymous with periods of reduced thermal gradient. An assessment of differences in the magnitude of the thermal gradient during periods of high flow (25-15% exceedance flow), and periods of high flow and gravel entrainment (two sample t-test)[7], did not identify a significant difference at the 0.01 confidence limit. Therefore, with the data available, it was not possible to distinguish between the effect of gravel entrainment and the influence of hydraulically driven increases in surface-subsurface exchange during periods of high flow.

[6] Bed entrainment was not recorded at the River Test; therefore the analysis is restricted to the River Aran and River Blackwater.
[7]As it was not possible to asses the same discharges above and below the bed entrainment threshold, the analysis was carried out on a range of discharges above and below the threshold, but within the 25-15% flow exceedance range.

6.3.4 Discussion

6.3.4.1 Subsurface flow paths

Based on the hydraulic head information recovered from the mini-piezometers, it is apparent that surface flow conditions influenced intragravel flow paths. Across the sinusoidal bedform, the general intragravel flow trend was for downwelling to occur at the upstream face and upwellng to occur at the downstream face. This trend is characteristic of flow through sinusoidal features (including dunes, salmon redds and riffles) (Cooper, 1965; Vaux, 1968; Savant *et al.*, 1987; Thibodeaux and Boyle, 1987; Harvey and Bencala, 1993). Typically, sinusoidal features induce downwelling in the zone of increasing velocity at the upward incline. At the crest, the pressure differential declines and lateral flow may be observed. Finally, a negative pressure differential on the lee of the dune induces an upwelling return flow. Across the flat bed, downwelling was the dominant flow path. This flow trend was conjectured to have been an artefact of the flume set-up. The lowered tailgate induced a 0.02 m drop in stage between the upstream and downstream sampling locations.

Based on the hydraulic head data, a conceptual rationalisation of potential flow paths through the sinusoidal bedform is proposed (Figure 6.3.12). It is theorised that the increased surface flow induced increased downwelling and elongated flow paths. Downwelling within the sinusoidal bedform was induced by the pressure differentials across the morphological feature. Water entered the riffle at the upstream incline and exited at downstream decline.

These laboratory observations of the influence of surface flow on subsurface flow paths are in agreement with the field observations of increased coupling of surface and subsurface water during high flow events (Wickett, 1954; Bretshko, 1992; Vervier et al., 1992; Panek, 1994; Brunke and Grosner, 1997; Angradi and Hood, 1997; Soulsby *et al.*, 2001, Malcolm *et al.*, 2003). Previous studies have highlighted relationships between surface flow conditions and the hydrochemical characteristics of the intragravel environment (Soulsby *et al.*, 2001; Malcolm *et al.*, 2003). Within riverbeds receiving groundwater inputs, the depth at which hydrochemical indicators are characteristic of groundwater inputs has been shown be veiy dependent on surface flow conditions (Soulsby *et al.*, 2001; Malcolm *et al.*, 2003). During periods of high flow, the mixing zone between upwelling groundwater and surface derived water has been shown to migrate downwards into the riverbed. Once low flows return, the mixing zone migrates towards the surface (Malcolm *et al.*, 2003). Based on the results of the flume experiment, it is suggested that this variable groundwater/surface-water mixing zone results from variations in hydraulic head associated with changes in the surface flow conditions.

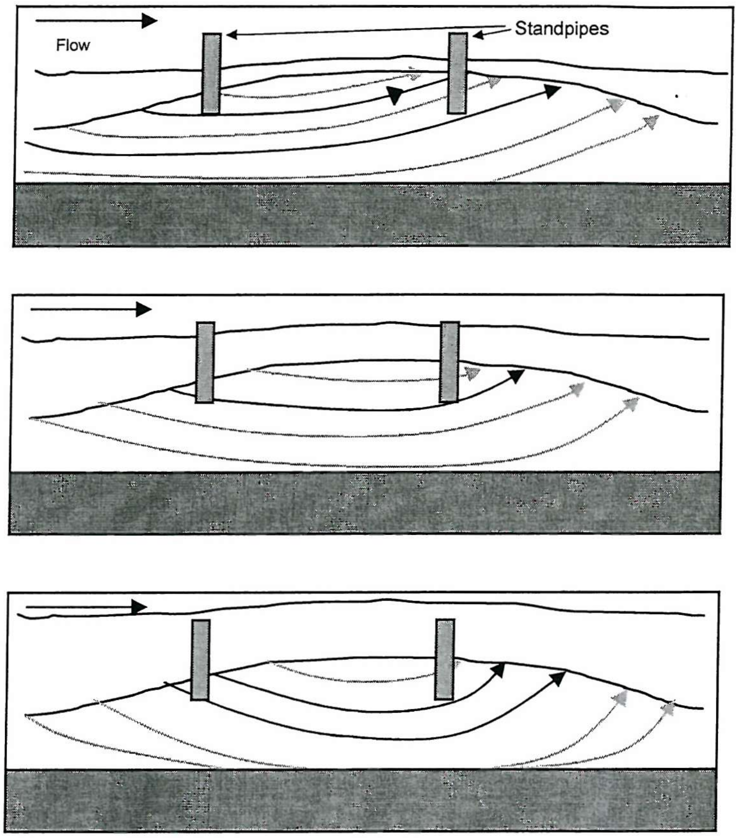


Figure 6.3.12 Conjectured graphical representation of intragravel flow paths occurring under increasing discharge across the sinusoidal bedform. (a) × 1 discharge, (b) ×2 discharge, (c) ×3 discharge. The black lines represent the flow paths potentially passing the monitoring locations.

6.3.4.2 Intragravel flow velocities

Intragravel flow velocity was shown to increase with discharge. Applying Darcian principals, these increases may be partially explained by the changes in hydraulic gradient that were also shown to occur under varying surface flow conditions. However, the increases in velocity estimated with the conductiometric standpipe were greater than the increases that would be estimated to occur applying Darcy's Law. Two explanations for this trend are proposed. First, it is possible that the conductiometric standpipe overestimated higher intragravel flow velocities. The velocities recorded in the flume were above the range of velocities tested during the calibration procedure (Appendix 1), therefore, it is possible that an upper response threshold exists, and that this was exceeded in the flume, resulting in erroneous intragravel flow velocity.

Second, at the depths monitored, it is possible that intragravel flow was influenced by non-Darcian principles. Previous investigations of the effects of surface flow on intragravel flow velocities across flat beds have proposed that turbulence at the bed surface induces a slip velocity in the upper gravel layers that exponentially decreases with depth into the bed. Across a flat bed, the depth of penetration of slip-induced velocities is typically reported to be around 0.1m. In this experiment, intragravel flow velocities were monitored at a depth 0.25m. This depth is beyond that typically associated with slip-induced velocities. However, it is possible that an interaction between pressure driven and momentum driven subsurface flow occurred, resulting in the velocity increases recorded. Additionally, the range of discharges investigated in this study exceeded those investigated in previous studies. It is possible therefore, that the greater discharges monitored in this study resulted in greater penetration depths of turbulent momentum driven flow.

6.3.4.3 Broad implications

In practicable terms, these observations have important implications for investigations into the ability of riverbeds to support incubating salmonid embryos. Previous investigation into factors influencing intragravel flow have typically focused on the impact of fine sediments on gravel permeability (Chapter 1). The results of this study suggest that increased consideration should be given to the potential detrimental impact of low flows and the positive influence of high flows and, potentially, associated bed entrainment. Over the incubation period, fluctuating discharges may result in variable intragravel flow conditions. High flows may provide a mechanism for providing increased exchange of surface water with the riverbed, promoting increased intragravel flow within the riverbed and the supply of oxygen to incubating embryos and alevins. Furthermore, increased intragravel flow may reduce the relative influence of sedimentary oxygen demands on intragravel oxygen concentrations, thereby providing a mechanism to maintain higher intragravel dissolved oxygen concentrations. Periods of low flow would have a reverse effect on the intragravel environment, reducing intragravel flow and increasing the impact of sedimentary oxygen demands. Changes to the hydrological regime that result in intermittent or prolonged periods of low flow, have been linked to impoundment and land drainage activities (Robinson, 1986, 1990).

In addition to the direct influence of surface flow on subsurface flow patterns, the indirect influence of riverbed scouring must also be considered. The dislodgement of salmonid eggs during scour events has been reported in a number of studies (Montgomery *et al.*, 1996; De Vries, 1997). However, observation of surface-subsurface interactions coupled with the results of this experiment suggest that under some circumstances scouring may also have a beneficial influence over potential embryonic survival.

In essence, scour events reduce egg burial depths. This reduction may be transient were the riverbed gravels are temporarily mobilised before settling to pre-mobilisation bed morphology, or they may be permanent in environments where bed adjustments are occurring. If the distance between incubating eggs and the bed surface is reduced, increased exchange of surface water with the riverbed may be induced. This increased exchange may result from localised turbulent driven momentum exchange (Shimizu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993) or from temporary flushing of fine sediments and its consequent affect on pressure driven exchange (Vaux, 1968). The resultant increase in the exchange of surface water with the riverbed may provide a mechanism to replace older, lower oxygen concentration water retained in the riverbed with higher oxygen concentration surface water, thereby increasing the availability of oxygen to incubating embryos. The longevity of this increase in oxygen availability will be dependant on the nature of the bed mobilisation event and on post mobilisation bed conditions. If bed mobilisation is coincident with the infiltration of fine sediments into the incubation environment, the potential influx of oxygen consuming materials combined with reduced gravel permeability may result in a quick return to lowered oxygen concentrations. However, if the mobilisation event results in a net reduction in fine sediment levels within the riverbed, the increased oxygen concentrations and flow velocities may be sustained for a longer period.

6.3.4.4 Implications at field sites

With respect to trends in embryonic survival recorded at the field sites, the increased exchange of surface water during the high flow events at the River Aran and Blackwater may have enhanced the supply of oxygenated water to the incubating embryos. Conversely, prolonged periods of low flow, particularly following a period of high flow and the potential infiltration of fine sediments into the incubation environment may have reduced the exchange of surface water with the riverbed and impeded the exchange of oxygenated water to incubating embryos. Although at the River Ithon sampling difficulties negated a direct analysis of the influence of surface flow on the intragravel environment, the principles discussed above can be applied.

At the River Ithon, a dramatic decline in intragravel oxygen concentration and flow velocity was recorded during a prolonged period of low flow that followed a prolonged period of high flow (5^{th}-26^{th} March[8]). It is probable that the period of high flow resulted in the infiltration of fine sediment into the incubation environment, and that the prolonged period of low flow that followed exacerbated the impact of the deposited material on intragravel oxygen concentrations and flow velocities.

Finally, as detailed in Section 5.6, the potential presence of upwelling groundwater was identified at the River Blackwater. Upwelling groundwater has been shown to influence intragravel oxygen concentrations, with low oxygen content groundwater having a negative impact on intragravel oxygen concentrations (Malcolm *et al.,* 2003). In circumstances where surface exchange is impeded, for example by the presence of high levels of fine sediment or during periods of low flow, the influence of groundwater upwelling may be more pronounced (Malcolm *et al.,* 2002, 2003). The high intragravel oxygen concentrations recorded at the River Blackwater suggest that: (i) the oxygen content of any groundwater inputs were of similar oxygen concentration to surface derived water, (ii) groundwater upwelling was restricted to a spatially discrete area in close proximity to the thermister column, or (iii) the high flux of surface water into and through the riverbed resulted in surface-water-dominated intragravel environment, which diluted or removed the potential detrimental influence of low oxygen content groundwater at the range of depths monitored. The low oxygen concentrations recorded in the presence of low intragravel flow velocities at redd 3 (Section 6.2) potentially indicate the presence of low oxygen concentration groundwater at this location. However, this trend may also be indicative of the influence of an oxygen demand induced by deposited material (Section 6.4).

[8] The intragravel oxygen concentration and flow data for this period is located in Section 6.1.

6.3.5 Summary

The influence of surface flow on the subsurface environment has been highlighted. It was shown that increases in discharge result in increased negative hydraulic head in zones of downwelling and increased positive hydraulic head recorded in zones of upwelling. It was also shown that intragravel flow velocities increase under increasing discharge. Two mechanisms for this increase in flow velocity were outlined. First, the increased hydraulic gradients recoded under high flow resulted in a consequent increase in intragravel flow velocity. Second, based on comparisons of estimates of intragravel flow based on Darcy's law and from the conductiometric standpipe, it is also hypothesised that non-Darcian flow was occurring at the monitoring depths. Field evidence of temporally variable temperature gradients between surface water and water at 0,4m depth into the riverbed, supported the notion of increased influx of surface water during highflow events. With respect to future research, consideration should be given to the effectiveness of Darcy's law to accurately estimate intragravel flow at depths within the hyporheic zone that may be influenced by surface flow effects. Additionally, the impact of low flow on the flux of oxygenated water through salmon spawning gravels requires further field and flume based investigation.

6.4 Impact of fine sediment accumulation on intragravel oxygen fluxes and salmonid incubation success.

The following section provides an examination of the impact of fine sediment accumulation on intragravel oxygen fluxes and incubation success. The section includes (i) a summary of the sedimentary character of the study sites, (ii) an analysis of the ability of commonly reported granular metrics of incubation success to explain variations in survival, and (iii) an assessment of the impact of fine sediment accumulation on intragravel flow velocity and oxygen concentration.

6.4.1 Introduction

Sediment accumulation within salmon spawning gravels has been identified as a factor contributing to poor incubation success (Chapman, 1988; Bjorn and Reiser, 1997; Reiser, 1998). However, previous investigation into the impact of fine sediment accumulation has largely been limited to the development of simple metrics of survival, which are based on a quantitative description of the sedimentary character of spawning gravels. Commonly reported granular metrics of survival include percent fine sediment below an empirically defined threshold, geometric mean and Fredle index (McNeil and Ahnell, 1964; Koski, 1966, 1975; Hall and Lantz, 1969; Bjorn, 1969; Phillips, 1975; McCuddin, 1977; Platts, 1979; Shirazi *et al.*, 1981; Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Cederholm *et al.*, 1981; NCASI, 1981; Tappel and Bjorn, 1983; Tagart, 1976, 1984; McCrimmon and Gots, 1986; Chapman, 1988; Tappel and Bjorn, 1989; Young *et al.*,1991). However, although providing statistically relevant relationships, with respect to pre-hatching incubation success, bulk sedimentation of the riverbed is not directly linked to survival. Rather, it is the impact of sediment on oxygen flux through the riverbed that influences survival[9].

The influence of sediment accumulation on oxygen flux through salmon spawning gravels can be categorised into two distinct components. First, the physical blocking of pore spaces by infiltrated sediments, organic and inorganic, reduces gravel permeability and restricts the flow of water into and through the riverbed (Chapman, 1988). Second, the infiltration of organic material, or inorganic substances attached to sediment particles, may impart an oxygen demand that depletes oxygen from interstitial water (Chevalier and Murphy, 1985). Different sediment size classes will have a variable impact on permeability and therefore intragravel flow (Chevalier and Carson, 1985), and the impact of sedimentary oxygen demands will vary dependant on the magnitude of the demand induced by deposited materials (Whitman and Clark, 1982; Chevalier and Murphy, 1985; Sterba *et al.*, 1992). Furthermore, although these two processes are distinct, the impact of oxygen demands within the riverbed is influenced by the rate of passage of water through the riverbed, with lower flow rates resulting in longer contact times with oxygen consuming materials and, therefore, greater reductions in dissolved oxygen concentration.

Potential intra and inter site variations in the relative influence of the two sedimentary related processes influencing intragravel oxygen fluxes raises concerns regarding the application of simple granular metrics of embryonic survival. Furthermore, empirical relationships that have been developed for one system, or spawning reach, may not be transferable to localities in which a different interaction of sedimentary related factors influence the flux of oxygen to incubating embryos. There is a requirement therefore, to better understand the processes and mechanism by which fine sediment accumulation influences the flux of oxygenated water through spawning gravels and, thereby, embryonic survival.

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[9] Section 6.2 highlighted the potential impact of clay material on the exchange of oxygen across the egg chorion. However, further research is required to assess this potential oxygen inhibiting mechanism and its implications in river systems.

This section details the results of an investigation into the impact of fine sediment accumulation on the flux of oxygen through salmonid spawning gravels. Four study sites, selected to represent a range of UK spawning habitats, were investigated over two spawning and incubation periods (2001-2002 and 2002-2003) (Section 5.3). The overarching aim of this section was to investigate the processes by which fine sediment infiltration influences oxygen availability and, therefore, incubation success. Within this broad aim, the investigation centred on the following key objectives:

(i) A summary of the sedimentary character and suspended sediment loads at the study sites.
(ii) An assessment of the composition of infiltrated sediments at the study sites.
(iii) An assessment of the ability of currently proposed granular metrics of incubation success to delineate potential embryonic survival at the study sites.
(iv) An investigation of the impact of fine sediment on intragravel flow velocity.
(v) An investigation of the impact of sedimentary oxygen demands on intragravel oxygen concentrations.
(vi) Identification of the specific sedimentary related factors influencing incubation success at the study sites.

Additionally, an assessment of variations in the composition and availability of sediment for infiltration at each study site was undertaken. As highlighted in Section 5.6, one of the project constraints was a lack of high quality data pertaining to suspended sediment and bed load concentrations. Therefore, the analysis of sedimentary material available for infiltration at each study is restricted to an estimate of suspended sediment load at each field site.

Finally, it should be noted that this study is restricted to investigation of survival to hatching (Section 2.1). Post hatching, sedimentation may directly influence survival by physically impeding the emergence of fry from the gravel substrate. However, at present, information regarding the ability of salmon fry to migrate through varying mixtures of gravels and fine sediments is limited (Crisp, 1993). Furthermore, delineation of mortalities resulting from low oxygen availability and restricted emergence was beyond the scope of this study. Consequently, all results are restricted to assessments of survival to hatching.

6.4.2 Methods[10]

6.4.2.1 Monitoring strategy

Four interrelated studies, developed within the larger monitoring framework outlined in Section 5.6, were undertaken to investigate the impact of fine sediment accumulation on embryonic survival. First, a detailed analysis of the hydrological and granular character of the study sites was undertaken to aid delineation of the precise sedimentary related pressures at each study site. Second, an assessment of embryonic survival in relation to granular properties of the incubation environment. Third an assessment of the impact of sediment accumulation on intragravel flow velocities was performed. Finally, an analysis of the impact of sedimentary oxygen demands on intragravel oxygen concentrations was undertaken.

Each study used artificial redds to assess conditions within the incubation environment (Section 5.6). As described in Section 6.1, all redds were created at appropriate spawning times and locations for each river system. Furthermore, each redd was carefully constructed to mimic important granular and morphological characteristics of natural redds. As discussed in Section 5.6, three types of redds were created to monitor the impact of sediment accumulation on intragravel oxygen fluxes and embryonic survival: (i) survival redds (Type I) were used to assess a) total sediment accumulation over the incubation period, b) granular properties of the incubation environment and c) embryonic survival, (ii) sediment accumulation redds (Type II) were used to quantify the cumulative accumulation of sediment over the incubation period and temporal trends in intragravel flow and oxygen concentration, and (iii) sedimentary oxygen demand redds (Type III) were used to obtain sediment samples for laboratory analysis of sedimentary oxygen demands (Figure 5.15). Details of the investigations associated with these redds are outlined below.

Assessing survival and granular properties of the incubation environment

A series of artificial redds (Type 1) were used to monitor survival to hatching of Atlantic salmon embryos and sedimentary properties of the incubation environment. Total sediment accumulation over the incubation period was monitored using sediment pots and freeze cores. Sediment pots were composed of plastic coated rolled steel mesh and were deployed within a steel mesh sump (Figure 6.4.1). To aid recovery of deposited sediments, a retractable rip-stop

[10] Information from all four study sites is presented. The reader is referred to Section 5.3 for a description of the study sites.

nylon bag was attached to each pot. At the end of the sampling period, the pots were removed and sediments were retained for particle size analysis (Section 6.4.2.5). Careful consideration was given to mimicking the granular structure of natural redds, and larger particles were placed in the bottom of each sediment pot (Section 2.1). To allow an analysis of rates of sedimentation, and to mimic the cleansing spawning activity of the hen salmon, pots were filled with a heterogeneous mixture of gravel that was truncated at 4mm. Gravels were truncated at 4mm on the basis that particles greater than 4mm would be too large to infiltrate the riverbed, therefore, the sediment pots allowed accurate assessments of sediment accumulation across all potential sediment deposition size classes. However, it is important to note that naturally cut gravels would only be partially cleansed of fine material (Section 3.1.2.4) (Kondolf *et al*, 1993). Therefore, with respect to sedimentary composition, the pots should be considered only partially representative of natural spawning gravels. Over the 2001-2002 monitoring period (River Test and River Ithon), two pots were deployed (front and rear) within six artificial redds at each field site. Over the 2002-2003 monitoring period, a single pot was deployed within five redds at each study site (Figure 6.1.1).

Freeze cores taken from within each artificial redd at the end of the monitoring period provided supplementary granular data and allowed an assessment of sediment accumulation in gravels that were undisturbed by the presence of sediment pots or influenced by the artificial truncation of fine sediments. At the River Test and River Aran, the freeze cores were also used to assess trends in the vertical accumulation of fine sediments. The vertical structure of the redd gravels was assessed by placing a number of freeze cores on divider trays (three 80mm compartments: top, middle and bottom). As the freeze cores thawed, the sedimentary material separated into the appropriate compartments.

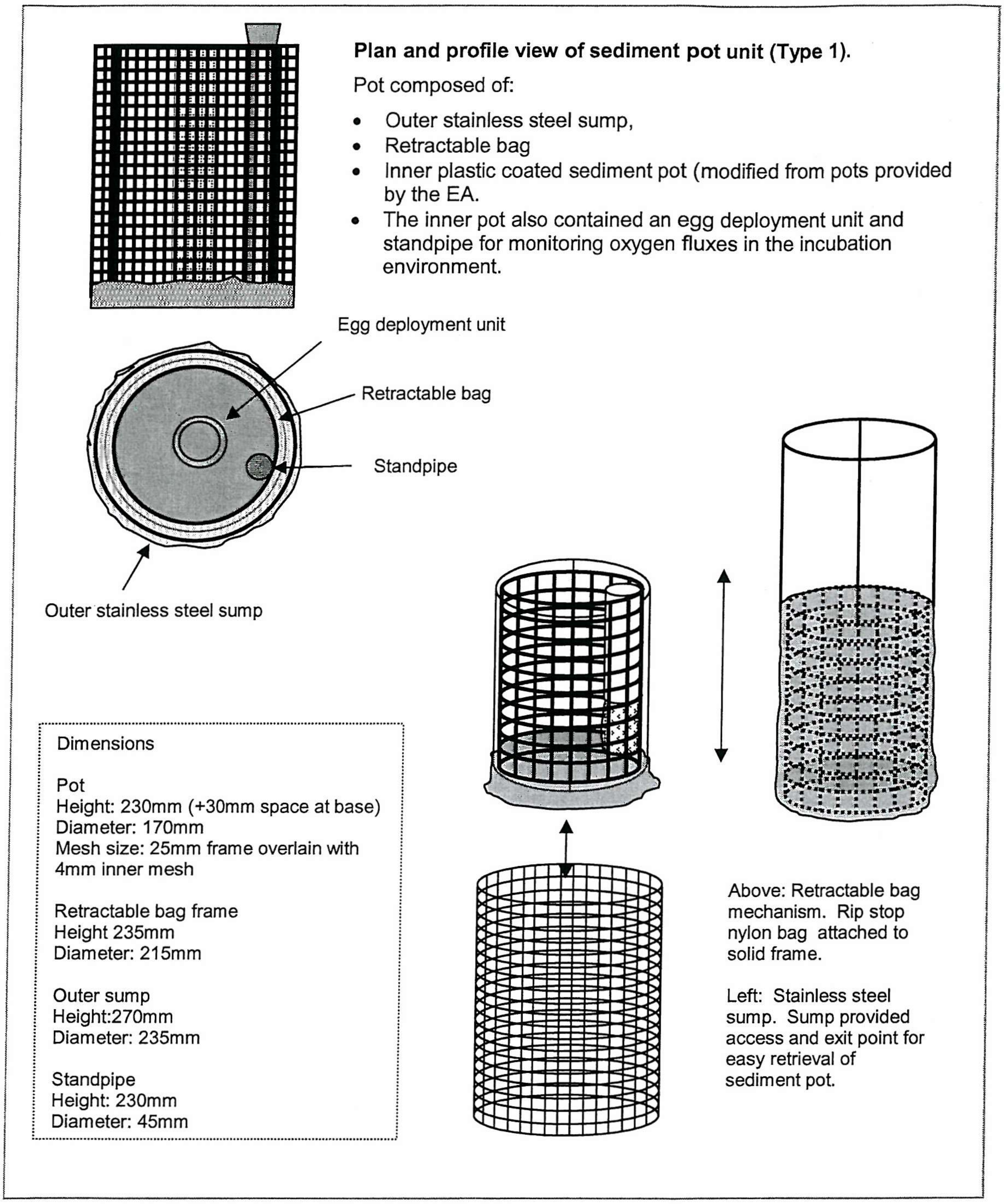

Figure 6.4.1 Schematic of sediment pot design (Type 1).

Survival to hatching of Atlantic salmon embryos was based on the survival of hatchery-reared salmon eggs deposited within sediment pots and inserted directly into redd gravels. Section 6.1 and Appendix 2 provide a detailed description of the techniques developed and procedures followed to quantify embryonic survival.

At the River Blackwater and River Aran, variations in gravel permeability were assessed over the incubation period. Permeability measurements were taken in the standpipes located adjacent to the sediment pots. The permeability measurement was based on a pump test method proposed by Pollard (1955) (Figure 6.4.2). Permeability was assessed three times over the incubation period: post redd creation, at embryonic eying and at hatching. As the standpipes were of similar design to the ones used by Carling and Boole (1986), the empirical equation linking Darcian permeability to pumping rate developed by Carling and Boole (1986) was applied (Section 6.3).

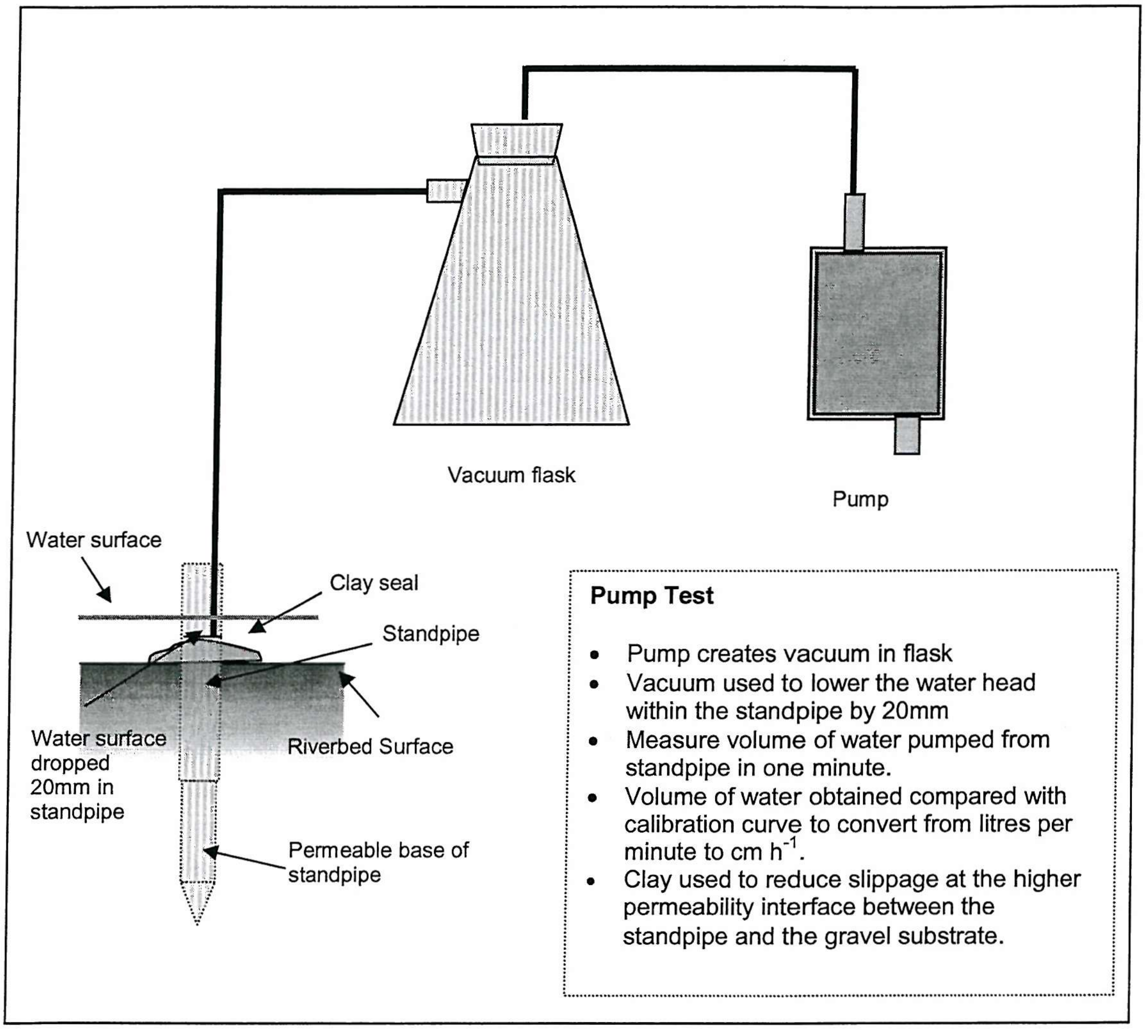

Figure 6.4.2 Diagram of procedure followed and equipment utilised for permeability test.

Assessing the impact of fine sediment accumulation on intragravel flow velocity

Large artificial redds were used to assess the rate of fine sediment accumulation and its affect on intragravel flow velocity (Figure 6.4.3). Twelve small sediment pots organised in a grid formation, were inserted into each redd. Two pots were then removed sequentially, one from the front and one from the rear, at 14-day intervals, and the contents were retained for particle size analysis (Section 6.4.2.5). Standpipes, of the same design described in Section 6.1.2.2, were inserted into each redd to provide access points for monitoring the intragravel incubation environment.

Intragravel flow velocities were estimated using the recalibrated conductiometric standpipe technique (Carling and Boole, 1987) described in Section 6.1.1.2 and Appendix 1. Intragravel flow velocities were also recorded at bi-weekly intervals.

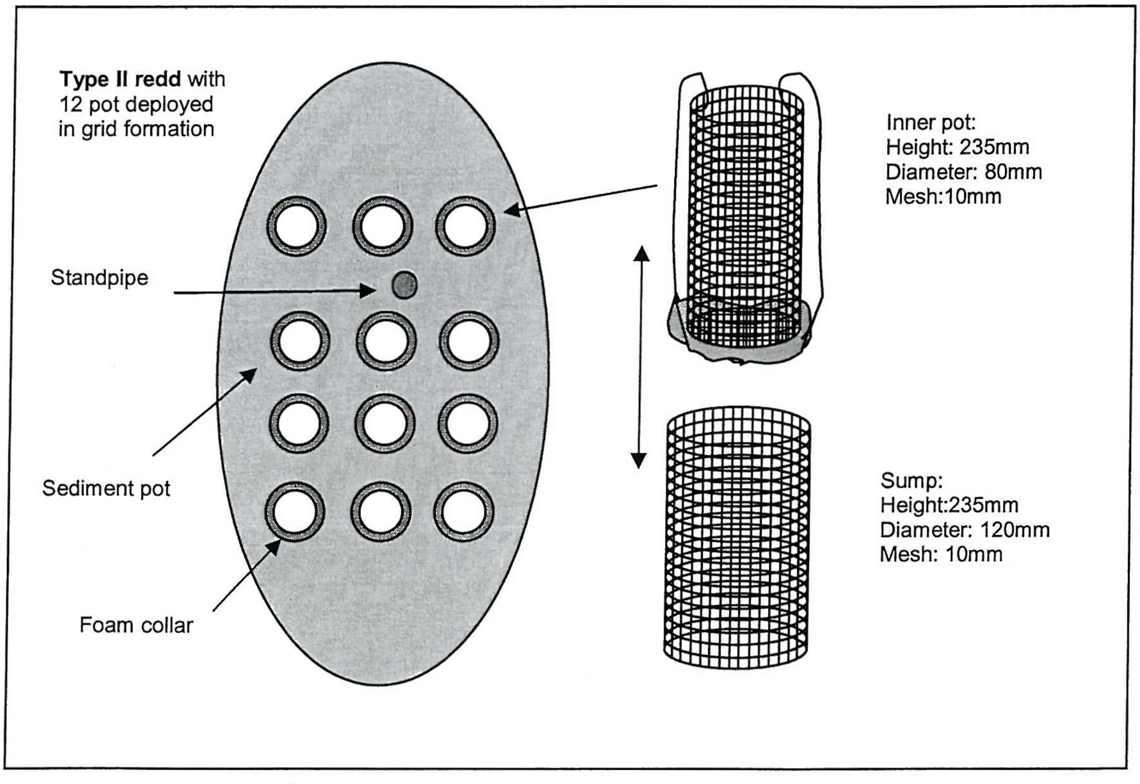

Figure 6.4.3 Sediment accumulation redd (Type II). Also outlined is the location and design of the small sediment pots.

Assessing oxygen demands of material deposited in riverbed gravels

To allow acquisition of sediment samples for determination of oxygen demands associated with materials deposited in the riverbed, two sedimentary oxygen demand redds (Type III) were created at each field site (Figure 6.4.4). Each redd contained three small sediment pots that were removed sequentially during the monitoring period. Samples of fine sediment were retained for laboratory analysis of associated oxygen demands. Two-three replicate sub-samples (2-5g) were taken from each field sample. Long term (25 day) oxygen demands of sedimentary material were carried out using a Biochemical Oxygen Demand Oxitop control system in association with an Oxitop OC 110 controller (WTW instruments). Nitrogen demands of samples taken from the River Test and River Ithon were assessed following the same procedure but with the addition of a nitrogen inhibitor. The difference in demand between the non-nitrogen-inhibited sample and the nitrogen-inhibited sample provided an estimate of the total nitrogen demand (and the carbon demand). All incubations were carried out at 20°C. Ignition analyses (450°C) of sub-samples were performed to determine the organic content of each sample.

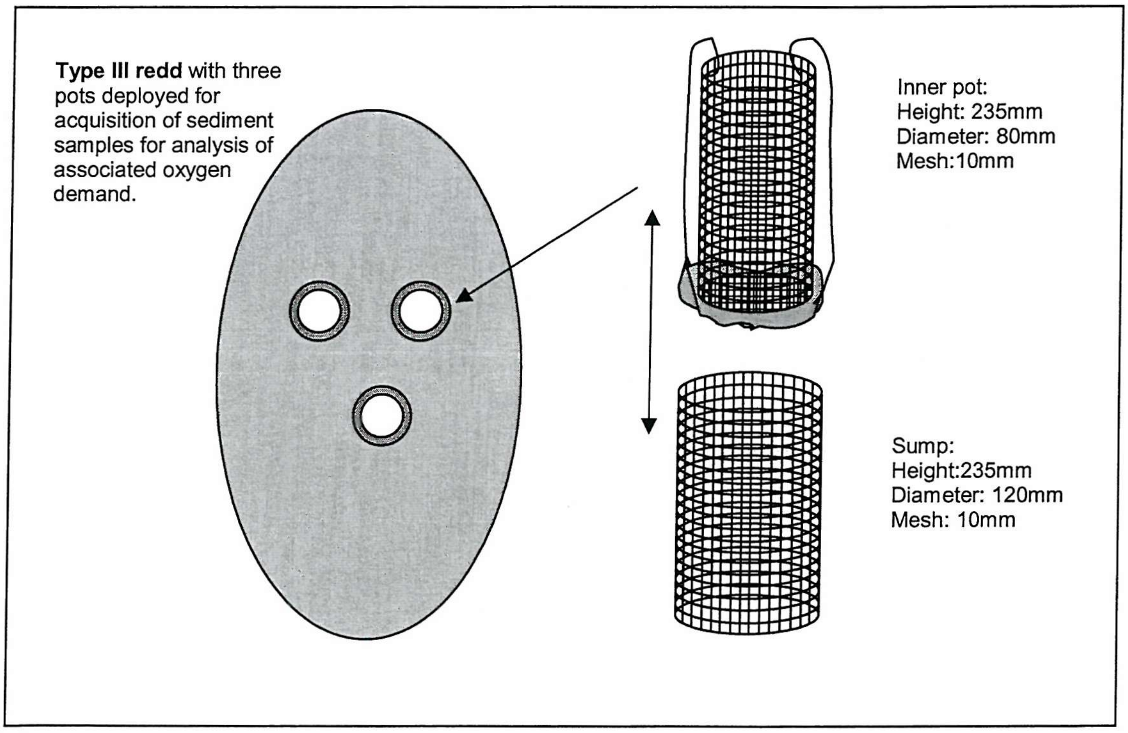

Figure 6.4.4 Sediment oxygen demand redd (Type III). Also detailed is the design of the sediment pot used to obtain sediment samples for subsequent laboratory analysis of oxygen demands.

6.4.2.2 Particle size analysis

A two-stage particle size analysis was performed on all field samples. For particles greater than 710 microns, dried samples were sorted on a mechanical shaker at ½ phi intervals and the samples retained on each sieve were weighed. For particles below 710 microns, sub-samples of between 3-8 grams were taken for Coulter analysis (Coulter Counter™ LS 100). Coulter Counters allow rapid analysis of fine sediment samples within the clay to sand size range. Based on the influence of particle volume on the electrical current passing an aperture, the Coulter Counter can determine the number of particles in a given size range. Based on the average of three replicates, the output from the coulter counter (number of particles in each size class) was multiplied by the total dry weight to provide an estimate of total weight of material in each size class. The data from the Coulter Counter was then combined with the data from the sieve analysis to provide a complete particle distribution across the entire particle size range.

For each substrate sample a series of particle distribution parameters were computed. To improve cross-site comparisons, all samples were truncated at 31.5mm prior to particle size analysis (Church, 1985). A graphic geometric approach was adopted to investigate distribution parameters, and all data sets were computed in mm. Table 6.4.1 summarises the particle distribution parameters investigated. Finally, the organic content of each sample (<710 microns) was determined by loss on ignition.

Distribution parameter	Equation	Reference	Eq. No.
Geometric mean (D_g)	$d_g = [D_1 w_1 \times D_2 w_2 .....D_n w_n]$	Lotspeich and Everest (1981)	6.4.1
Sorting coefficient (S_0)	$S_o = \sqrt{\frac{D_{75}}{D_{25}}}]$	Trask (1932)	6.4.2
Skewness (Sk)	$Sk = \sqrt{\frac{D_{16} \times D_{84}}{S_o}}$		6.4.3
Kurtosis	$K = \frac{D_{75} - D_{25}}{2(D_{90} - D_{10})}$	Trask (1931)	6.4.4
Fredle index	$Fi = \frac{D_g}{So}$	Lotspeich and Everest (1981)	6.4.5

Table 6.4.1 Summary of gravel distribution parameters and computation procedures adopted.

6.4.2.3 Suspended sediment loads

To determine suspended sediment loads, calibration curves were generated between measured turbidity values (averaged for the hour around time of pump sampling) and a single daily sample of suspended solids. Suspended sediment samples were obtained using an ISCO™ automatic pump sampler and were subsequently retained for laboratory processing. The pump sampler intake nozzle was located at roughly 0.6 depth, and 500ml samples were extracted. Samples were filtered, dried and weighed. All filter papers (Whatman, 0.45µm) were weighed prior to filtration and the weight of each paper was subtracted from the total paper and filtered sediment sample weight (weighed to the nearest 0.1mg). At the River Test, Aran and Ithon, turbidity was supplied from YSI™ 950 sondes deployed by the Environment Agency. Importantly, these units had self-cleansing lens to reduce bio-foiling. At the River Blackwater, a calibrated Partech™ IR4000 turbidity probe (range 0-1000mg l^{-1}) was deployed. Scatter in the curves was particularly high for low (more frequently sampled) discharges. The data was therefore averaged in bins to reduce scatter and compensate for the higher sampling frequency. However, at the River Ithon, sampling difficulties limited the size of the suspended sediment concentration data set, resulting in the poor relationship recorded at this site. At the River Aran, there was a stronger relationship with discharge than with turbidity, therefore a rating relationship between discharge and suspended sediment was developed (Table 6.4.2). The resulting rating curves were then applied to the turbidity records at each site to provide estimates of suspended sediment concentration.

Site	**Regression model**	r^2
Test	$SS = 0.0851x+14.379$	0.860
Blackwater	$SS = 1.717.3y$	0.672
Ithon	$SS = 1.9975x$	0.23
Arran	$SS = 5.654Q^2+9.5947Q$	0.501

SS = *suspended solids* (mgl^{-1}), x = Turbidity (NTU), y = Turbidity (mV), Q = discharge (m^3s^{-1})

Table 6.4.2 Rating equations for discharge and suspended sediment concentration.

At the River Ithon discharge was supplied from an Environment Agency Gauging station located immediately upstream from the study reach. At the remaining field sites, stage discharge curves were developed for the study reaches using a standard handbook estimation based on the Manning's roughness formula (Section 6.3.2.2).

The sampling equipment and resources available for determining suspended sediment loads were limited and consideration must be given to the limitations of the adopted approaches. Depth integrated sampling was not undertaken across the channel cross section to assess lateral and vertical variations in suspended sediment concentration (Hicks and Gomez, 2003). However, sampling was undertaken in straight section of channel and, wherever possible, the water sampler was located in a section of riffling flow, thereby reducing potential lateral and vertical sediment stratification. Second, sampling at daily intervals, although providing multiple samples across a range of flows, did not allow for a comprehensive analysis of trends in concentration across the full spectrum of flows experienced at each field site. Potential bias may have resulted from limited sampling at higher discharges and limited information pertaining to trends associated with rising and recession flows, for instance increased concentrations on rising limbs due initial to 'flush' effects (Christian and Thompson, 1978; Walling and Webb, 1988). Third, pump samplers can be susceptible to isokinetic-induced bias in the sediments samples, for example underestimates of sand sized fractions (Hicks and Gomez, 2003). Finally, at the River Test, River Blackwater and River Aran, the discharge data used to compute the rating relationships was calculated from synthetic discharge estimates based on Manning's roughness formula (Section 6.3.2.2). The strength of these relationships may have influenced the representativeness of the rating relationships developed at each site.

Finally, bulk water samples at the River Ithon and River Test provided samples for particle size analysis of suspended sediments. However, at the River Blackwater and River Aran, samples were obtained from sampling sediments released from the riverbed by gentle agitation of the surface gravel. Accurate characterisation of the size of the sediments available for infiltration requires a more rigorous sampling regime that recognises potential variations in the size characteristics between high flow events, and lateral and vertical variations in particle size within the water column (Hicks and Gomez, 2003). Therefore, it was deemed inappropriate to apply this dataset to undertake a detailed assessment of the relationship between suspended sediment and the composition of infiltrated material. Therefore, information presented by other researchers regarding the relationship between the composition of suspended sediment and infiltrated material was assumed to be indicative of the relationships at the field sites (Section 6.4.3.2).

6.4.3 Results and analysis

6.4.3.1 Substrate composition and suspended sediment load

Composition of uncut gravels

Based on the sedimentary data obtained from freeze cores taken at the end of the monitoring period, a detailed particle size analysis of uncut riverbed gravels at each field site was undertaken. The purpose of the analysis was to characterise the composition of undisturbed gravels within the study reaches, and to provide reference data for a comparative assessment of the composition of uncut and cut gravels at the end of the incubation period (Section 6.4.3.2).

The particle size analysis indicated that uncut gravels at each field site can broadly be classified as coarse, poorly sorted, coarsely skewed and leptokurtic (highly peaked) to very leptokurtic (Figure 6.4.5, Table 6.4.3). Additionally, based on the particle distribution data, the presence of two grain size populations was evident (Figure 6.4.6). Bimodality is a common characteristic of riverbed gravels, and the two size classes are generally separated into framework and matrix populations (Carling and Reader, 1982). Framework gravels form the main stream deposits and are composed of large self supporting interlocking gravels (Church *et al.*, 1987). The interstices between these deposits are filled with the finer grade (matrix) materials deposited from the water column. Typically, matrix material is defined as material less than 2mm (or 1mm) (Carling and Reader, 1982). However, in view of the artificial truncation of particles at 4mm within the sediment pots, for the purposes of this study a matrix cut-off point of 4mm has been adopted.

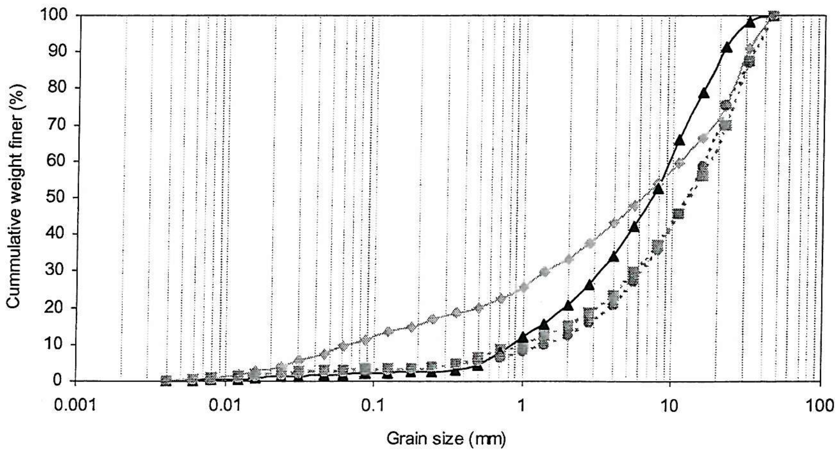

Figure 6.4.5 Cumulative grain size curves for uncut gravels at each field site

River Test —◆— ; River Blackwater —▲— ; River Ithon - -■- - ; River Aran - -●- - .

Gravel descriptor	Aran	Blackwater	Ithon	Test
D_{50} (mm)	10.41	7.07	11.89	6.33
D_g (mm)	6.36	4.98	4.96	3.27
Fi	2.9	2.26	1.43	0.67
Sorting	2.21	2.21	3.47	4.84
skewness	1.55	1.4	1.9	1.9
kurtosis	2.44	2.01	1.82	5.26
% <4mm	26.04	33.34	33.44	42.97
%< 1mm	11.43	13.28	19.48	25.42
% < 0.063	4.69	2.28	6.20	9.30

Table 6.4.3 Granular character of uncut gravels at each field site. Data based on mean of freeze core samples taken at each field site (Number of samples: Test-3, Ithon-3, Blackwater-2, Aran-2).

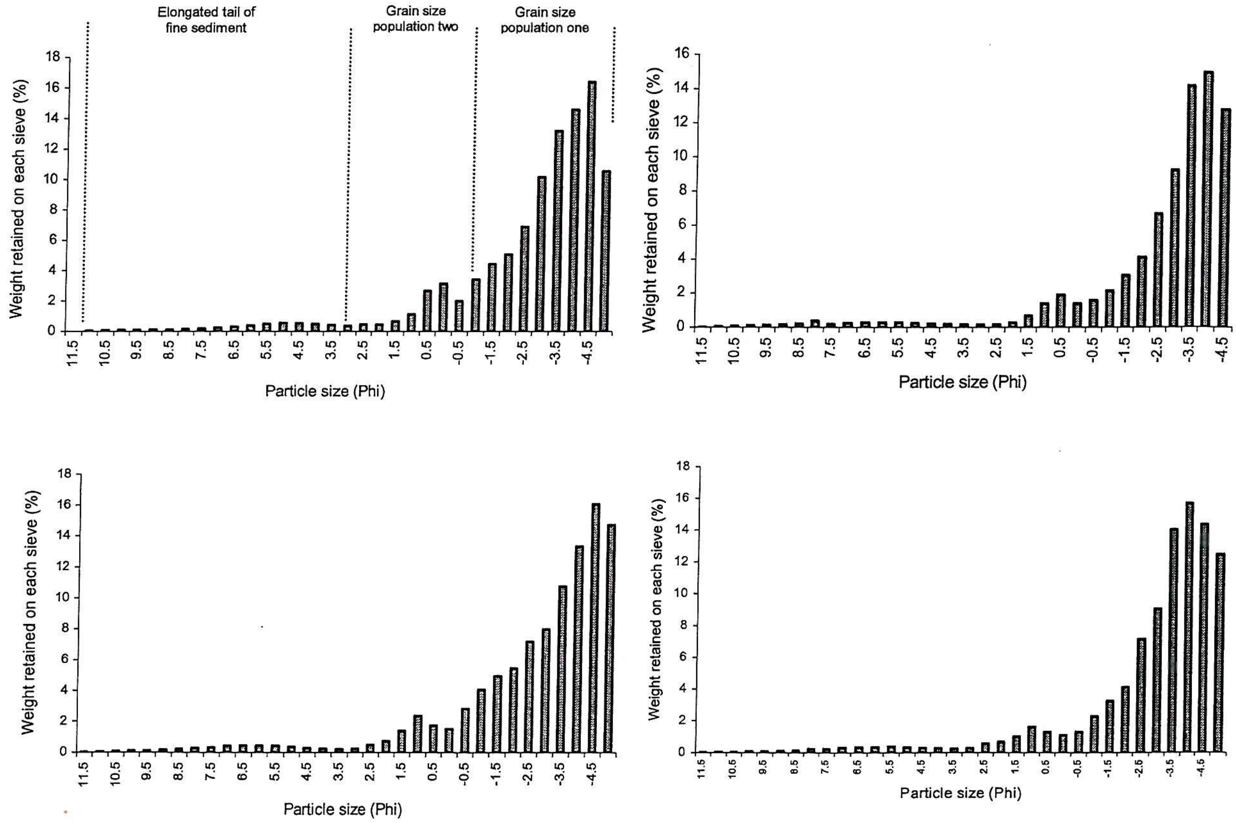

Figure 6.4.6 Summary of particle distributions of uncut gravels, highlighting the presence of two grain size populations: (a) River Test, (b) River Blackwater, (c) River Ithon, (d) River Aran. The elongated tail of fine sediment is a result of the sampling and analysis programme, which was weighted towards characterisation of the fine sedimentary material.

Salmonid spawning is typically restricted to gravels containing less than 20 percent fine sediment (1mm) (Crisp and Carling, 1989; Moir, 1998; Armitage *et al.*, 2002). At the River

Test field site, fine sediment levels in excess of this threshold were recorded. However, salmon and trout spawning was observed at the field site during the spawning season, furthermore, the site has a record of salmon spawning, although spawning densities have declined in recent years (Environment Agency personal communication, Mark Fidebottom). The higher level of fine sediment recorded within the riverbed of this study reach is indicative of the hydrogeomorphic characteristics of lowland groundwater systems (Sear *et al.*, 1999). Bed entrainment, and, therefore flushing flows are infrequent in groundwater-dominated systems (Sear *et al*, 1999). Consequently, sediments deposited in the riverbed may reside for long periods without disturbance (Acornley and Sear, 1999), and gravels therefore have a tendency to become saturated with fine sediments.

Suspended sediment loads

Before undertaking an analysis of the amount and composition of material deposited within the artificial redds, variations in hydrology and fine sediment availability (load) at each site were investigated. Based on the continuous (15 minute intervals) discharge and turbidity data, estimates of suspended sediment load were calculated from the product of discharge and suspended sediment concentration. Figure 6.4.7 shows the suspended sediment loads recorded over the monitoring period at each field site. As would be expected, the freshet systems display peaky suspended sediment loads that are closely linked to discharge (Section 6.3). Conversely, the River Test, which is an example of a groundwater system, displays a more stable hydrological response (Section 6.3.3) and suspended sediment load regime with muted peaks in concentration.

The total flux of suspended sediment (kg) through each system was calculated from the following equation:

$$\text{Suspended sediment load} = = \sigma \sum_{i=1}^{n1} QC \qquad (6.4.6)$$

Where, σ is the time interval between sampling (seconds), Q is discharge (m^3s^{-1}), C is suspended sediment concentration (kg m^{-3}) (Webb *et al.,* 1997). The River Test and River Ithon were monitored over the 2001-2002 spawning and incubation period (December to March) and recorded total sediments over this period of 339 tons and 4288 tons respectively. Over this period the River Ithon and River Test recorded higher than average rainfall: 107% and 114% of mean rainfall respectively (Centre for Ecology and Hydrology monthly summary statistics), therefore, the potential runoff and consequent suspended sediment loads and rates of sediment accumulation may have been slightly higher than those typically experienced at these field sites. The Rivers Aran and Blackwater were monitored between December and March 2002-2003, and recorded total sediment loads of 269 tons and 281 tons respectively. With respect to rainfall, these sites experienced lower than average precipitation for this period: 71% and 73% of mean rainfall respectively (Centre for Ecology and Hydrology monthly summary statistics). Consequently, the suspended sediment loads and rates of sediment accumulation recorded at these field sites may have been lower than typically experienced.

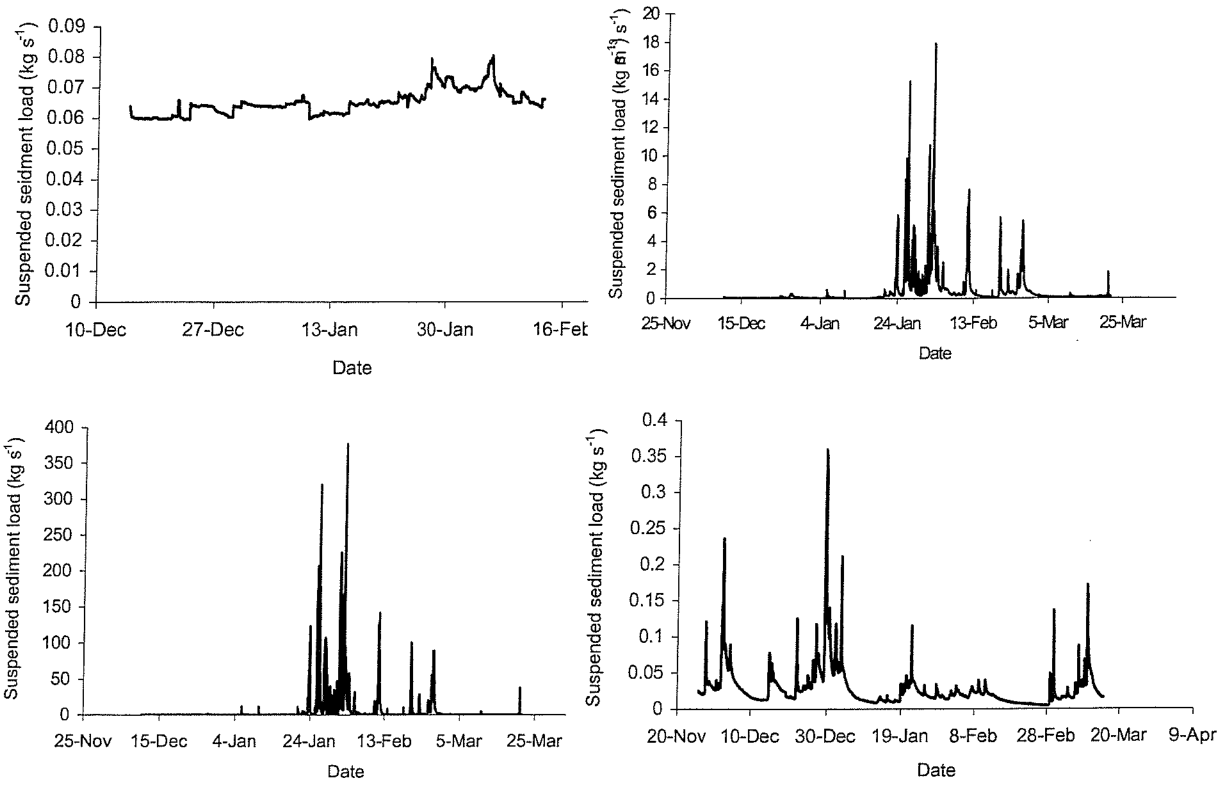

Figure 6.4.7 Temporal fluctuations in suspended sediment load recorded over the incubation period at each field site. (a) River Test, (b) River Blackwater, (c) River Ithon, (d) River Aran.

To provide the basis for a comparative assessment of sediment load at the field sites, the total sediment load estimates at each site was divided by the channel width. This value represents the total suspended sediment passing a 1m transect of the riverbed. This width is roughly representative of the width of the artificial redds constructed at each field site (1-1.5m) and therefore provides an approximation of the total amount of suspended sediment passing each redd over the incubation period (Table 6.4.4). As highlighted in Table 6.4.4, the River Test recorded the lowest total sediment load across a one metre transect, and the River Ithon recorded the highest total load. However, this analysis does not compensate for variations in near bed sediment concentration or bedload (see below) at each field site. Both these factors can potentially influence the sediment available for infiltration (Sear, 1993; Hicks and Gomez, 2003), therefore, the estimates are provided for a comparative assessment of sediment load, and are not intended to reflect the potential sediment available for infiltration at the field sites.

	River Test	River Blackwater	River Ithon	River Aran
Suspended sediment load (tons m^{-1})	32.93	48.04	4728.54	56.20

Table 6.4.4. Total suspended sediment load passing a one metre transect at each field site.

Figure 6.4.8 outlines the particle size distribution of the suspended sediment in each system. As described in Section 6.4.2.6, the particle distribution is based on a limited data set that does not fully represent temporal variations in the size of suspended sediment or potential variations in size composition within the water column. The data presented suggests similar suspended sediment size composition at the River Test, River Blackwater and River Aran, and a finer size composition at the River Ithon. However, the River Ithon sample was taken from the water surface during a period of exceptional high flow (late January), and may be unrepresentative of the depth integrated distribution of particles through the water column (Hicks and Gomez, 2003).

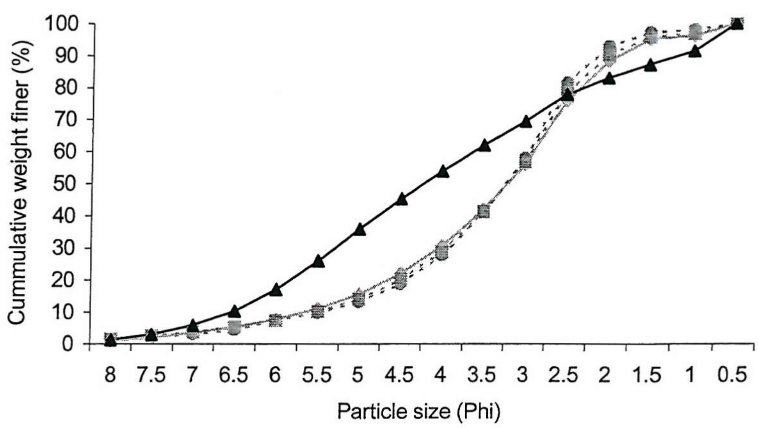

Figure 6.4.8 Particle size distributions of suspended sediments at each field site.

- -●- - River Blackwater, - -■- River Aran, —◆— River Test, —▲— River Ithon.

A further limitation of the monitoring strategy was the lack of information pertaining to bedload. The water sample inlet hoses were positioned to provide a representative assessment the suspended sediment concentration, and, with the resources available, it was not possible to supplement this information with bedload sampling. The bedload traps provided an indication of the timing of gravel entrainment, however, they provided limited information on quantity of bedload in each system. The data obtained from the bedload traps indicated that bedload transport was occurring at the River Ithon and River Blackwater, however, in the River Test and River Aran, fine sediment transport was dominated by suspended sediment. The observation from the River Test is in agreement with trends reported in previous studies, which have indicated limited bedload transport in this system in comparison with freshet systems (Acornley and Sear, 1999).

In freshet systems, it has been shown that bedload can comprise up to 80% of the total material deposited in riverbed gravels (Lisle, 1980). Beyond highlighting a potential bedload component at the freshet sites, it was not possible to assess the amount of bedload in each system or its relative contribution to infiltration rates or total fine sediment accumulation (Section *6.4.3.2*).

6.4.3.2 Composition and amount of fine material deposited over the incubation period

Accumulation of inorganic material over the incubation period

Based on the data obtained from the sediment pots (Type I), bivariate scatter plots were used to identify inter and intra site differences in the total amount of fine sediment that accumulated in the redds over the incubation period (Milne, 1983). Figure 6.4.9 shows percent fine sediment (<4mm and <0.710mm, <0.063) deposited over the incubation period in relation to the geometric mean of the framework gravel. The plot provided a graphical representation of intra and inter site variations in amount of fine sediment deposited over the incubation period. Vertical separation between data groups highlights inter-site difference in total sediment accumulation, whereas intra-site variations are highlighted by the spread of data within each group.

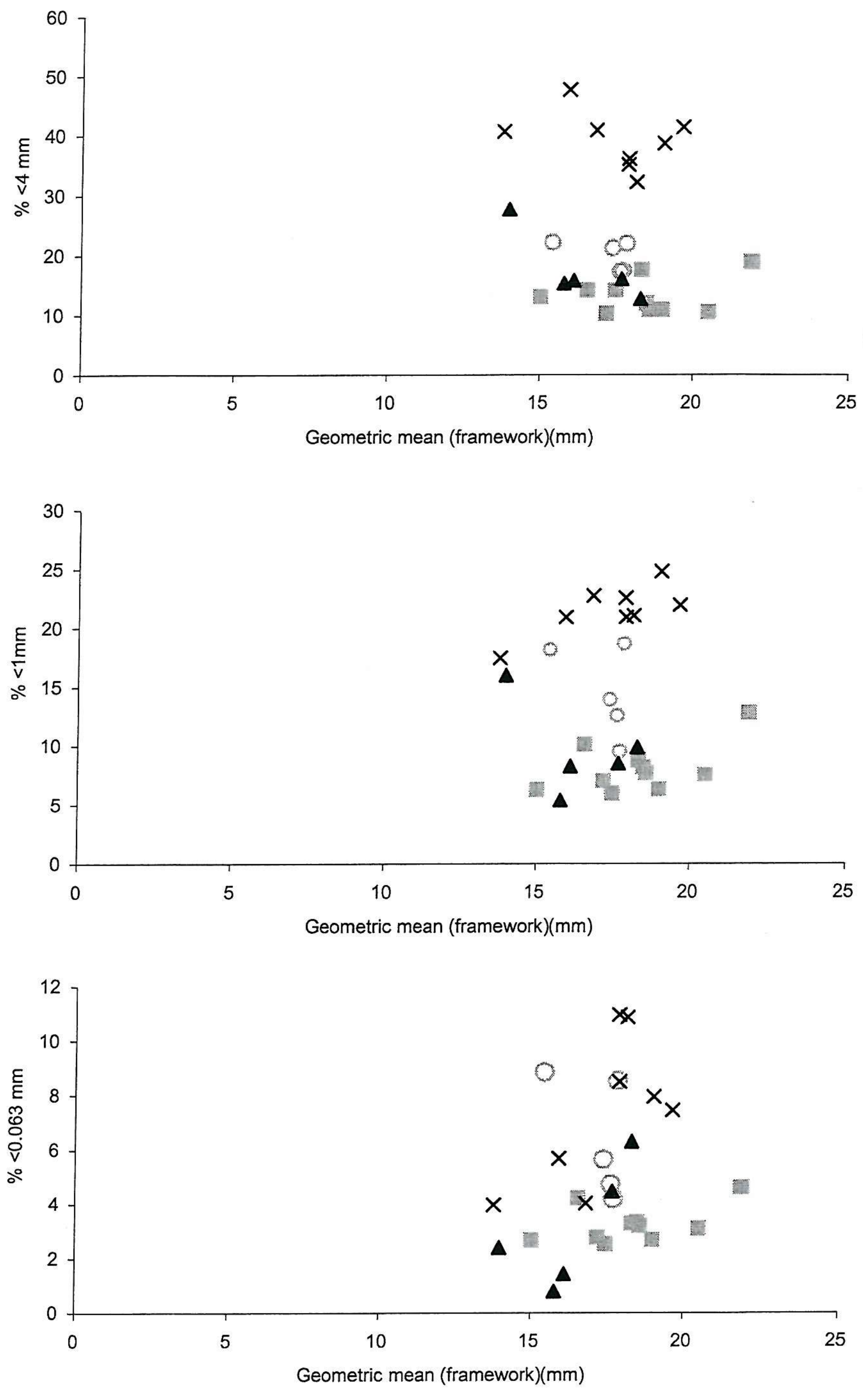

Figure 6.4.9 Bivariate scatter plots of geometric mean (framework) and % fine sediment in three size classes. ■ Test ▲ Blackwater × Ithon ○ Aran

For the periods monitored, the River Ithon experienced the highest total accumulation of fine sediment <4mm and the River Test recorded the lowest. The greatest intra-site spatial variability in total sediment accumulation (<4 mm) was recorded in the River Blackwater and River Ithon and the lowest was recorded in the River Test. However, it should be noted that although the River Blackwater recorded high intra-site variability in total sediment accumulation, this was strongly influenced by a single outlying data point. Over the range of particles < 1mm a similar trend is apparent, although greater intra-site variability is present in the River Aran. Over the clay and silt size range (<0.063), all freshet streams recorded high intra-site variability and, consequently, there is less distinction between sites in total sediment accumulation. However, in broad terms the River Test and River Blackwater recorded lower total sediment accumulation in the silt and clay range than the River Aran and River Ithon.

Variations in total sediment accumulation are partially a result of the availability of sediment for deposition. Based on the data provided in Section 6.4.3.1, the total amount of sediment accumulation over the incubation period is broadly coincident with the magnitude of the sediment load for this period at each field site. However, as highlighted in Section 6.4.3.1, suspended sediment load is only one of a number of factors influencing sediment accumulation, therefore, without information on bed load, it is difficult to comment on the direct relationship between sediment availability and infiltration.

Vertical distribution of fine sediments within the redds

A number of studies have commented on the vertical distribution of sediments deposited within riverbed gravels. In short, the ratio of pore size to matrix material size largely determines whether a particle is obstructed, becomes trapped near the surface, or passes through to the base of the bed (Besheta and Jackson, 1979; Frostick *et al.*, 1984, Lisle, 1989). Matrix particles that can infiltrate upper gravels layers, but are too large to pass through the sub-layer gravels, become trapped near the surface of the riverbed (Besheta and Jackson, 1979). These fines form successively smaller interstices that trap successively smaller matrix particles. As a result, the subsurface layer becomes plugged, preventing deeper penetration of matrix particles (Besheta and Jackson, 1979). The development of such 'seals' has been cited as an important factor inhibiting the emergence of fry from the gravel substrate (Section 1.2, Chapman, 1988). Conversely, matrix particles that are much finer than the surrounding framework gravel pass through the framework interstices unhindered and settle at the base of the permeable gravel layer, and fill the gravel bed from the base upward (Einstein, 1968;

Carling 1984). Bottom-up infilling has been attributed to lowered intragravel flow velocities and rates of oxygen supply to incubating salmon embryos (Meyer, 2003). As the deposition of coarser, seal forming particles can inhibit deeper deposition of finer material, the mixture of matrix material sizes exerts an important control over the level and amount of 'bottom- up' deposition.

Based on the freeze cores extracted from artificial redds at the River Test and River Ithon, Table 6.4.5 outlines the results of the analysis of the vertical distribution of fine sediments at the end of the sampling (incubation) period. Generally, a 'bottom-up' trend in sediment accumulation is apparent at the two study sites, with the amount of fine sediment increasing with distance from the bed surface. This trend suggest that bottom-up infilling of the redd gravels was the dominant accumulation process at these field sites, and similar trends have been reported for other U.K rivers (Petts, 1988, Acornley and Sear, 1999). This observation has important implications for potential incubation success. First, the lack of a significant seal towards the bed surface suggests that in these reaches, the dominant impact of sediment accumulation was on intragravel oxygen fluxes rather than inhibiting emergence. Second, as eggs are typically contained in the lower portion of the egg pocket, when assessing the relationship between incubation success and sediment composition, it may be appropriate to place greater emphasis on conditions in the lower portion of the redd (Meyer, 2003).

	River Test				River Ithon			
	Redd 3	Redd 4	Redd 5	Redd 6	Redd 2	Redd 3	Redd 4	Redd 6
Top (0-0.08m)	12	10	14	17	14	9	4	33
Middle (0.08-0.16m)	29	17	70	31	66	54	139	49
Bottom (0.16-0.24m)	45	52	105	31	76	90	85	128

Table 6.4.5 Vertical structure of fine sediment accumulation with artificial redds (grams).

Comparison of uncut and cut gravels at hatching

Previous studies have commented on the rate of infilling of spawning gravels (Sear, 1993, Acornley and Sear 1999, Soulsby *et al.*, 2001) and the implications for gravel cleaning operations (Shackle *et al.*, 1999). Comparison of the uncut gravel data with the freeze core data obtained from the redds at embryonic hatching, indicated that at the River Aran, River Blackwater and River Test, total fine sediment accumulation (<4mm) remained lower than the surrounding uncut gravels, suggesting that in these systems infiltration over the incubation period was not sufficient to saturate redd gravels (Table 6.4.6). Conversely, in the River Ithon, the redd gravels at hatching contained fine sediment equivalent to the surrounding uncut gravel that was sampled. This indicated that infiltration of fine sediments over the incubation period was sufficient to fill these gravels to pre-cut conditions. However, it is important to recognise that the rates of sediment accumulation recorded are influenced by hydrological events experienced over the monitoring period. In view of the hydrological conditions at each field site, the amount of material deposited over the incubation period in the River Test and Ithon may be in excess of those recorded in typical years, whereas, the amount deposited at the Aran and Blackwater may be lower than those recorded under typical climatic conditions.

	Test	Blackwater	Ithon	Aran
% < 1mm (uncut)	25.42	13.5	19.48	11.43
% < 4mm (uncut)	49.97	33.34	33.4	26.04
%<1mm (end of monitoring period)	9.99	7.31	17.21	12.3
%<4mm (end of monitoring period)	24.23	15.82	25.3	16.45

Table 6.4.6 Comparison of uncut gravels with sediment accumulation over the monitoring period. Values based on averages of all freeze core samples obtained at each field site.

These trends are in agreement with previous studies that have commented on the effectiveness of gravel cleaning (Shackle *et al*, 1999). Based on this data, it is suggested that unless gravel cleansing was repeated on a bi-yearly or tri-yearly basis, potential improvements in incubation habitat quality would be not be maintained.

Particle size and composition of material deposited over the incubation period

To assess variations in the amount and composition of deposited sediments, Table 6.4.7 summarises a suite of frequently cited gravel descriptors. The data highlights the mean and standard deviation of the sediment samples obtained from the sediment pots (Type I) and the freeze cores taken at the end of the monitoring period (hatching). The River Ithon recorded the highest total fine sediment accumulation (< 4mm) and the River Test recorded the lowest. For particles <1mm, a similar trend in accumulation was recorded. For particles < 0.63 mm, the River Ithon again records the highest total accumulation, however, this is closely followed by the River Aran, indicating a relative increase in the proportion of fine sediment in this size class at this field site. Additionally, it is important to note variations between sampling locations. As highlighted in Table 6.4.7, within the fine sediment size range, the River Test and River Aran recorded the lowest variation in size composition between monitoring locations, and the River Ithon and River Blackwater recorded the highest variation.

Gravel descriptor	Aran	Blackwater	Ithon	Test
D_{50}	**12.03 (1.04)**	**11.80 (2.15)**	**7 (1.6)**	**14.06 (2.2)**
	13.45 (4.19)	*14.19 (3.21)*	*15.47 (4.13)*	*12.88 (3.53)*
D_g	**6.48 (1.37)**	**7.98 (1.52)**	**3.19 (0.24)**	**9.48 (1.02)**
	9.66 (3.08)	*7.21 (1.14)*	*8.15 (1.94)*	*8.15 (1.94)*
Fi	**3.3 (0.75)**	**4.32 (1.07)**	*1.1* **(0.2)**	**5.14 (0.67)**
	5.34 (2.64)	*3.46 (0.85)*	*3.46 (1.40)*	*3.17 (1.35)*
Sorting	**1.97 (0.05)**	**1.88 (0.17)**	**3.65 (0.55)**	**1.85 (0.10)**
	1.97 (0.46)	*2.13 (0.25)*	*2.60 (0.43)*	*2.33 (0.47)*
Skewness	**1.37 (0.22)**	**1.45 (0.13)**	**1.96 (0.23)**	**1.43 (0.18)**
	1.48 (0.14)	*1.66 (0.157)*	*1.59 (0.12)*	*1.48 (0.14)*
kurtosis	**3.57 (0.93)**	**4.19 (2.07)**	**1.04 (1.59)**	**2.80 (1.1)**
	5.4 (3.00)	*4.5 (2.74)*	*3.48 (3.15)*	*2.43 (1.95)*
% <4mm	**20.00 (2.48)**	**17.48 (5.89)**	**39.16 (4.73)**	**13.23 (2.98)**
	17.02 (9.71)	*17.97 (4.79)*	*25.1 (6.38)*	*14.19 (6.19)*
%< 1mm	**14.55 (3.85)**	**9.58 (3.92)**	**21.53 (2.10)**	**8.06 (2.06)**
	8.44 (3.65)	*8.66 (2.68)*	*10.00 (4.31)*	*9.33 (2.60)*
% < 0.063 mm	**6.38 (2.16)**	**3.07 (2.11)**	**7.43 (2.75)**	**3.2 (0.68)**
	2.71 (0.89)	3.51 (2.69)	*0.37 (0.17)*	*0.15 (0.28)*
% < 0.002mm	**0.56 (0.20)**	**0.43 (0.25)**	**0.80 (0.32)**	**0.14 (0.03)**
	0.32 (0.13)	*0.19 (0.076)*	*0.10 (0.03)*	*0.057 (0.01)*

Table 6.4.7 Gravel descriptors. Bold figures are based on sediment pots and figures in italics are based on freeze cores. Figures in brackets are standard deviations (mm).

It is also important to note variations in the size composition of infiltrated sediments recorded by the sediment pots and freeze coring sampling techniques. Generally, the freeze cores recorded lower levels of fine sediment than the sediment pots, and greater differences in sediment composition between sampling locations (higher standard deviations). Under estimation of fine sediment levels is a common problem associated with freeze coring techniques (NCASI, 1986), and results from the cone shaped cores that are generally obtained. The small samples obtained from the freeze coring programme potentially explains the higher variability in sediment composition between sampling locations (Church, 1985).

Trends in the size composition of fine sediments recovered from the sediment pots (Type I) are further exemplified in Figure 6.4.10 and 6.4.11. Figure 6.4.10 provides a spatial representation of the composition of the fine sediments deposited at each field site. The chart highlights variations in the skewness and geometric mean of sediments deposited over the incubation period at each field site. Coarser matrix material distributions plot towards the upper right portion of the diagram, whereas, finer sediment distributions plot towards the lower left portion of the diagram. From Figure 6.4.10 it can be seen that with respect to the size composition of deposited sediments, the River Ithon and River Blackwater recorded higher intra site variability than the River Aran and River Test. Furthermore, although intra-site variability masks potential inter site differences, the River Test and River Aran generally recorded finer matrix deposits.

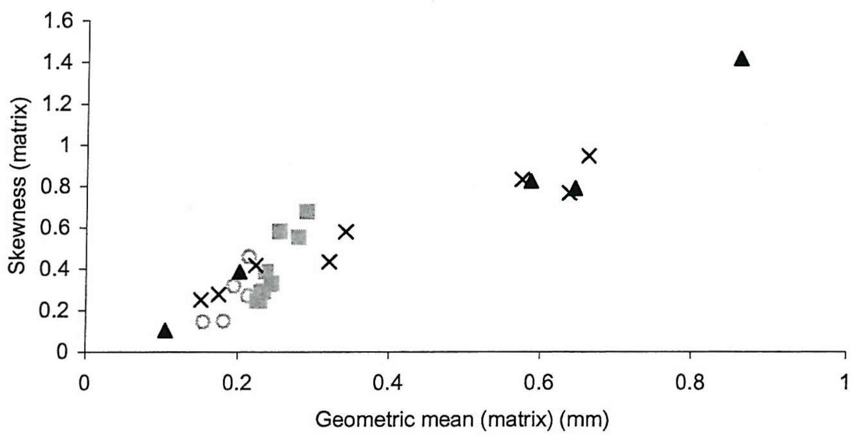

Figure 6.4.10 Bivariate scatter plot of geometric mean and skewness (matrix)

■ Test ▲ Blackwater ✕ Ithon O Aran

Figure 6.4.11 summarises the amount of fine sediment within each size class as a proportion of the total fine sediment accumulated over the incubation period. Figure 6.4.11 shows the higher proportion of material in the <1mm and <0.063mm size classes at the River Aran and River Test. Also highlighted by Figure 6.4.11 is the lower proportion of infiltrated clay sized sediments at the River Test.

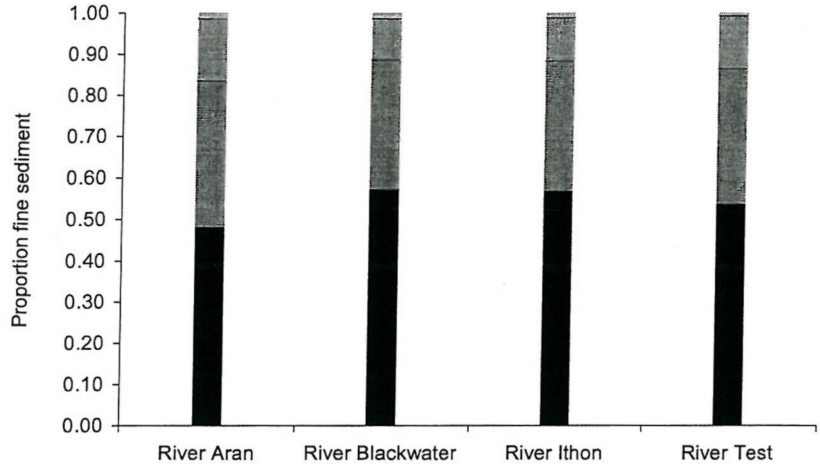

Figure 6.4.11 Stacked column chart (100%), highlighting the relative proportion of material with in four size classes: ■ <4mm, ■ <1mm, ■ <0.063mm, ■ <0.002mm.

Figure 6.4.12 shows box-and-whisker plots (Tukey, 1977) of the data recovered from the sediment pots. The boxes encompass the middle 68% of the distribution (limited by the 'hinge's of the D_{16} and D_{84} values) with a horizontal line marking the D_{50}. The whiskers extending above and below the boxes represent the D_5 and D_{95} values. The box-and-whisker plots provide a clear representation of the range and central tendency of the gravel and sediment size distributions and allow simple comparisons between multiple data samples (Kondolf and Wolman, 1993, Kondolf, 2000). The plots highlight the limited intra-site variability in the River Test particle distributions and outline the higher variability at the River Aran and River Blackwater. Additionally, the comparatively lower D_{50} of the River Ithon samples is highlighted

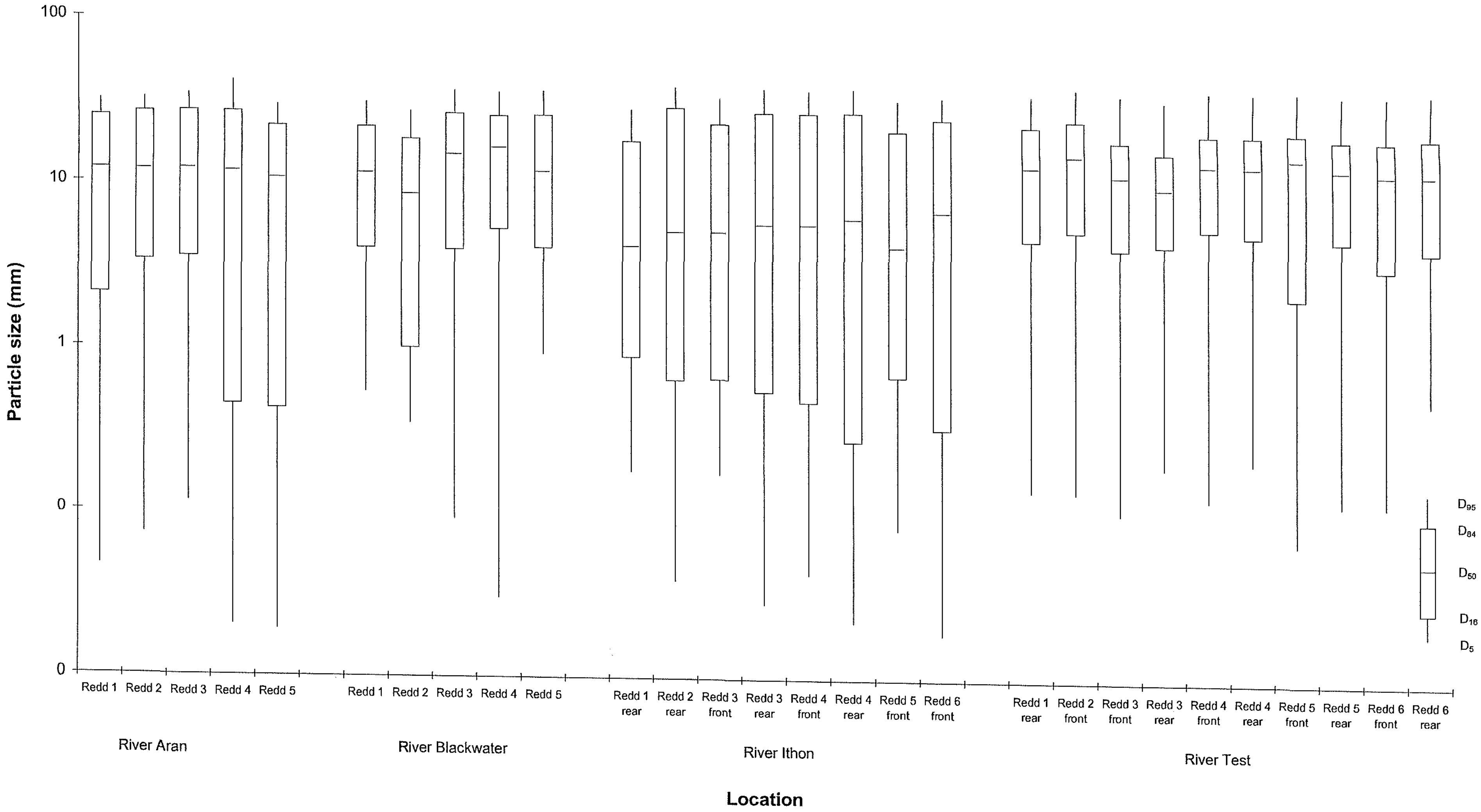

Figure 6.4.12 Box-and-whisker plots (Tukey, 1977) of the data recovered from the sediment pots at each field site.

The size composition of infiltrated sediments is influenced by the size composition of suspended sediment and bedoad material, surface and subsurface interstitial pore spaces, local sediment sources and local hydraulics (Einstein, 1968; Carling and McCahon, 1987; Lisle, 1989; Carling, 1992; Sear, 1993). In light of the limited information pertaining to the size composition of suspended sediment and bedload material, a detailed analysis of infiltration processes and trends was beyond the scope of this study. However, integration of the field observations with information presented in previous studies investigating infiltration process, allows the development of some simple interpretations of variations in the size composition of infiltrated sediments recorded at the field sites.

The River Test and River Aran recorded finer infiltrated sediments and lower spatial variability in size composition than the River Ithon and River Blackwater. Both the River Test and River Aran recorded limited bed load movement (Section 6.3.3), consequently, the materials infiltrated were predominately composed of suspended sediments, which are typically smaller than bedload derived sediments. At the River Test, observations in previous studies, which highlighted limited bedload in the River Test, support this conjecture (Acornley and Sear, 1999). With respect to the smaller variations in particle size composition between sampling locations, the deposition of suspended sediments has been shown to be distributed fairly evenly across the channel (Frostick *et al.*, 1984; Carling and McCahon, 1987; Lisle, 1989; Sear 1993; Acornley and Sear, 1999). Furthermore, many of redds constructed at these field sites were created in zones of similar flow depth and velocity (Section 5.3). Therefore, the local hydraulics and bed shear stress would have been fairly similar, thus, similar infiltration trends should be expected.

At the River Ithon and River Blackwater, the infiltrated material was generally coarser than at the River Test and River Aran. Furthermore, the variations in particle size distribution between sampling locations were greater than at the other study sites. Both these field site experienced periods of bedload movement. Therefore it is probable that the infiltrated sediments were composed of both suspended and bedload derived particles. Variations in the particle size distribution of infiltrated sediment between sampling locations probably resulted from variations in surface flow hydraulics and localised areas of sediment availability (Figure 6.4.13). At the River Blackwater, the coarser deposits were associated with higher energy flow areas and, therefore, potentially higher rates of bedload derived sediment infiltration (Sear, 1993).

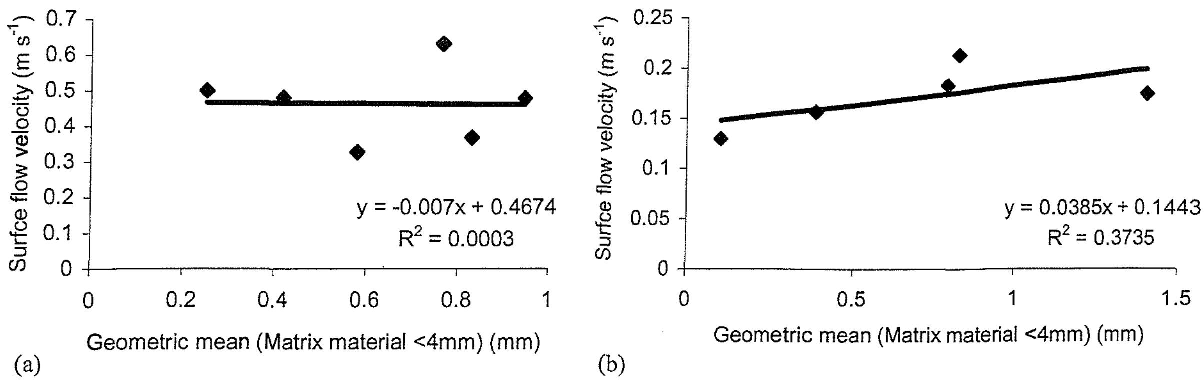

Figure 6.4.13 Relationship between surface flow velocity and particle size of deposited material (Geometric mean (*dg*)): (a) River Ithon, (b) River Aran.

At the River Ithon, there is no correlation between flow velocity and the particle size of infiltrated sediments. This may be partly explained by the relatively high flow velocities at each monitoring location (redd), which exceeded those recorded at the River Blackwater at all locations. As a consequence, infiltration may have been dominated by bedload derived materials, thus reducing potential variations in the size of infiltrated sediments related to spatial variation is the proportion of suspended and bedload derived sediments (Carling, 1992; Sear, 1993; Alonso *et al.*, 1996). Additionally, a local area of sediment supply may have influenced the size distribution of deposited sediments. Directly upstream form the monitoring site was a large gravel bar. The bar was composed of a mixture of fine and coarse gravels and coarse sands. The River Ithon experienced a number of exceptionally high flow events, each of which would have mobilised material from this bar. It is likely that the vicinity of this bar influenced both the amount and size composition of infiltrated materials of accumulation. Although not highlighted on Figure 6.4.14, there is evidence of decreasing particle size of infiltrated material with distance from the point bar. It is possible that the bar acted as local source of course bedload material, thus influencing the observed trends in sediment infiltration.

Accumulation of organic material

As highlighted in Section 3.2, in addition to inorganic sediments, it is also important to consider the amount of organic material infiltrating redd gravels. To summarise, inorganic material influences oxygen fluxes through riverbeds by blocking pore space, provides a basis for the development of oxygen demands and promoting the growth of biofilms within the riverbed (Chen and Li, 1999). Table 6.4.8 summarises the results of the loss-on-ignition analysis of infiltrated sediments at each field site. The River Test recorded a higher organic content than at the freshet sites, suggesting that there was greater availability of organic material for deposition in the River Test. This observation is documented by other studies (Welton, 1980). Generally, chalk streams have high instream densities of macrophyte vegetation. As this vegetation dies back in autumn and winter, increased amounts of organic detritus are present within the water column and potentially available for deposition (Welton, 1980). Importantly, organic material is of a lower specific gravity than inorganic material, consequently, there is often a propensity for particulate organic material to be flushed from the riverbed when gravels dilate or become entrained during high flows (Shapely and Bishop, 1965, Garvin, 1974, Ringer and Hall, 1987, Alonso *et al.*, 1996). However, as described in Section 6.3.3, chalk rivers seldom experience periods of gravel entrainment (Sear *et al.*, 1999), consequently, materials deposited in the riverbed will have long residence times. These factors may explain the higher amount of organic material present within the riverbed of the River Test. The values of organic material recorded in the freshet systems are also in agreement with values reported in previous studies (Sear, 1993).

	Aran	**Blackwater**	**Ithon**	**Test**
Mean % organic <0.71mm	7.52	3.43	5.3	19.78
Standard Deviation	0.69	0.84	1.1	2.3

Table 6.4.8 Organic material deposited over the monitoring period at each field site.

6.4.3.3 Correlations between survival and granular properties of the incubation environment

To test the ability of previously proposed granular determinants of survival, the sedimentary data gathered in each system was compared with recorded survival rates. This assessment was based on both the data recovered from the sediment pots and from the freeze cores. As in Section 6.1, the analysis is divided into two stages, first an assessment of the data collated from all field sites (Table 6.4.9) and, second, a site specific analysis (Table 6.4.10). Generally, granular metrics of survival were poor descriptors of incubation success. Furthermore, in many instances the direction of the correlations opposes those reported in other studies (McNeil and Ahnell, 1964; Koski, 1966; Hall and Lantz, 1969; Bjorn, 1969; Phillips, 1975; Koski, 1975; McCuddin, 1977; Platts, 1979; Shirazi *et al.*, 1981; Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Cederholm *et al.*, 1981; NCASI, 1981; Tappel and Bjorn, 1983; Tagart, 1976, 1984; McCrimmon Gots, 1986; Chapman, 1988; Tappel and Bjorn, 1989; Young *et al.*, 1991).

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

Table 6.4.9 Pearson correlation coefficients based on data collated from all sites.

	D_{50}	*Dg*	*Fi*	% <4mm	% < 1mm	% < 0.067mm
Test pots	0.068	0.16	0.36	-0.27	0.01	0.06
Test freeze cores	-0.57	-0.53	-0.30	0.19	0.27	0.29
Blackwater pots	-0.28	-0.58	-0.52	0.67	0.68	0.11
Blackwater freeze cores	0.69	-0.1	-0.083	-0.54	0.4	0.79
Ithon pots	-0.001	0.35	0.14	-0.028	-0.11	-0.39
Ithon freeze cores	0.35	0.3	0.29	-0.27	-0.30	-0.07
Aran pots	-0.27	-0.49	-0.48	0.31	0.65	0.65
Aran Freeze cores	0.6	0.43	0.28	-0.1	-0.21	0.0049

Table 6.4.10 Site specific Pearson correlation coefficients (r). *Dg* based on power analysis (Platts, 1983).

Gravel permeability, which is a measure of the ability of gravels to transfer water, was assessed at the River Aran and River Blackwater. Applying a simple linear relationship between gravel permeability (cm h^{-1}) (at hatching) and embryonic survival to hatching, a weak linear relationship with survival was observed (r^2 =0.257) (Figure 6.4.14). However it should be noted that a relatively narrow range of gravel permeabilites was assessed across a limited number of data points. Chapman (1988), using data supplied by Koski (1966) and McCuddin (1977), assessed the relationship between gravel permeability and survival in two North American rivers. McCuddin (1977) data showed a strong correlation with survival (r^2 = 0.83) across permeability values ranging from around 2000 cm h^{-1} to 70 000 cm h^{-1}. Using the data supplied by Koski (1968) a weaker correlation with survival was identified (r^2 = 0.33). However, this relationship was based on a different range of permeabilities (300-20 000 cm h^{-1})

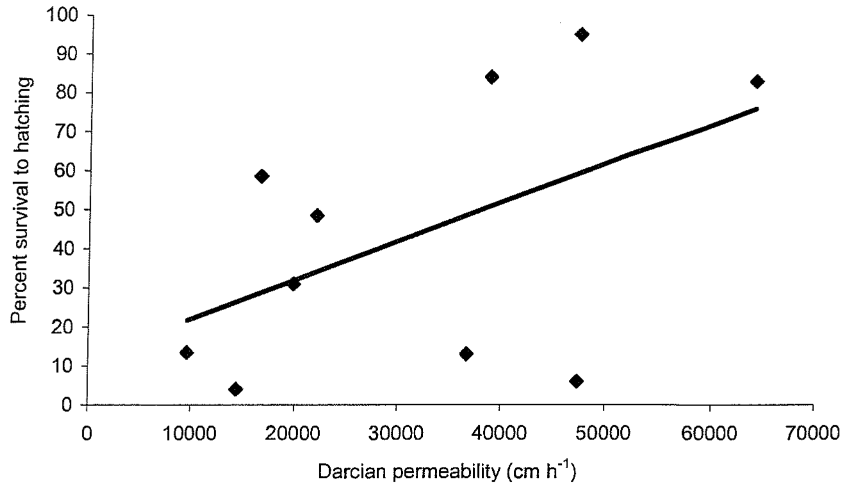

Figure 6.4.14 Relationship between permeability and embryonic survival. Linear relationship of the form y= a x + b, where y is percent survival to hatching, a is 0.001, b is permeability (cm h^{-1}) and b is 12.088 (r^2 = 0.257).

6.4.3.3 Impact of fine sediment on intragravel flow velocity

Sampling difficulties experienced at the River Test and River Ithon resulted in the abandonment of the multi-pot sediment accumulation experiment at these field sites, therefore the following analysis is restricted to the observations made at the River Aran and River Blackwater. From the data recovered from the sediment accumulation redds (Type II), rates of sediment accumulation were shown to be closely related to flow over the monitoring period, with greater deposition occurring under higher flow events (Frostick *et al.*, 1984; Carling and McCahon, 1987; Lisle, 1989; Sear, 1993) (Figure 6.4.15).

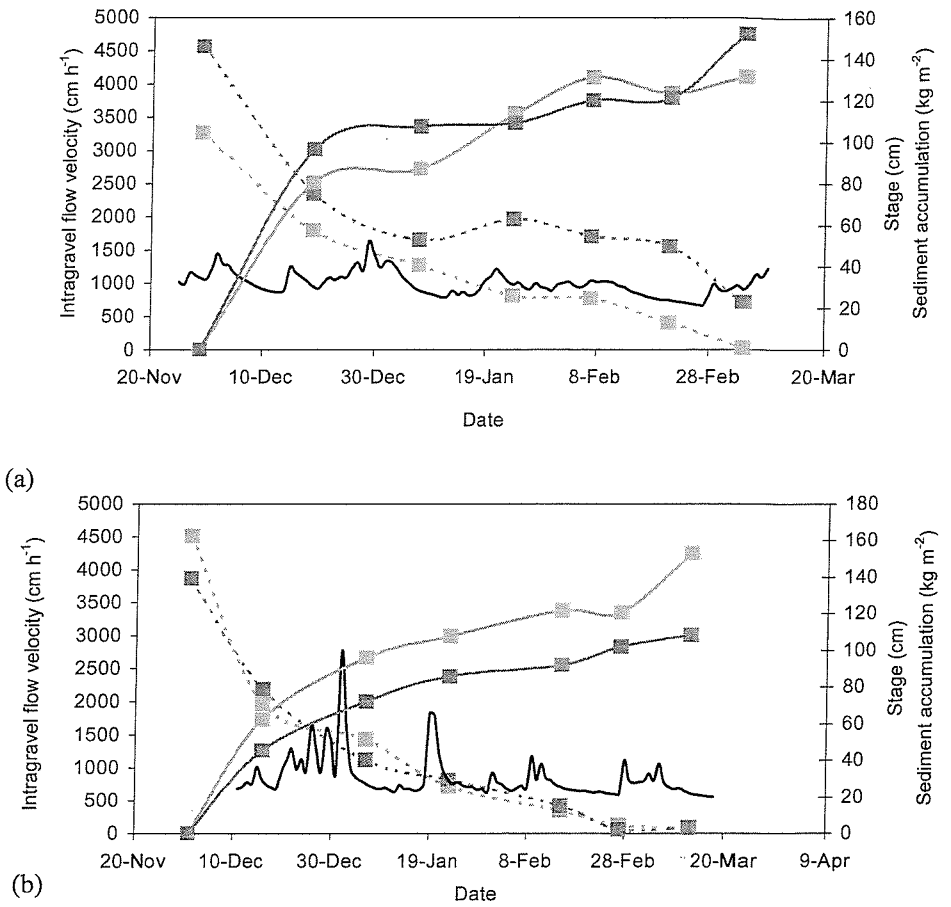

Figure 6.4.15 Relationship between flow, sediment accumulation and intragravel flow velocity. (a) River Blackwater. (b) River Aran. ——— Stage (cm) ——— Sediment accumulation (kg m^2) (Redd 1) ——— Sediment accumulation (kg m^2) (Redd 2) - - - - - Intragravel flow velocity (cm h^{-1}) (Redd 1) - - - - - Intragravel flow velocity (cm h^{-1}) (Redd 1)

It is also interesting to note the general decline in the rate of sediment accumulation recorded after the initial peak post redd creation. Although this trend may be partially explained by high flow events directly post redd creation, it may also be indicative of variations in the mechanisms controlling the influx of fine sediment into the riverbed. Specific data relating to potential processes influencing infiltration rates were not obtained in this study. However, based on the findings of other studies, it is possible to identify some potential explanations for this trend. First, it is possible that the interstices between the surface gravels became partially blocked by sediments depositing near the gravel surface, resulting in reduced rates of infiltration (Besheta and Jackson, 1979). In the River Blackwater, periods of gravel entrainment (Section 6.3.3) may have cleansed the surface layers, reducing this blocking mechanism. However, at the River Aran, limited gravel entrainment was recorded, therefore, it is possible the obstruction of surface gravel interstices may have influenced rates of fine sediment infiltration. Second, the lateral movement of sediments through riverbed gravels (Sear, 1993) may have influenced rates of sediment accumulation. Discrete pockets of gravels with higher permeabilities than the surrounding gravel may enhance the lateral movement of sediment. Directly post redd creation, the redd gravels are cleansed of fine sediment and are of greater permeability than surrounding uncut gravel (Chapman, 1988). Therefore, increased lateral movement of fine sediment may have occurred directly post redd creation, contributing to the high initial rates of sediment accumulation. This process may also help explain the accumulation of sediment in the absence of flow events. Third, the shape of the redd has been shown to promote downwelling flow, potentially enhancing the infiltration of fine sediment into redd gravels (Cooper, 1965). Finally, surface gravel adjustments may have influenced the size and availability of pore spaces in the redd gravels post construction. Directly post redd creation, the redd gravels are openwork and the interstices between gravels are dilated (Kondolf *et al.,* 1993). This contrasts with riffle gravels, which generally display a level of compaction and sorting, with interlocking gravels and small interstices between particles (Sear, 1996). Over time, it is possible that redd surface gravels adjust to a level of sorting and compaction more characteristic of riffle gravels, thereby reducing the interstitial pore spaces and potential rates of infiltration.

Also highlighted in Figure 6.4.15 is the decline in intragravel flow velocities recorded over the incubation period. Fine sediments that infiltrate riverbed gravels block interstitial pore spaces and reduce gravel permeability, thereby inhibiting intragravel flow velocities (Chapman, 1988). A Pearson correlation analysis of sediment accumulation and intragravel flow velocity was undertaken to investigate the relationship between gravel composition and intragravel flow velocity. Four metrics describing gravel composition were analysed; % fine sediment < 4mm, % fine sediment < 1mm, geometric mean and D_{50}. The results of the analysis are presented in Table 6.4.11. With the exception of median particle diameter (D_{50}), granular descriptors were significantly correlated with intragravel flow velocity (95% confidence limit) at all sampling locations.

Descriptor	Aran L1	Aran L2	Blackwater L1	Blackwater L2
D_{50}	0.29	0.61	0.55	0.83
D_g	0.86	0.98	0.88	0.86
% <1mm	-0.89	-0.97	-0.93	-0.71
% <4mm	-0.98	-0.97	-0.98	-0.85

Table 6.4.11 Pearson correlations between intragravel flow velocity and granular descriptors.

Applying a linear regression model (Table 6.4.12), the relationship between sediment accumulation and percent fine sediment < 4mm was investigated. As outlined in Figure

6.4.16 and Table 6.4.12, a strong relationship between intragravel flow velocity and sediment accumulation was recorded at each sampling location. However, the relationships are site specific, and are not spatially transferable. This site specificity can be explained by intra and inter site variations in sedimentary composition and hydraulic gradient. For example, the finer particle size composition of sediment deposited at the Aran may have resulted in a greater impact on intragravel flow velocity, resulting in the steeper gradient of the relationship between flow and sediment accumulation observed at each sampling location. Intra-site variations may be explained by variations in hydraulic gradient, between sampling locations, with higher hydraulic gradients resulting in higher intragravel flow velocities. The influence of hydraulic gradient potentially influenced the impact of fine sediment on intragravel flow, resulting in the lateral displacement of the relationship between intragravel flow and sediment accumulation (Figure 6.4.16). Factors influencing hydraulic head include surface topography and surface flow characteristics (Section 3.2, Section 6.3). An interrogation of the hydraulic gradient data (Section 5.4) indicated that the locations with higher hydraulic gradients recorded higher intragravel flow velocities.

	Linear regression model	r^2
Blackwater (L1)	y = -98.506x + 3331.8	0.95
Blackwater (L2)	y = -109.72x + 4598	0.98
Aran (L1)	y = -135.03x + 4216	0.95
Aran (L2)	y = -158.37x + 3828.5	0.99

Table 6.4.12 Linear regression models: where y is intragravel flow velocity (cm h^{-1}) and x is sediment accumulation (<4mm) (kg m^{-2}). All relationships significant at the 95% confidence limit.

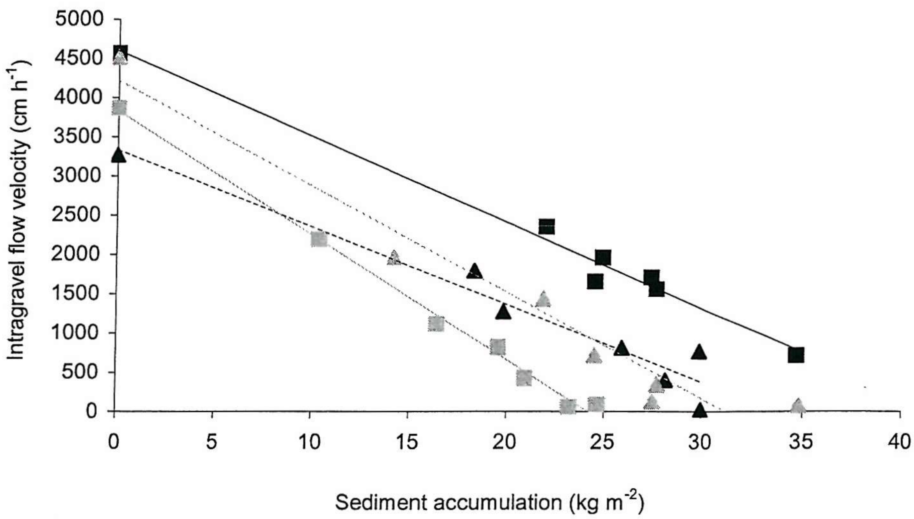

Figure 6.4.16 Relationships between sediment accumulation (<4mm) and intragravel flow velocity. Fitted lines based regression models outlined in Table 6.4.12.

These results highlight the direct influence of fine sediment on intragravel flow velocity. As intragravel flow is controlled by the influence of fine sediment on gravel permeability, hydraulic gradient and surface flow conditions (Section 6.3), it is proposed that for locations of similar hydraulic gradient and surface flow conditions, measures of the composition of the riverbed may provide site specific information on potential intragravel flow velocities.

6.4.3.4 Impact of sediment accumulation on intragravel oxygen concentration

Field derived datasets

The oxygen demands induced by materials deposited at each field site are shown in Table 6.4.13. As oxygen demands are generally associated with organic materials, oxygen demand values are reported in mg of oxygen per gram of organic material (dry weight) (mg O_2 g^{-1}). It should be noted that this value relates to the total oxygen demand induced by all materials and substances contained in the sediments and does not distinguish between biological oxygen demands (BOD) and nitrogen oxygen demands (NOD) or chemical oxygen demands (COD) (Section 3.2). Both 5-day and 25-day oxygen demand values are reported. The five-day demand is a standard laboratory protocol for determining BOD demands. However, in light of the retention time of sediments and the potential influence of longer term nitrogen based demands, a 25-day test was performed to provide a better indication of the total oxygen demand imposed by the deposited organic material.

Location and date	**5-day (mg O_2 g^{-1})**	**25-day (mg O_2 g^{-1})**	**Time from last high flow event (days)**
Test 23/1/02	10.96	57.73	N/A
Test 10/1/03	16.15	62.17	N/A
Blackwater 13/3/03	43.79	105.85	5
Ithon16/2/02	49.81	189.13	3
Ithon 21/2/03	32.86	70.82	15-20
Ithon 13/3/03	11.42	54.49	5-10
Aran 7/1/03	16.04	43.69	6
Aran 21/2/03 (a)	61.72	143.80	14
Aran 21/2/03 (b)	35.23	75.86	14

Table 6.4.13. Oxygen demands of sediments recovered at each field site. Demands based on dry weight of organic material. Infiltration assumed to be related to high flow events (Section 6.4.3.3). Note: the stable hydrological regime and limited variation in suspended sediment concentration at the River Test did not allow an accurate assessment of time from infiltration event.

The oxygen demand values display spatial (intra and inter site) and temporal variability. In broad terms, the River Test recorded the lowest demand. Furthermore, the demand recorded in successive years remained similar. The sediments from the River Ithon sampled on 12th February 2002 recorded the highest total oxygen demand. However, this system also recorded the highest temporal variability, with oxygen demand values obtained in 2003 less than half those recorded in the previous monitoring period.

Temporal and intra-site variations in oxygen demand may have resulted from variations in the age of sampled materials and variations in composition of materials deposited in the riverbed. The demand induced by the oxidation processes reduces over time (Section 3.2.4), therefore, if fresh materials are not supplied to the intragravel environment, the oxygen demand of infiltrated material will reduce over time (Chevalier and Murphy, 1985). The timing of sampling can therefore influence the magnitude of the oxygen demands recorded. As highlighted in Table 6.4.13, the samples recording higher oxygen demands are often associated with samples extracted closer to deposition events. With respect to composition of deposited materials, agricultural waste and animal faeces will typically record higher oxygen demands than more naturally occurring organic detritus (Section 3.2.4). The spatial variability in oxygen demand recorded at the River Aran also suggests that the composition of infiltrated materials may vary significantly over small spatial distances (further details of the sources of the oxygen demands at each field site, and potential reasons for variations in measured oxygen demands are outlined below).

Consideration must also be given to the representativeness of the samples used to assess the oxygen demands. Representative samples for assessment of oxygen demands are difficult to obtain as they are typically based on small samples (1-5grams) that may not be representative of larger bulk sediments. For instance, if a sub sample contains small amounts of high oxygen inducing material, for instance animal faeces, the oxygen demand may be overestimated. Consequently, multiple replicates should be performed, thereby allowing a detailed analysis of variances between samples. Project limitations restricted field sampling to two bulk samples from two locations in season one and two sets of two bulk samples from two locations in season two. In the laboratory, these samples were subdivided into two replicates. In view of the limited replication, it is possible that some oxygen demand values may not be representative of conditions in the riverbed.

When interpreting the potential impact of oxygen demands on intragravel oxygen concentrations, it is important to consider the amount of oxygen consuming material contributing to the demand, and its availability within the gravel substrate. As organic matter is the primary source of oxygen demands (Section 3.2.4), an assessment of the organic material recorded within the artificial redds in each system, provided a basis for assessing the amount of material contributing to the oxygen demands at each site (Table 6.4.8). To provide an estimate of the relative impact of a given oxygen demand on intragravel oxygen concentration, a subset of oxygen consumption values reported in Table 6.4.13 were adjusted to account for differences in the amount of organic material present in the sediment samples from each site. To achieve this, the amount of organic material in contact with one litre of interstitial water was determined and an oxygen demand (mg O_2 g $(\text{organic})^{-1}$ h^{-1}) was applied to the organic material. To determine the amount of organic material in contact with in one litre of sediment the amount of organic material in one litre of substrate was multiplied by the gravel porosity. As porosity was not quantified at the field sites, a standard porosity value of 0.25 was adopted (Chevalier and Carson, 1985).

Table 6.4.14 summarises the potential demand imparted on one litre of water at each field site. Temporal variability and inter site differences in oxygen demand remain, however, the values provide a more representative assessment of the actual demands present within the riverbed at each field site. The oxygen demand present within the riverbed of the River Blackwater was lower then at the other field sites. This is simply because this system recorded the lowest accumulation of fine sediment and the lowest organic content, therefore, the availability of oxygen consuming material was lowest in this system. The River Aran (7/1/03) recorded the highest potential demand and this was due to high oxygen demand and relatively high availability of oxygen consuming material in this system.

Location and date	**Mean Percent organic material**	**Oxygen demand mg O_2 g $(\text{organic})^{-1}$ h^{-1}**	**Demand imparted on one litre of water (mg O_2 $l^{-1}h^{-1}$)**
Test 23/1/02	19.78	3.21	0.0045
Blackwater 13/3/03	3.43	4.86	0.0009
Ithon16/2/02	5.3	7.36	0.0057
Aran 7/1/03	7.52	2.41	0.0021
Aran 21/2/03 (b)	7.52	7.98	0.0071

Table 6.4.14 Demand imparted on one litre of interstitial water at each field site.

The results presented thus far have focused on the total oxygen demand at each field site. Figure 6.4.17 highlights the relative contribution of BOD and NOD demands at the River Test and River Aran. This data indicates that carbon based oxygen demands were dominant in the River Test, whereas at the River Aran nitrogen demands composed a significant proportion (50%) of the total oxygen demand. This observation is consistent with the oxygen demand time trends produced for these samples, which indicated a two-stage response. Although NOD tests were not carried out on all samples, a temporal analysis of the oxygen demand curves provided an indication of the potential NOD for each sample (Figure 6.4.18). All samples exhibit an oxygen demand extending beyond 12 days; suggesting the presence of a second stage demand curve. However, as an NOD test was not performed, it is not possible to determine whether these trends are induced by a nitrogen demand or a result of a second stage carbon demand. Potential sources of nitrogen-based demands include fertilisers and organic manure.

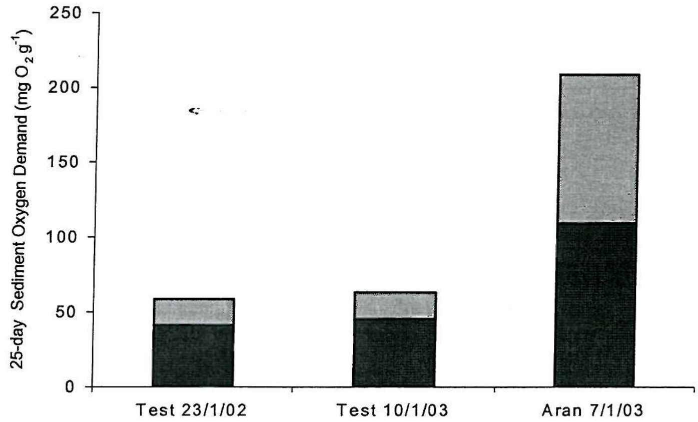

Figure 6.4.17 Total oxygen consumed (mg O_2 g^{-1}) over 24-day period.

■ Carbon Demand ▢ Nitrogen Demand

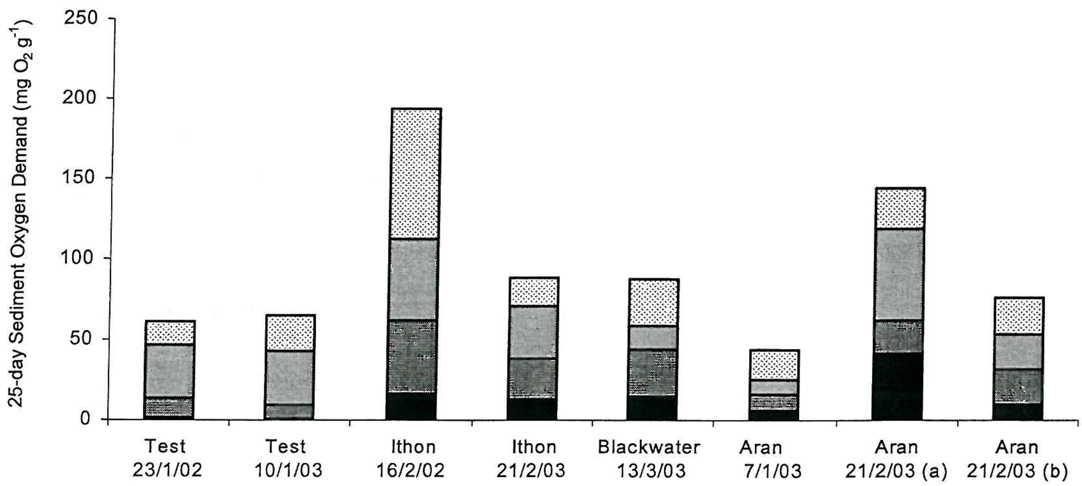

Figure 6.4.18 Staked column chart outlining temporal oxygen demand trends for sediments recovered from field sites: ■ 1-day ▩ 5-day ▢ 12-day ▧ 25-day

Based on data presented above, on the land use activities in each study catchment (Section 5.3) and on observations made during the monitoring period, a general assessment of the source materials contributing to the oxygen demands recorded at each field site can be undertaken. At the River Ithon a high oxygen demand was recorded on the 12th February 2002. Prior to the extraction of the sediment sample there was a period of overbank flow. The dominant landuse activity in the surrounding catchment is agricultural. At the study site, grazing cattle and sheep were observed on the floodplain at the study site. It is possible that the bank exceedance flow increased the risk high oxygen demand substances entering the watercourse from the adjacent land surface. Potential high oxygen demand materials include animal faeces, fertilisers that had been applied to the land, and poorly or inappropriately stored agricultural waste (Chevalier and Murphy, 1985; DEFRA, 2002). In 2003, the sediments extracted from the River Ithon recorded a lower demand. These samples were extracted after a period of low flow. It is probable that reduced inputs of materials from the adjacent land surface, resulted in the lower oxygen demand recorded. The River Aran is contained within a locality of similar land-use pressures, it is possible therefore, that materials of similar composition to those entering the River Ithon were present at this system, resulting in the high demand recorded at the River Aran 21/2/03 (a).

At the River Test, the dominant land-use is arable agriculture. With respect to inputs of materials and substances with high oxygen demands, the primary risks are associated with fertilisers and agricultural waste. However, as surface runoff is lower in this catchment than at the freshet sites and as bank exceedance was not exceeded during the monitoring period, it is probable that there were lower inputs of catchment derived sources of oxygen consuming materials than at the River Ithon and River Aran. A major source of oxygen consuming material in the River Test was organic detritus (Section 6.4.3.2). However, although large quantities of organic material were recorded in the River Test sediments, organic detritus has a lower associated oxygen demand than agriculturally derived materials, hence the lower oxygen demand oxygen recorded.

At the River Blackwater, mixed forest is the dominant landcover. Consequently, sources of high oxygen demand materials are lower in this system. However, a relatively high oxygen demand was recorded, suggesting the presence of high oxygen demand material. Potential sources of this oxygen demand include organic debris and detritus from the riparian vegetation.

A modelling approach to assessing the impact of oxygen demands on oxygen concentrations

The impact of sediment oxygen demands on intragravel oxygen concentrations can by modelled using a simple streamline approach (Chevalier and Carson 1985). Oxygen concentrations at a given point within the riverbed are calculated from streamlines along which velocities are assumed to be equal. Along each streamline, a differential equation describes the influence of sedimentary oxygen demands on intragravel oxygen concentrations.

$$v\frac{dC}{ds} = -SOD \tag{6.4.7}$$

where, *SOD* (sediment oxygen demand) is the demand imparted on one litre of interstitial water, s is the distance along the streamline (m), v is the intragravel velocity (cm h^{-1}) and C is initial oxygen concentration (mg l^{-1}). Integrating this equation gives:

$$Co\int_{Co}^{C} dC = \frac{-SOD}{V}\int_{o}^{s} ds \tag{6.4.8}$$

$$C = Co - \left(\frac{SOD}{V}\right)s \tag{6.4.9}$$

Assuming steady state conditions, the oxygen concentration at any distance along a streamline can be determined. It should be noted that this model is a simplified facsimile of a complex system in which variable flow velocities, variations in sedimentary structure and diffuse processes also influence oxygen concentrations. However, for the purposes of describing the potential impact of oxygen demands, it provides a workable model of the intragravel environment.

Application of the SOD model, allowed estimates of the impact of the oxygen demands on oxygen concentration across a range of intragravel flow velocities (Figure 6.4.19). As intragravel flowpath lengths were not recorded at the study sites, estimates were based on the location of artificial redds in relation to areas of downwelling, observations of hydraulic head at sampling locations, and reference to previous research (Chevalier and Murphy, 1985; Boulton, 1998; Edwards, 1998; Malard *et al.*, 2002). At the freshet sites, redds were located at the interface between pools and riffles. At these locations downwelling would be expected. Measures of hydraulic head at each sampling redd validated this assumption (Figure 5.17).

Based on the assumption that downwelling was indicative of a short flow path between the point of surface-subsurface exchange and the sampling location, a flow path length of 1.0m was adopted. At the River Test, typical pool-riffle morphology was not present, however, the redd morphology was retained for the duration of the monitoring period. The redd morphology would have induced downwelling (Stuart, 1955, Thebodeaux and Boyle, 1987). Based on the distance between the upward lea of the redd and the location of the monitoring equipment, an average flow path of 0.75m was assumed representative of flow paths at the River Test.

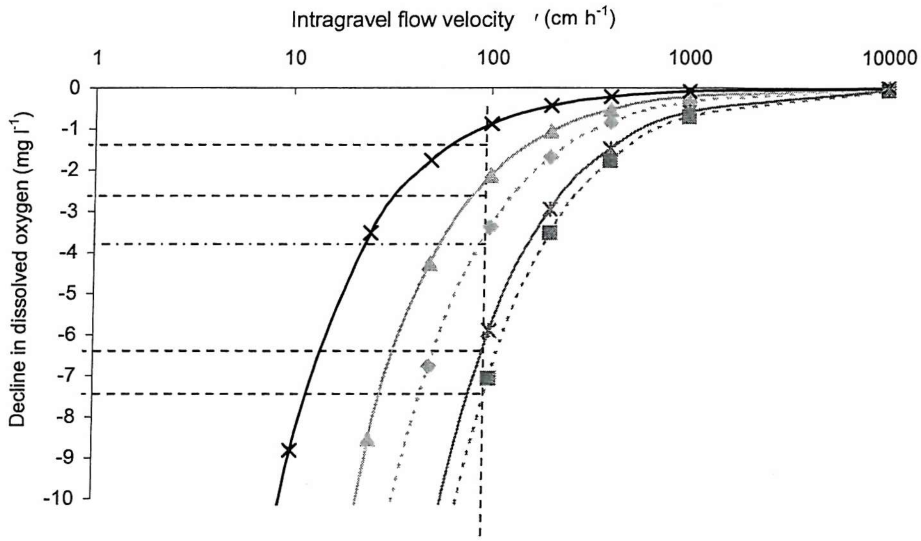

Figure 6.4.19 Results of SOD model. Plot show decline in dissolved oxygen concentration for a range of SOD values and intragravel flow velocities. Dashed lines highlight oxygen concentrations at intragravel flow velocities of 100cm h^{-1} for each field site.

Test 23/1/02 — Blackwater 13/3/03 — Ithon 16/2/02

Aran 7/1/03 — Aran 21/2/03 (a)

As highlighted by Figure 6.4.20, intragravel flow velocity is an important control over the impact of oxygen demands on intragravel oxygen concentrations. For the range of oxygen demands and flow paths lengths assessed, the model predicts that intragravel flow velocities above 1000 cm h^{-1} have limited affect on oxygen concentrations. However, at intragravel flow velocities of around 100 cm h^{-1} the model suggests that the oxygen demands recorded at the River Aran (21/2/03 (a) and the River Ithon (16/2/02) would result in oxygen within in the range reported to be harmful to incubating embryos (Section 1.2). This observation is of particular relevance as intragravel flow velocities recorded during the monitoring programme were frequently below 100 cm h^{-1}.

To test the accuracy of the models predictions, the output form the model was compared with the results obtained during the field-monitoring programme. To assess the relationship between the oxygen concentration and intragravel flow velocity at the field sites, logarithmic regression models (Table 6.4.15) were fitted to the oxygen concentration and intragravel flow velocity data recorded at each field site (Figure 6.4.20). As highlighted by variations in the gradients of the relationships at each site, there is strong inter-site variability in the impact of SOD on intragravel oxygen concentrations, with the River Ithon recorded the highest impact and the River Blackwater recording the lowest. The large scatter in the dissolved oxygen concentrations recorded for similar intragravel flow velocities is probably indicative of spatial variations in intragravel flow path length and sedimentary oxygen demands.

Site	Regression model	r^2
Test	y = 0.375 ln (x) – 2.850	0.43
Blackwater	y = 0.172 ln (x) – 1.683	0.20
Ithon	y = 0.891 ln (x) – 7.791	0.69
Aran	y = 0.824 ln (x) – 6.944	0.66

Table 6.4.15 Summary of regression models used in SOD analysis.

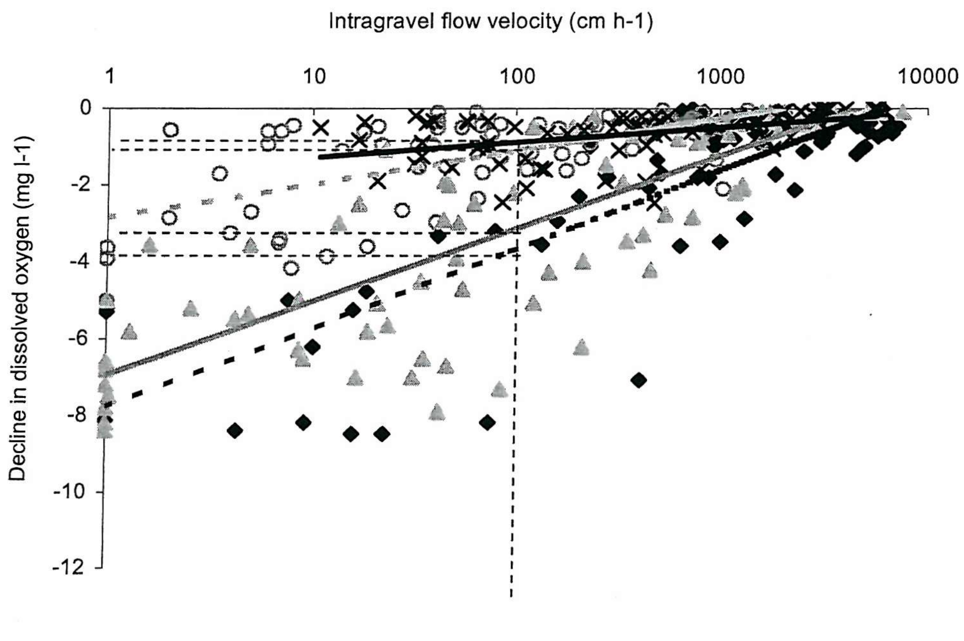

Figure 6.4.20 Intragravel flow and decline in oxygen concentration recorded at field sites. Data points represent oxygen concentrations and intragravel flow velocities at a given point in time, thick lines show regression models outlined in Table 6.4.16. Dashed lines show oxygen concentrations at 100 cm h^{-1} based on fitted regression models at each site.

○ - - Test ✕ — Blackwater ▲ — Ithon ◆ - - Aran

The logarithmic relationship between flow and oxygen concentration recorded in the field does not conform to trend displayed by the SOD model, however, in relative terms the dissolved oxygen responses observed at the field sites are similar to those estimated applying the SOD model (Table 6.4.16). The largest declines in dissolved oxygen were recorded in the River Ithon and Aran, and lowest were recorded in the River Blackwater and River Test. However, the magnitude of the decline in oxygen concentration with intragravel flow velocity estimate by the SOD model varies from the declines recorded in the field. Generally, the model overestimated the impact of sedimentary oxygen demands on intragravel oxygen concentration, particularly at high oxygen demand values.

	Aran 7/1/03	**Blackwater 13/3/03**	**Ithon 16/2/02**	**Test 23/1/02**
Decline in DO at 100 cm h^{-1} (field)	3.9	0.9	3.4	1.0
Decline in DO at 100 cm h^{-1} (Model)	-7	1	-6	3.3

Table 6.4.16 Comparison of field and model predictions of decline in intragravel dissolved oxygen concentration (DO) at a comparative intragravel flow velocity.

Three potential explanations for this discrepancy are proposed. First, the oxygen demand values obtained in the laboratory were unrepresentative of the oxygen demands present in the field (see above for a description of potential sources of error). Second, oxygen demands vary over time dependent on the residence time of organic material (Figure 3.2.9). The model uses a constant oxygen demand value that was based on the average rate of oxygen consumption determined from the 25-day test. In the natural river environment, oxygen demands will vary dependent on the age of organic material. If new material is not introduced to the riverbed, the potential oxygen demand induced by oxygen consuming material will diminish over time as the organic material degrades (Chevalier and Murphy, 1985), resulting in reducing impacts on intragravel oxygen concentrations. Although field data is limited, oxygen demand values support this premise (Table 6.4.13). Third, the model assumes a constant temperature, however, in the field, significant variations in temperature were recorded. Increased temperature induces increased synthesis of organic materials (Chevalier and Murphy, 1985) and higher oxygen demands. This would have resulted in temporally variable, temperature dependant oxygen demands within the riverbed. Finally, the model is sensitive to flow path length. Although efforts were made to estimate the potential flow path lengths at the field sites, it is possible that these estimates were unrepresentative of actual flow paths, furthermore, they did not recognise the potential spatial variability of flow path length at the field sites. A more accurate assessment of flow path lengths would be required to fully test the accuracy of the models outputs.

6.4.4 Discussion

6.4.4.1 Granular character of study sites

The total amount of sediment accumulated over the incubation period varied between the study sites. The sediment accumulation recorded at the study sties can be compared with previous investigation into sediment accumulation in salmon spawning gravels (Table 6.4.17).

Study site	**% fine sediment <2mm**	**Source**
Newmills Burn	23.1	Soulsby *et al.* (2001)
North Tyne	11.0	Sear (1993)
Great Eggleshope burn	10.0	Carling and McCahon (1987)
River Test	24.5	Acornley and Sear (1999)
Wallop Burn	17	Acornley and Sear (1999)
Turkey Brook	31	Frostick (9184)
River Piddle	22.6	Walling and Amos (1994)
River Test	10.0	This study
River Ithon	28.9	This study
River Aran	15.7	This study
River Blackwater	12.2	This study

Table 6.4.17 Documented values of total sediment accumulation within spawning gravels.

As highlighted in Table 6.4.17, the total sediment accumulations at each each field site recorded in this study were typical of the ranges recorded in previous studies. However, it is interesting to the note the lower total sediment accumulation recorded at the River Test in this study compared with that recorded by Acornley and Sear (1999). As highlighted in Section 6.4.3.1, sampling at this stream occurred during a drier than average period, and this may have resulted in lower rates of sediment infiltration recorded in this study. With respect to the high sediment accumulation recorded at the River Ithon, a local sediment supply feature (gravel bar) directly upstream of the monitoring site may have influenced the amount of material, particularly in the bedload size fraction, available for deposition at this field site. Samples of sediment from the gravel bar were not obtained in this study, therefore, a comparison of the sediment sampled within the redds with sediment contained within the gravel bar cannot be undertaken. However, a considerable decline in the size of the bar over the monitoring period suggests that it was acting as a local sediment source.

Variations in the amount of sediment deposited between sampling locations within each field site were also recorded (Figure 6.4.10). As discussed in Section 6.4.3.2, these variations were probably a consequence of local geomorphologic and hydraulic controls. However, with respect to characterising the quality of salmon spawning gravels, it highlights the importance of sampling multiple locations across a spawning riffle. Similarly, variations in sediment accumulation can result from temporal variations in sediment availability (sediment load) associated with different surface flow conditions and land use activities. Therefore, it is suggested that when assessing the quality of spawning gravels and incubation habitats, careful consideration should be given to spatial and temporal representativeness of sampling.

With respect to the particle size of deposited materials, these were also shown to vary within and between the study sites. Spatial and temporal variability in the size of deposited materials is a common characteristic of river systems, and is representative of the complex and dynamic process governing sediment mobilisation, transport and deposition or infiltration (Frostick et al., 1984; Carling and McCahon, 1987; Lisle, 1989; Sear 1993; Acornley and Sear, 1999).

6.4.4.2 Granular determinants of incubation success

The development of a simple granular based determinant of incubation success has been an enduring goal in fishery science, and a number of granular determinants of incubation success have been proposed (Section 6.4.1). However, for the range of conditions sampled in this study, granular metrics performed poorly as determinants of potential embryonic survival.

The disparity between the results presented in this study and those of previous researchers may result from distinctly different sampling environments. In this study, natural systems were investigated. Consequently, oxygen flux and incubation success was influenced by a compound of factors, including gravel permeability, sedimentary oxygen demands and variable hydraulic gradients. Furthermore, the magnitude and interaction of these factors may have varied significantly between the study sites dependant on hydrologic, geomorphic and land-use controls. In contrast, many of the relationships between incubation success and granular properties of the incubation environment proposed in the literature were developed in laboratory settings or artificial channels (Chapman, 1988). Consequently, they are based on investigations of simplified facsimiles of a complex environmental system. Under controlled conditions, sediment accumulation may be the dominant factor influencing incubation, and granular determinants may provide a good indication of incubation success. However, in a more natural environment, where a compound of factors influences the availability of oxygen to incubating embryos, simple relationships between sediment composition and incubation success will be uncommon.

It is also important to note that many of the relationships between granular characteristics of the incubation environment and incubation success that have been proposed in the literature were developed in North America. Land-use activities and pressures in North America, although not dissimilar, are distinct from those in the U.K. The dominant land-use in the U.K is agriculture, however, in North American many salmon bearing rivers are contained within forested catchments. Typically, some form of timber management is present in these forested catchments, and poor timber management practices are recognised as one of the primary pressures on salmon rivers in North America (Cederholm, *et al,* 1981, Chamberlin, *et al.*, 1993). Although many of the impacts of forestry and agriculture are similar, for instance increased sediment, agricultural practices introduce a number of pressures that are not associated with forestry, for instance fertiliser application, agricultural waste and cattle grazing. Therefore, the impact of oxygen demands on intragravel oxygen concentration may be more pronounced in U.K rivers. Thus, the precise factors degrading the quality of U.K salmon spawning and incubation environments may be more complex than those discussed in the literature from North America.

6.4.4.3 Impact of sediment accumulation on oxygen fluxes

Fine sediment infiltration into spawning gravels is recognised as one of the principal factors influencing the flux of oxygenated water through salmon spawning gravels. The results of this study have highlighted two mechanisms controlling the impact of fine sediment accumulation on oxygen fluxes through salmon spawning gravels: (i) the impact of sediments on intragravel flow velocity and (ii) the impact of sediments on intragravel oxygen concentrations.

With respect to the impact of sediment on intragravel flow velocity, it was shown that a simple linear relationship may be used to express the relationship between fine sediment accumulation and intragravel flow velocity. This linear response results from the direct impact of fine sediment on pore space and the interconnectivity of pore spaces, and thus gravel permeability. However, spatially variable hydraulic gradients dictate that this linear relationship is site specific. Furthermore, variations in the character of deposited sediments may also influence the relationship between sediment deposition and intragravel flow velocity. For instance, it has been shown that a one percent increase in silt and clay can result in a drop in intragravel flow equivalent to a 22 percent increase in sand (Chevalier and Carson 1985). Likewise, variable quantities of organic material within the riverbed may also influence the relationship between sediment quantity and intragravel flow velocity. As highlighted is this study, high quantities of organic material within the riverbed may result in larger drops in intragravel flow velocity than would be expected based on in quantities of inorganic sediment. Consequently, in view of spatially variable hydraulic gradient and spatial variations in the size and composition of deposited sediments, it is proposed that for locations of similar hydraulic gradient and granular properties, measures of the composition of the riverbed may provide a means of estimating intragravel flow velocities. However, the development of a spatially transferable relationship between the granular character of riverbeds and intragravel flow velocity appears inappropriate. A controlled flume investigation may provide a means to develop multivariate models of the impact of sediment accumulation on intragravel flow velocity.

The amount of organic material present in deposited sediments also varied between the study sites. In addition to blocking pore spaces on a volumetric basis, organic material promotes the growth of biofilms around particles that interstitial pore spaces. Bacteria attach to solid surfaces to consume organic molecules. As organism consume nutrients, they grow, reproduce and produce extracellular polymeric substances (EPS) that bind cells together. This aggregate of attached microorganisms, EPS and other particulate matter is termed a biofilm (Chen and Li, 1999). The availability of organic molecules influences the growth of biofilms, and as the biofilm thickness increases, the effective pore space between particles will decrease, resulting in reduced permeability and intragravel flow (Chen and Li, 1999). Furthermore, low pore velocities reduce biofilm detachment and promote biofilms growth (Chen and Li, 1999). It is suggested that the presence of organic matter and the growth of biofilms may impart a significant influence over intragravel flow velocities, and therefore availability of oxygen to incubating salmonid embryos.

The second process investigated was the impact of sedimentary oxygen demands on intragravel oxygen concentrations. Based on the intragravel flow velocities and the magnitude of the decline in intragravel oxygen concentrations recorded in each system, sedimentary oxygen demands were shown to exert an important control over intragravel oxygen concentrations. The decline in oxygen concentration was shown to be linked to the magnitude of the sedimentary oxygen demand, the rate of flow through the riverbed and the length of intragravel flow path.

Oxygen demands were shown to vary spatially and temporally within the study reaches. Spatial variability is probably indicative of the heterogeneous natures of the riverbed and spatial variations in the character of infiltrated materials, potentially resulting form local hydraulic conditions. Temporal variations may have been a consequence of variations in the age of deposited material or temporal variations in the composition of sediments entering the watercourses. As organic materials are degraded in the oxidation processes, the potential oxygen demand is reduced (Chevalier and Carson, 1985). If new sediments are not supplied to the intragravel environment, the oxygen demand of infiltrated material will reduce over time (Chevalier and Murphy, 1985). The temporal characteristics of this decline will be controlled by the composition of deposited materials, for instance if carbon demands are dominant, the oxygen demand may subside after 5-10 days, however if nitrogen demands, or extended carbon demands dominate, the demand may continue for upwards of 20 days (Chevalier and Murphy, 1985).

With respect to the composition of infiltrated materials, the dominant factors controlling inputs to watercourse are seasonal, anthropogenic and climatic variations in the supply of oxygen consuming materials. Increases in the availability of organic matter occur during succession when algal biomass is at a maximum, when inputs of leaf litter and other natural occurring organic detritus are high, for instance in autumn (Bunn. 1986). Anthropogenic controls are influenced by changes in land-use activities. For instance periods of clear cutting may provide increased inputs of organic detritus (Cederholm *et al.*, 1981; Scrivener and Brownlee, 1988). Similarly, changes in agricultural activities will also influence the supply of oxygen consuming material. For instance, application of fertilisers and silage, or proximity of grazing cattle and sheep to the river channel, will influence the availability of oxygen consuming material for input into watercourses (DEFRA, 2002). Finally, climatic variations, particularly the magnitude and longevity of precipitation events will influence inputs of oxygen consuming material. Under periods of prolonged rainfall, periods of overland flow may provide a pathway for increased inputs of agriculturally derived materials. Likewise, it has been shown that saturated soils result in increased subsurface transfer of nutrients from the land to watercourses, potential providing an additional source of oxygen demand inducing materials (Bechtold *et al.*, 2003).

These observations have important remediation and river management implications. As highlighted in Section 3.2.4, agriculturally derived materials, including fertilisers, agricultural water and sheep and cattle faeces have high associated oxygen demands. Inputs of these substances over the incubation period, either cumulatively or during an episodic event, may impart a considerable influence over oxygen availability and potential embryonic survival. It is suggested that greater attention should be given to agricultural activities that may provide a source and pathway for inputs of oxygen demand materials and substances into watercourses during the incubation period.

6.4.4.4 Delineation of sedimentary related pressures at the field sites

With knowledge of the sedimentary character of the study sites and the processes by which sediments influence oxygen availability and embryonic survival, an assessment of the impact of sediment accumulation at the field sites was undertaken. The results of this analysis are outlined in Table 6.4.18.

River	Potential sedimentary factors influencing intragravel oxygen fluxes
River Test	• The accumulation of fine sediments and its impact on intragravel flow velocity. However, it should be noted that the amount of material < 1mm was lower than the other field sites (10%.). • High percentage organic material (20%) further reduced gravel permeability, resulting in low intragravel flow velocities. Additionally, the presence of high levels of organic material may have promoted the growth of biofilms further lowering intragravel flow velocities. • Limited bed mobility, reducing the potential cleansing of fine material from redd gravels. • Oxygen demands of materials deposited in the riverbed, potentially induced by high organic content,, lowered intragravel oxygen concentrations.
River Blackwater	• Fine sediments deposited in the riverbed were slightly courser than in the other systems. Therefore, the impact of fine sediment accumulation on gravel permeability was lower than in the other systems. • Low levels of organic material, reducing the impact of the oxygen demand on interstitial water. • Loose, openwork and mobile gravels, promoted the influx of oxygenated surface water into the riverbed. • Location of poor survival influenced by of low intragravel flow velocity and oxygen demand of deposited material.
River Ithon	• High levels of fine sediment (<1mm) accumulation (22%). Potentially influenced by a local source of fine sediment. • High oxygen demand of material deposited in the riverbed reduced intragravel oxygen concentrations.
River Aran	• The accumulation of fine sediments and its impact on intragravel flow velocity (<1mm 15%). • High oxygen demands within the riverbed, although high temporal and spatial variability was recorded, reduced intragravel oxygen concentrations.

Table 6.4.18 Summary of sedimentary related factors influencing intragravel oxygen fluxes at each field site.

In addition to identifying the sedimentary related factors contributing to intragravel oxygen concentrations and intragravel flow velocities, for managerial purposes, it is important to identify the critical factors influencing incubation success within each system. Furthermore, it is also important to consider the likelihood that the identified pressures are contributing to an overall reduction in productivity within these systems: is incubation survival a factor limiting productivity in these systems?

Before assessing site-specific pressures, it is important to recognise the broader population scenarios at each field site. As detailed in Section 1.1, over the last 50 years there has been a dramatic reduction in Atlantic salmon populations in many U.K. rivers. Furthermore, there is documented evidence suggesting a far longer-term decline in salmon populations (Theurer *et al.*, 1998). This downturn in population size is characteristic of the current state of the Atlantic salmon populations at the River Test, River Ithon and River Aran (Environment Agency, 1997, 1998, 1999). One of the consequences of reduced population size is a reduction in the ability of the pollution to absorb small 'blimps' in productivity at a given life stage. This places increased pressure on individual salmon life stages, and on associated habitat zones to attain a level of productivity that will not result in a further reduction in the size of the population. Consequently, at the River Test, Ithon and Aran, there is a requirement for all spawning zones to maintain a level of productivity that will not compound existing pressures on the populations in these systems

At the River Test field site, the high level of organic material infiltrating the incubation environment was recognised as a factor contributing to the low intragravel flow velocities and poor rates of embryonic survival. In view of the low sediment accumulation and low sediment oxygen demands recorded at this field site, the high organic content appears to be the dominant factor influencing incubation success. High densities of macrophyte vegetation are synonymous with U.K chalk rivers (Welton, 1980; Berrie, 1992), therefore, if conditions at this field site are representative of conditions within this system it is probable that high accumulations of organic material within the riverbed is a long-term feature of these river systems. It is also possible therefore, that low incubation survival is also a long-term feature of this field site. This is not to say that low incubation survival is a natural occurrence at this site, rather, current environmental conditions, which are heavily influenced by human alteration, are not conducive to high rates of embryonic survival. It is also possible that it is reduced productivity at the other life stages (Environment Agency, 1997) that has placed new pressures on incubation success.

At the River Ithon, it is probable that a combination of high oxygen demands and high sediment accumulation resulted in the poor rates of incubation success recorded. However, unlike the River Test, these factors can be attributed to relatively recent changes in land-use within the catchment. The application of fertiliser to agricultural land has increased over time as have stocking densities (DEFRA, 2002), consequently inputs of high oxygen demand materials may have also increased. Similarly, bank erosion and excess sedimentation in this system are recognised as a problem by the Environment Agency (personnel communication, Grant McMellin). In light of changes in stocking density and increased infringement of agriculture into the riparian margins, it is probable that sedimentation and inputs of high oxygen demand materials has increased over time. However, it is also important to recognise that the flow conditions over the incubation period may have contributed to the accumulation of sediment and high oxygen demand material. Overbank flows were recorded for prolonged periods at this field site. These overbank flows may have resulted in a greater influx of land derived materials, including agricultural waste and animal faeces than during years when overbank flows do not occur. The oxygen demand data recovered from this field site, which indicated lower demands in 2003, supports this premise. Similarly, the large gravel bar directly upstream from this study site probably acted as a zone of sediment supply, potentially influencing the accumulation of sediment recorded at this field site. Further investigation would be required to assess the typicality of conditions monitored at this site and whether they are representative of conations elsewhere in this system. In light of the low embryonic survival recorded at this site, and probable long term changes in land use and sediment availability, poor incubation success may be contributing to poor productivity within this system.

At the River Aran, recorded survival was higher than at the River Test and River Ithon, However, during the study period, lower than average precipitation was recorded (Section 6.4.3.1), consequently it is likely that total sediment accumulation was lower than would expected in years experiencing typical rainfall levels. Therefore, further assessments of incubation success are required at this site to determine the existence of oxygen related pressures on incubation survival.

6.4.4.5 Considerations for defining incubation habitat quality

As discussed above, the development of a method of defining the quality of salmonid spawning gravels is key requirement for the ongoing preservation and rehabilitation of U.K salmonid rivers. For instance, the European Union Habitats Directive has recently suggested a 'favourable condition' fine sediment threshold of 10% for salmon spawning gravels. However, as highlighted in this study, granular based determinants of incubation success may have limited application in systems experiencing a concurrent problem of inputs of high oxygen demand material into the riverbed. Likewise, as was highlighted at the River Test, the amount of organic material within the riverbed may also exert an important control over intragravel flow velocities and therefore incubation success. Furthermore, as highlighted in the preceding sections, additional factors may also influence the availability of oxygen within salmon spawning gravels; including surface flow conditions, frequency of gravel entrainment and the accumulation of fine clay sized particles at the egg surface

In light of these observations, it is proposed that there is a requirement to replace current granular based methods of defining the ability of U.K riverbeds to support salmonid pollutions, with more comprehensive measures of the riverbed environment that appreciate the complex and dynamic processes that govern their ability to support salmon spawning and incubation requirements. Section 6.5 provides on overview of a new method of defining the quality of incubation environments. However, this method is focused on defining the potential ability of the incubation environment to support the oxygen requirement of incubating embryos, and does not quantitatively assess factors contributing to reduced oxygen availability. Therefore, to supplement this information, methods and techniques for assessing the causes of low oxygen availability, and the sources of these factors, must be developed. Although it is beyond the scope of this thesis to provide a detailed examination of potential methods and strategies for assessing the quality of spawning gravels, the key findings presented in this section, and in the preceding sections, can be used to define a set of potential criteria for assessing the quality of U.K spawning gravels (Table 6.4.19).

Key considerations for defining spawning and incubation habitat quality
• The factors influencing incubation success may vary considerably between river systems, or within systems, dependent on local and catchment scale pressures. Measures of habitat quality should be transferable between river systems, and therefore should consider all potential factors influencing habitat quality.
• The infiltration of high oxygen demand materials and substances into the incubation environment may exacerbate existing problems associated with the excess sedimentation.
• The impact of fine sediments on intragravel flow velocities and therefore oxygen availability to incubating embryos is influenced by the size composition of infiltrated sediments. As particle size decreases, its impact on intragravel flow increases. Therefore, greater consideration should be given to the range of fine sediment particle sizes present in the riverbed, rather than solely on the percent below an arbitrary threshold.
• Clay particles can severely reduce the supply of oxygen to and the potentially the rate of exchange across the egg membrane. The impact of very fine particles on oxygen availability and embryonic respiration should be considered.
• Organic material, in addition to inducing oxygen demands, can influence gravel permeability and intragravel flow velocities. Therefore, in addition to the impact of inorganic sediment accumulation, consideration should be given to accumulation of organic materials.
• Bed mobility and gravel entrainment processes may provide a mechanism to promote increased exchange of surface water into the riverbed, thus enhancing the availability of oxygen to incubating embryos. Thus, the mobility and/or degree of compaction of riverbed gravels may affect ability of riverbeds to support incubating embryos.
• Conversely, in highly mobile environments, bed entrainment may result in excessive scouring and disturbance to the incubation environment resulting in pre-emergent mortalities.
• Sediments deposited in the base of redds will influence incubation conditions. The infiltration of larger sediments may potentially restrict deep penetration of fine sedimentary material, thus enhancing the flux of oxygen deeper within the redd. However, excess sedimentation in the upper gravel layers can create 'seals' that can entomb emerging fry. Thus greater consideration should be given to the vertical distribution of sediments within the redd.
• Increased exchange of surface water with the riverbed can occur during periods of high flow. Conversely, low flows can reduce this exchange mechanism. Thus, in addition to granular characteristics of the riverbed, hydrological regimes may also influence the ability of spawning gravels to support incubation requirements.
• As the spawning process cleanses the incubation environment of fine material, assessments of uncut gravels may provide an unrepresentative indication of conditions within incubation gravels. This is particularly true when sediments within a riverbed have accumulated over an extended time period or when antecedent conditions have promoted uncharacteristically high infiltration rates.

Table 6.3.19 Summary of key factors and processes that should be considered when developing assessment of spawning and incubation habitat quality.

6.4.5 Summary

The results presented in this study have highlighted the interaction of factors influencing the impact of sediment accumulation on oxygen availability and incubation success. Intragravel controls on oxygen flux were separated into factors influencing intragravel flow velocities and factors influencing intragravel oxygen concentration. Intragravel flow velocity was shown to respond linearly to sediment accumulation. However, spatial variations in sedimentary composition and hydraulic gradient dictated that relationship were site specific. In addition to the impact of sediment accumulation, the potential influence of organic material was assessed. Based on field observations of the impacts of organic rich material on intragravel flow velocities, it was suggested that consideration should be given to the organic composition of deposited sediments. With respect to intragravel oxygen concentrations, the interaction of sedimentary oxygen demands with the retention time of water within the riverbed was assessed. Results indicated that the magnitude of sedimentary oxygen demands varied between the study sites. Furthermore, it was shown that intragravel flow velocity influences the impact of sedimentary oxygen demands on intragravel oxygen concentrations.

These observations suggest that simple granular based determinants of incubation success may not be sufficient to assess the range of factors potentially influencing embryonic survival. It was suggested that dependent on catchment and channel characteristics, the precise factors influencing incubation success would vary between spawning localities. Consequently, greater attention should be placed on delineating catchment, or reach, specific factors influencing oxygen fluxes and embryonic survival.

6.5 Application of mass transport theory as a measure of habitat quality and potential incubation success

This section details the application of mass transport theory to the problem of determining oxygen deficiency related mortalities. A discussion of the limitations associated with this approach is provided.

6.5.1 Introduction

The previous sections have detailed the importance of oxygen availability within salmonid spawning and incubation environments. It was shown that oxygen availability was dependent on both intragravel oxygen concentration and intragravel flow velocity, and that these factors displayed high spatial and temporal variability. Consequently, embryonic mortalities may result from either oxygen concentrations exceeding critical levels, or from combinations of oxygen concentration and intragravel flow velocity that are insufficient to support respiration.

Assessments of current metrics of survival indicated variable performance at the study sites. Of the metrics tested, oxygen flux, defined as the product of oxygen concentration and discharge past an incubating embryo, was the best overall predictor of incubation success. However, it was recognised that this approach performed poorly in environments that did not exhibit a range of intragravel flow, oxygen concentrations or rates of embryonic survival. Additionally, it was recognised that the field results only provide a simple empirical basis for delineating survival based on oxygen availability. A process-based method of assessing potential survival would provide a more robust method of assessing potential incubation success.

In response to these observations, a new approach to assessing potential incubation success, which centred on the application of mass transport theory, was tested. Mass transport theory is a series of process-based equations that describe heat and solute transport. The theories of mass transport were first applied to the problem of determining embryonic respiration by Daykin (1965), and refinements to the original model were proposed by Wickett (1975), Chevalier and Carson (1985) and Alonso *et al.* (1996). At present, application of the theories of mass transport is typically restricted to assessing potential rates of embryonic oxygen consumption (Alonso *et al.*, 1996). However, it was recognised that mass transport theory can also be applied to assess oxygen related embryonic mortalities (Daykin, 1965; Wicket, 1975; Chevalier and Carson, 1985). Applying this rationale, the following section describes the application of mass transport theory as a tool for assessing potential incubation success.

6.5.2 Overview of mass transport theory

Mass transport theory states that a solute boundary layer exists in the fluid surrounding a sphere and that solute is transferred across the layer at a rate proportional to the concentration gradient across the layer. As detailed in Section 3.2.2, with respect to incubating embryos, oxygen is diffused across the egg membrane from a thin boundary layer at the egg surface (Figure 3.2.2). The rate of oxygen transport across the boundary layer is proportional to the concentration in the external and internal egg environment (Daykin, 1965). Oxygen is supplied to the boundary layer primarily by an oxygen gradient that exists between the boundary layer and the surrounding macroenvironment, although natural convection and advection have also been shown to influence supply (O'Brien, 1979). The oxygen required to support the exchange of oxygen between the macroenvironment and the boundary layer and between the boundary layer and the egg capsule is supplied by advected flow through the riverbed. Mass transport theory can be applied to determine oxygen availability at the egg surface under varying oxygen concentrations and flow velocities. Theoretically determined values of oxygen availability can be compared with experimentally determined oxygen consumption rates to assess whether availability meets respiratory requirements.

The model applied in this paper is based on the refined model of mass transport proposed by Wickett (1975). This model synthesises Daykin's original work on the transfer of oxygen across the boundary layer with improved awareness of solute transport between the boundary layer and the egg capsule. The model is divided into two stages, an examination of the oxygen concentration required at the egg surface to meet the respiratory requirements of the egg and, an assessment of the oxygen concentration available at the egg surface for a given set of conditions within the surrounding macroenvironment. The model described also integrates a function modelling natural convection (Alonso *et al.*, 1996).

6.5.2.1 Stage 1 Evaluation of oxygen requirements in the microenvironment

The first stage in the application of mass transport theory is to determine the oxygen concentration required at the egg surface to support respiratory requirements. The Fickian equation for diffusion across a plane is used to represent solute transport across the egg membrane:

$$N = \frac{4\pi r^2 (C_o - C_e) D_c}{\delta} \qquad (6.5.1)$$

where N is rate of transfer of solute to the sphere (mg s^{-1}), r = sphere radius, C_e is the concentration in the pervitelline fluid (mg cm^{-3}), C_o = solute concentration at the sphere surface (assumed uniform over the sphere), D_c = mass transport coefficient (cm^2 s^{-1}) and δ is the capsule thickness (cm). Solving equation 6.5.1 for C_o, the concentration required at the egg surface to support a given rate of embryonic oxygen consumption is:

$$C_o = \frac{N\delta}{4\pi r^2 Dc} + C_e \qquad (6.5.2)$$

6.5.2.2 Stage 2 Evaluation of conditions within the macroenvironment

Once the required oxygen concentrations are determined, an assessment of potential oxygen concentrations at the egg surface (C_o) for various egg diameters, rates of consumption, water velocities, oxygen concentrations in the macroenvironment, viscosities, and diffusion constants can be undertaken. For transfer from the surrounding fluid to a sphere, the rate of mass transport is given by:

$$C_o = \frac{N}{4\pi r^2 k} - C_1 \qquad (6.5.3)$$

Where C_1 is solute concentration outside the solute boundary layer (mg cm^{-3}), and k is the mass transport coefficient (cm^2 s^{-1}). The mass transport coefficient is calculated from a dimensionless number, referred to as the Sherwood number (S_h):

$$S_h = \frac{k2r}{D_w} \qquad (6.5.4)$$

where D_w is the diffusion coefficient of water (cm^2s^{-1}) defined for varying temperatures as:

$$D_w = \frac{\left[0.721^{-9}(T+273)\right]}{\mu} \qquad (6.5.5)$$

where T is the temperature (°C) and μ is the kinetmatic viscosity of water (g cm^{-1} s^{-1}). The Sherwood number is a function of three other dimensionless numbers, the Reynolds number (N_{re}), the Grashof number (G_r) and the Schmidt number (S_c):

$$R_e = \frac{2rv}{\mu}$$ (a measure of fluid hydrodynamic stability) (6.5.6)

$$G_r = \frac{g(2r)^3 \Delta\gamma}{\mu^2}$$ (a measure of the ratio of buoyant and viscous force) (6.5.7)

$$S_c = \frac{\mu}{D_w}$$ (A measure of the ratio of viscosity to molecular diffusion) (6.5.8)

where v is intragravel flow velocity (cm s^{-1}), g is the gravitational constant (980) (cm^2s^{-1}) and Δγ is the density difference between non-aerated (D_o) and aerated water (D_{os}) (g cc^{-1}):

$$\Delta\gamma = 0.0000055 \frac{D_o}{D_{os}}. \qquad (6.5.10)$$

Combining equations 6.5.6, 6.5.7 and 6.5.8, the Sherwood number can be estimated from the following equation:

$$S_h = 2 + 0.569(G_r S_c)^{0.25} + 0.347(R_n S_c^{\ 0.5})^{0.62} \qquad (6.5.11)$$

Equations 6.52 and 6.5.3 can be used to determine the required oxygen concentration at the egg surface and the potential oxygen concentration at the egg surface for a given set of variables and, therefore, whether the oxygen available exceeds the demand imposed by the incubating embryo. Similarly, equations 6.5.2 and 6.5.3 can be combined and solved for N to provide an estimate of the physically possible oxygen consumption rate for a given set of environmental and biological variables.

The solved equation takes the form:

$$N_{obtainable} = \frac{\left[4\pi r^2 C\left(_o - C_e\right)\right]}{\left[\left(\frac{1}{k}\right)+\left(\frac{\delta}{D_w}\right)\right]} \quad (6.5.12)$$

This equation can be used to compare obtainable oxygen consumption with required rates of oxygen consumption (*N*). If the required rate exceeds the obtainable rate, then an oxygen deficit is present. Importantly, the model cannot distinguish between critical and limiting oxygen conditions. Therefore, the thresholds defined by the model assume that an oxygen deficit will result in mortalities. Table 6.5.1 contains reported values for parameters required for application of the model.

Parameter	Definition	Value	Species	Reference
σ	Egg capsule thickness	6 x 10 $^{-3}$ cm	Chinook salmon	Daykin (1965)
		4 x10 $^{-3}$ cm	Steelhead trout	Daykin (1965)
		3.5 x 10 $^{-3}$ cm	Brown trout	Wickett (1975)
D_c	Diffusion constant of egg	**0.18 x 10 $^{-5}$ cm²s⁻¹**	Chinook/steelhead	Daykin (1965)
C_e	Concentration in	3.0 mg l^{-1}	Chinook/steelhead	Daykin (1965)
	pervitelline fluid	2.5 mg l^{-1}	Chum salmon	Wickett (1975)
		1.6 mg l^{-1}	Sockeye salmon	Wickett (1975)
		2.0 mg l^{-1}	Chinook/steelhead	Alonso *et al* (1996)
R	Egg radius	0.3 cm	Atlantic Salmon	

Table 6.5.1 Basic data compilation for theoretical calculations. Values in bold type were adopted in the following analysis.

6.5.2.3 Stage 3 Determining values of consumption (N)

Embryonic oxygen consumption varies with temperature, stage of development and oxygen availability (Hamor and Garside 1978). Generally, consumption increases with temperature, oxygen availability and stage of development. (Wicket 1975; Hamor and Garside, 1977, 1979; Silver *et al.*, 1963; Shumway *et al.*, 1964; Cooper, 1965; Rombough, 1987; Hayes *et al.*, 1951). A range of oxygen consumption rates for a variety of species, stages of embryonic development and environmental conditions have been reported in the literature (Lindroth, 1942; Hayes, 1951; Hamor and Garside, 1979; Sigurd, 2003). Consideration of this information allows estimation of oxygen requirements for various stages of development, temperatures and oxygen concentrations.

For the purposes of defining incubation habitat quality, maximum rates of oxygen consumption for a given set of environmental conditions are of most relevance. Reported values of oxygen consumption at hatching vary significantly between studies. However, the weight of evidence indicates that at 5 °C oxygen consumption by Atlantic salmon embryos is around 0.003 mg O_2 egg $^{-1}$ h $^{-1}$ (Hayes 1951, Sigurd 2003, Section 6.2). Using this value of oxygen consumption as a reference point, an assessment of oxygen consumption under varying temperatures and oxygen concentrations was undertaken. The assessment was based on trends in oxygen consumption provided by Hamor and Garside (1978). However, it should be noted that while Hamor and Garside (1978) provided a detailed analysis of the influence of temperature and oxygen concentration on oxygen consumption, the values of consumption reported in that study are an order of magnitude higher than the rate of consumption adopted in this study (see Section 6.2 for a further discussion of the anomaly). Therefore, for the purposes of this study, although the trends in consumption outlined by Hamor and Garside are utilised, the actual values of consumption have been replaced.

The data provided by Hamor and Garside (1978) indicates a drop in temperature from 10 °C to 5 °C results in 50% decline in consumption. Therefore, over this temperature range, a 1°C drop in temperature equates in a 10% decline in consumption. This observation is validated by other studies of oxygen consumption that also report a similar trend in consumption with temperature (Hayes 1951). Hamor and Garside (1978) also assessed the influence of oxygen saturation on rates of consumption. Applying the relative changes in consumption reported by Hamor and Garside (1978), a simple analysis of the effect of oxygen concentration on oxygen consumption was undertaken (Table 6.5.2). It should be noted that the analysis was based on a limited dataset and therefore, only provides an estimate of environmental controls on oxygen consumption. However, application of this model provides a reasonable approximation of rates of oxygen consumption reported in the literature (Table 6.2.2).

Oxygen concentration	**11 mg l^{-1}**	**5.5 mg l^{-1}**	**3.3 mg l^{-1}**
Oxygen consumption $mgO_2egg^{-1}h^{-1}$ at10°C	0.0043	0.0034	0.0016
Oxygen concentration	**12.6 mg l^{-1}**	**6.3 mg l^{-1}**	**3.78 mg l^{-1}**
Oxygen consumption $mgO_2egg^{-1}h^{-1}$ at5°C	0.0022	0.0015	0.0012

Table 6.5.2 Summary of oxygen consumption ($mgO_2egg^{-1}h^{-1}$) rates estimated applying the analysis described above.

6.5.3 Application of mass transport as a measure of oxygen deficiency related embryonic mortalities

Applying the theory of mass transport, an analysis was undertaken to determine the oxygen concentrations and intragravel flow velocities required to support respiratory requirements at hatching across a range of water temperatures (Figure 6.5.1). As shown in Figure 6.5.1, as oxygen concentration declines, the interstitial velocities required to support respiration increase, conversely, as intragravel flow velocity declines oxygen concentrations must increase to support respiratory requirements. Additionally, as water temperature increases, the consequent increase in consumption must be supported by increased oxygen availability. Therefore, as temperature increases, the intragravel flow velocities and oxygen concentrations required to support respiratory requirements also increase. These trends are in agreement with laboratory observations reported by Silver et al. (1963). In an assessment of the influence of oxygen concentration and intragravel flow velocity on incubation success, Silver *et al.* (1963) concluded that intragravel flow velocities of 700 cm h^{-1} at 6 mg l^{-1} provided similar incubation conditions as velocities of 6 cm h^{-1} at 11 mg l^{-1} (Silver et al. 1963).

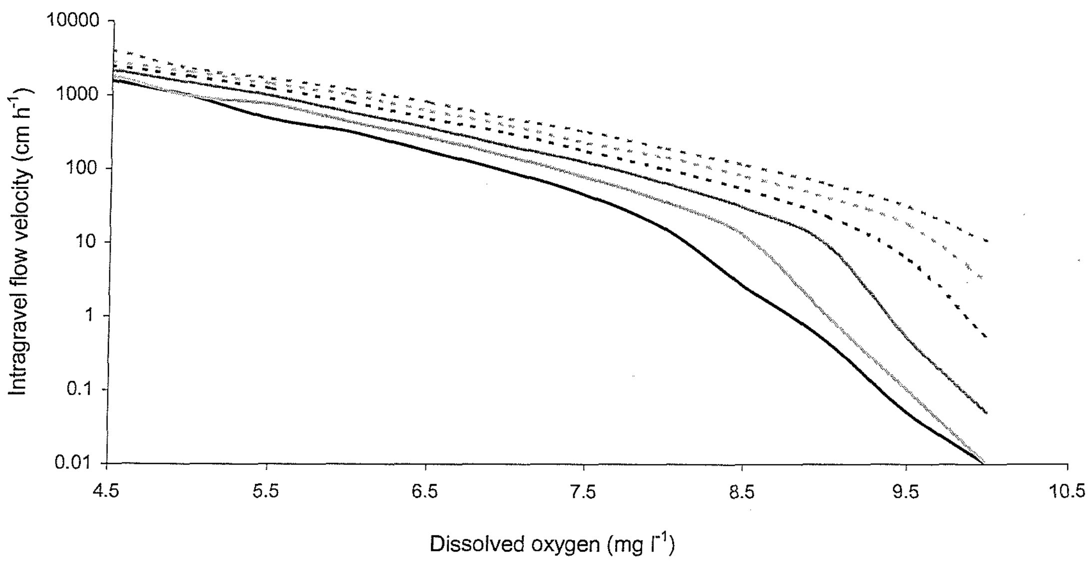

Figure 6.5.1 Range of intragravel velocities and oxygen concentrations required to support respiratory demands at five temperatures.

------ Threshold at 10°C	------ Threshold at 9°C	------ Threshold at 8°C
——— Threshold at 7°C	——— Threshold at 6°C	——— Threshold at 5°C

With respect to intragravel water temperatures, the literature contains a number of references to the potential benefits of elevated water temperatures, for instance reduced incubation time (Cloern, 1976). However, as highlighted by the results of the mass transport analysis, and by laboratory studies of embryonic respiration (Hamor and Garside, 1978), higher water temperatures induce increased respiratory demand, which must be supported by higher levels of oxygen availability within the incubation environment. This trend has important implications for environments suffering concurrent problems of low oxygen availability and increased water temperature over the incubation period. Potential causes of elevated water temperatures include increased periods of low flow resulting from abstraction or impoundment, climatic fluctuations, upwelling groundwater or channel shading (Brosofske, 1997; Bartholow, 1989; Poole and Berman, 2000).

To assess the potential effectiveness of mass transport theory for determining incubation success in the natural environment, the oxygen concentration, intragravel flow and survival data recovered during the field monitoring programme was compared with the threshold of survival determined by mass transport at a temperature (7°C) representative of conditions recorded at the field sites at hatching (Figure 6.5.2).

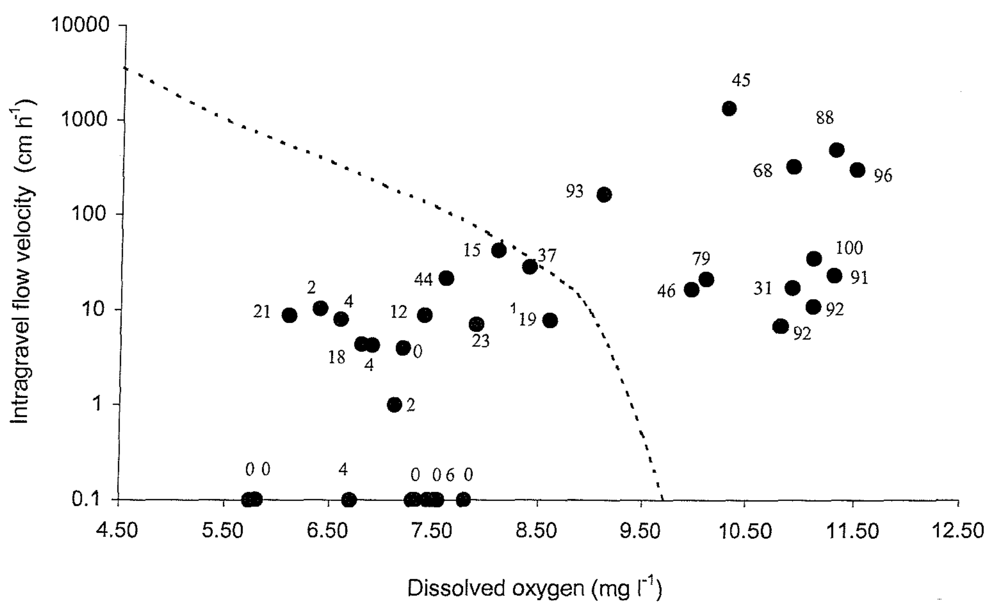

Figure 6.5.2 Comparison of survival recorded in the field with the threshold of survival recorded by the application of mass transport theory.

As shown in Figure 6.5.2, increased survival is recorded above the threshold defined by mass transport. However, in broader terms, survival increases towards the upper right portion of the diagram and decreases towards the lower left portion of the diagram. Applying this process-based model as a framework, it is possible to develop a conceptual model describing trends in survival in relation to combinations of intragravel flow and dissolved oxygen concentrations. Furthermore, integration of the findings of the field and laboratory studies with the findings of previous research, allows identification of a suite of factors that can result in a specific oxygen supply status (Figure 6.5.3).

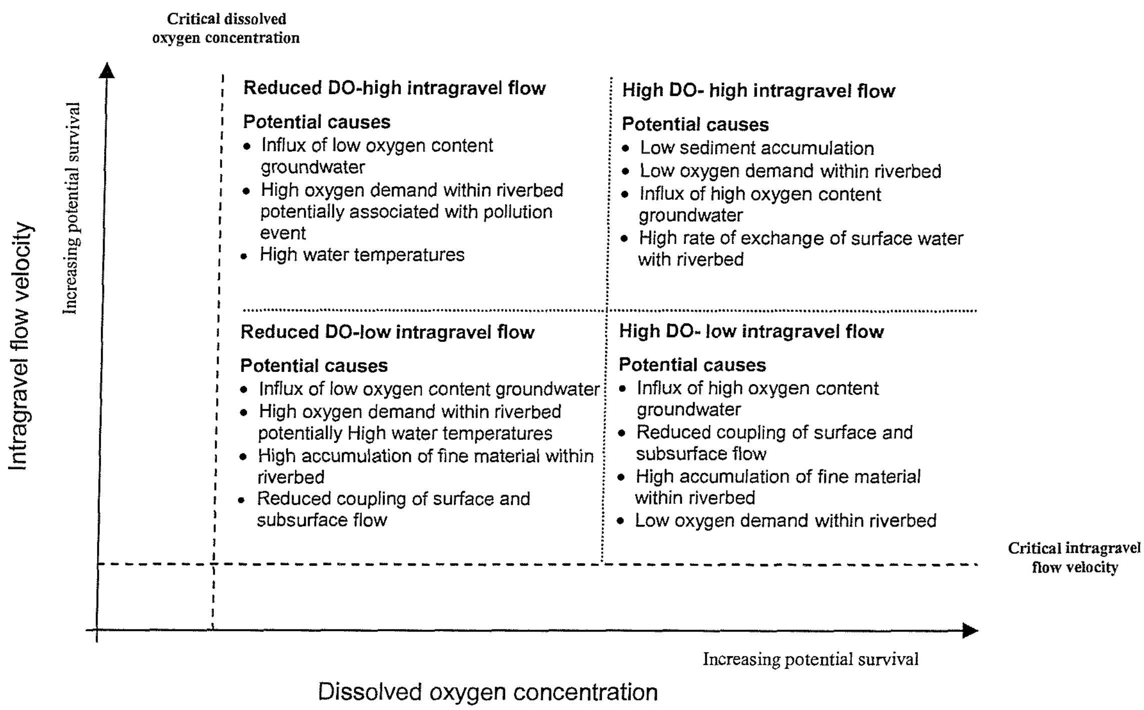

Figure 6.5.3 Conceptual model of the relationship between oxygen supply (flux) and embryonic survival. Also detailed are hypothetical scenarios potentially influencing oxygen fluxes.

In its present form, mass transport theory requires accurate oxygen concentration and intragravel flow data pertaining to conditions within the microenvironment directly surrounding a developing embryo to determine potential survival. Unfortunately, field sampling restrictions mean that information pertaining to conditions within the environment directly surrounding incubating embryos is unobtainable. Rather, assessments of intragravel incubation conditions are limited to spatially-averaged measures of conditions within the macro-environment. As highlighted by the spatial variability in conditions recorded within artificial redds detailed in Section 6.1, bulk assessments of intragravel incubation conditions may not provide accurate information pertaining to the environment directly surrounding incubating embryos. Consequently, application of the theories of mass transport to the problem of assessing potential incubation survival in the natural environment requires modification of the model to allow delineation of potential survival based on bulk measures of macro-environment conditions within spawning gravels.

To allow application of the theory of mass transport to define incubation success based on bulk measures of oxygen availability, the field monitoring data obtained in this study was integrated with the results of a mass transport analysis to produce an empirical model of potential incubation success under varying oxygen concentrations and intragravel flow velocities (Figure 6.5.4). The survival threshold determined by mass transport theory was modified to define boundaries of oxygen concentration and intragravel flow velocities that fell into three classes of survival, or levels of habitat quality: poor (0-25%), intermediate (25%-75%) and high (75%- 100%). The thresholds were created by modifying the output from equation 6.5.12 to define values of $N_{obtainable}$ that would encapsulate the three defined classes of survival (± 5%). The upper threshold was created by increasing $N_{obtainable}$ by a factor of 0.25, and the lower threshold was created by reducing $N_{obtainable}$ by a factor of 0.25. In essence, the threshold of survival defined by mass transport theory has been modified to include an error bar that represents the spatial variability in survival and intragravel oxygen availability that exists within the incubation zone.

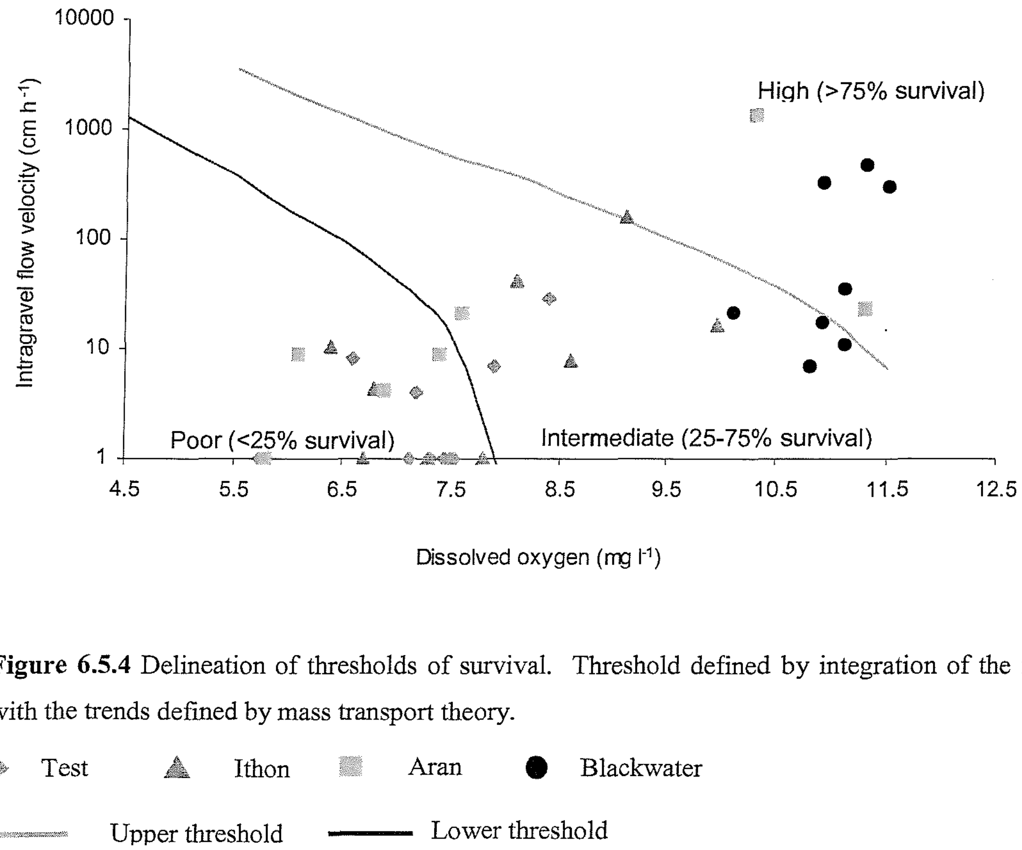

Figure 6.5.4 Delineation of thresholds of survival. Threshold defined by integration of the field data with the trends defined by mass transport theory.

In additional to the oxygen supply thresholds defined by mass transport, integration of the field data recorded in this study with reported thresholds of survival in the literature, allows delineation of critical oxygen concentration and intragravel flow velocities below which survival is negligible. The literature contains numerous references to critical oxygen concentration thresholds. Reported thresholds range from 4 to 8 mg l^{-1} (Table 1.1). However, the commonly adopted threshold value is 5 mg l^{-1}. The field observations reported in this study, which indicate limited survival below 5 mg l^{-1}, support this threshold[11]. With respect to intragravel flow velocity, mass transport theory suggests that even at low intragravel flow velocities, respiration will be sustained if suitably high oxygen concentrations are maintained. However, at low intragravel flow velocities, the accumulation of metabolic waste around incubating embryos may influence survival (Burkhalter and Kaya, 1977; McCabe *et al.,* 1985). At present, there is limited information pertaining to critical ammonia concentrations and rates of ammonia excretion by incubating embryos, therefore, it is difficult to identify intragravel flow velocities required to flush metabolic waste from the incubation zone. However, the results of the field study indicate that survival was negligible at intragravel velocities below 1cm h^{-1}. Therefore, a minimum intragravel flow velocity of 1 cm h^{-1} is proposed as a potential critical intragravel flow velocity. However, for management purposes, target intragravel flow velocities above 50 cm h^{-1} (Section 6.1.4) provide a basis for ensuring high rates of survival across a range of oxygen concentrations.

[11] The data presented in Figure 6.5.4is based on final oxygen concentrations. Therefore although the figure suggests a critical oxygen concentration threshold of around 7 mg l^{-1}, minimum oxygen concentrations were recorded a number of weeks prior to hatching. It is hypothesised that mortalities occurred during these periods of low dissolved oxygen concentration ($\cong$ 5 mg l^{-1}) (Section 6.1)

6.5.4 Limitations, requirements and potential applications

Although mass transport theory has been proposed as a potential method of assessing habitat quality, it is important to recognise the limitations and potential sources of error associated with this approach to defining incubation success.

First, with respect to the application of mass transport theory to delineate oxygen related mortalities, it should be noted that although based on a robust theoretical model of solute transport, it application to embryonic respiration has undergone a limited process of testing and validation. Therefore, there is a requirement for further assessments of the ability of mass transport theory to delineate oxygen related embryonic mortalities.

Second, a lack of information pertaining to some of the parameters utilised in the mass transport equations means that information has been pooled from external sources. For instance the diffusion constant of oxygen across the egg membrane is an estimation based on data provided by Hayes *et al.* (1951) and C_e is taken as the blood saturation value of haemoglobin (Chevalier and Carson, 1985). Additionally, the value of $C_{e\ \mathrm{was}}$ applied in the analysis was fixed. However, it is possible that C_e is in fact a variable that changes in relation to conditions in the external environment (Chevalier and Carson, 1985). There is a requirement for these values to be tested and validated.

Third, as described above and in sections 3.2 and 6.2, conflicting values of oxygen consumption have been reported in the literature. The accuracy of the survival thresholds defined by mass transport theory is dependent on the accuracy of the consumption values input into the model. Consequently, the production of detailed and reliable datasets pertaining to rates of oxygen consumption would potentially aid the effectiveness of mass transport theory to accurately predict potential survival.

Fourth, although a range of river types were assessed, the thresholds of survival are based on a limited number of data points. Additionally, although based on the trends defined by mass transport theory, the thresholds are based on simple statistical analysis. These thresholds could be improved and validated through a thorough laboratory based examination of the effect of oxygen supply on incubation success.

Finally, with respect to intragravel flow velocity, the technique adopted in this study (Appendix 1) provided reasonable estimates, however concerns remain regarding the accuracy of the probe. Based on the standard error produced by the recalibration, at velocities below 200 cm h^{-1}, the probe is only accurate to within 18 cm h^{-1}. Based on the results of the mass transport analysis, at the lower velocity thresholds, a small change in the rate of flow past an incubating embryo can significantly alter whether availability exceeds demand. Consequently, the development of an improved method of assessing intragravel flow velocities would appreciably improve the estimates of survival based on mass transport thresholds.

6.5.5 Summary

Mass transport theory was applied to the problem of determining potential incubation success. Integration of the results of the field monitoring programme with an examination of oxygen availability based on mass transport theory, allowed delineation of a series of empirically defined survival thresholds. For the range of incubation conditions investigated in this study, it is suggested that mass transport theory provides a means of assessing potential embryonic survival and, therefore, spawning and incubation habitat quality. With respect to future application, it was recognised that assessing intragravel flow velocities and oxygen concentrations provides limited evidence of broader causes of poor incubation survival. It was suggested that a potential avenue for future research is the development of a front end model, either theoretical or empirical, that would allow assessment of oxygen availability based on measures of the sedimentary character of spawning gravels.

Chapter 7. Summary of research findings

This concluding section summarises the information presented in the previous sections. Additionally, based on these findings, a series of research recommendations are proposed. Finally, a critique of the adopted research approach is also provided.

7.1 Introduction

The results presented in the previous sections have provided insights into the factors and processes influencing the flux of oxygen through salmon spawning gravels. Furthermore, synthesis of this information with knowledge of the respiratory requirements of salmonid embryos has provided a basis for assessing potential embryonic survival. This concluding chapter summarises the key findings presented in the thesis and describes a rational approach for advancing research into processes and factors affecting the quality of riverbed gravels. The chapter is divided into four sections: (i) a summary of scientific findings, (ii) an overview of the potential causes of embryonic mortalities at the field sites, (iii) a summary of key management and research implications, and (iv) a critique of the adopted research approach.

7.2 Scientific findings

7.2.1 Review of factors influencing the availability of oxygen to incubating salmonid embryos

Based on a comprehensive literature review, an appraisal of the evolution of research into incubation success was undertaken. This review indicated that incubation success has received extensive and intensive research attention. However, the evolution of this sphere of research is characterised by a series of disparate research arms associated with the different scientific disciplines investigating incubation success and associated channel and hyporheic processes. Therefore, the first stage in the development of this thesis was synthesis of this information and identification of the principal factors influencing embryonic survival. Based on this analysis, oxygen availability was identified as a primary factor influencing embryonic survival, and a holistic model of factors influencing the availability of oxygen to incubating embryos was proposed (Figure 3.2.7).

In summary, pre-emergent mortalities occur when oxygen concentrations drop below critical oxygen concentration thresholds or when oxygen supply rates are insufficient to support metabolic demands. Therefore, mortalities may occur as a consequence of periods of low oxygen concentration or as a result of combinations of oxygen concentrations and intragravel flow velocities that produce oxygen supply rates that are insufficient to support respiratory requirements at a given temperature and stage of development. Furthermore, mortalities can also occur if intragravel flow velocities are insufficient to remove toxic metabolic waste excreted by incubating embryos.

The supply of oxygenated water to incubating embryos can be separated into two processes: (i) the exchange of oxygenated water with the riverbed, and (ii) the flux of oxygenated water through riverbed gravels. The exchange of oxygenated water with the riverbed is controlled by pressure driven exchange processes and turbulent momentum coupling of surface-subsurface flow. Topographic features or changes in bed permeability induce pressure fields at the bed surface that drive flow into and through the bed (Vaux, 1968; Savant *et al.*, 1987; Harvey and Bencala, 1993). Turbulent coupling of surface-subsurface water results in increased exchange of surface water with the riverbed during periods of high flow (Shimizu *et al.*, 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Packman and Bencala, 2000). Additionally, temporally and spatially variable inputs of groundwater also influence intragravel oxygen concentrations. However, as the oxygen concentration of groundwater is dependent on the characteristics of the storage medium it was suggested that the influence of groundwater on the oxygen characteristics of the intragravel environment should be viewed on a system-to-system basis.

Within the riverbed, the rate of passage and oxygen concentration of interstitial water is influenced by the accumulation of fine sediments and surface flow conditions. The impact of fine sediment accumulation can be divided into two mechanisms. First, the impact of sediments on gravel permeability and intragravel flow velocities, and, second, the impact of oxygen demands associated with deposited materials on intragravel oxygen concentrations. With respect to surface flow, the results of flume studies over flat beds have indicated that non-Darcian driven flow can influence subsurface flow paths and velocities. Turbulent coupling of surface-subsurface water has been identified as a potential mechanism describing this flow interaction (Shimizu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993; Packman and Bencala, 2000).

7.2.2 Summary of research findings

As highlighted by the literature review, the key processes influencing the flux of oxygenated water through gravel riverbeds have been investigated in a number of studies, however, to date there has been little attempt to integrate these findings, or apply them to the problem of assessing embryonic survival. Based on this observation, the primary research aim of this thesis was investigation into the processes influencing the availability of oxygen to incubating salmon embryos, and identification of scenarios where oxygen availability will not meet embryonic respiratory requirements.

To inform this overarching aim, five research objectives were defined, and a series of complementary field and laboratory studies were undertaken to investigate the factors and process influencing the availability of oxygen incubating Atlantic salmon embryos. A summary of the key research findings relating to these research objectives is provided:

Objective one: Quantification of oxygen fluxes through salmon spawning gravels and assessment of oxygen flux as a potential measure of incubation success.

A field investigation into embryonic survival and oxygen fluxes through artificial salmon redds created in natural spawning gravels was undertaken. Survival was variable within and between the study sites. Minimum survival was zero at all sites. Maximum survival at the River Test, Blackwater, Ithon and Aran was 35%, 100%, 97% and 91% respectively. Mean survival was 22% at the River Ithon, 8.7% at the River Test, 71% at the River Blackwater and 28% at the

River Aran. With respect to oxygen flux, oxygen concentrations and intragravel flow velocities declined over the incubation period at all study sites. Maximum oxygen concentrations were recorded post redd creation and typical mirrored surface water oxygen concentrations. Minimum concentrations were typically recorded at hatching and ranged from 3 mg l^{-1} (River Ithon) to 12 mg l^{-1} (River Blackwater). Maximum intragravel flow velocities were also recorded post redd creation and ranged from >8000 cm h^{-1} (River Ithon) to 2000 cm h^{-1} (River Test). Minimum intragravel flow velocities were recorded at hatching, and ranged from <10cm h^{-1} (all sites) to 800 cm h-[1] (River Blackwater). The lowest intra-site variability was recorded in the groundwater-dominated system (mean standard deviations: 0.6 mg l^{-1} [oxygen concentration], 8 cm h^{-1} [intragravel flow velocity]) and was attributed to the less diverse flow and morphological character of the study site. The freshet sites recorded greater spatial variability, and this was attributed to the more complex flow and morphologic features found at these sites. In broader terms, the reference site (River Blackwater) maintained the highest flux of oxygen through the artificially created incubation environments (mean oxygen flux at hatching: 0.0029 mg 0_2 egg h^{-1}), whereas the heavily impacted sites (River Test and River Ithon) recorded the lowest fluxes of oxygenated water (mean oxygen flux at hatching: 0.006mg 0_2 egg h^{-1}(Test), 0.004 mg 0_2 egg h^{-1}(Ithon).

Based on data collected and collated from all field sites, an assessment of commonly proposed indices of incubation success was undertaken. The analysis indicated that oxygen concentration, intragravel flow velocity and oxygen flux performed well as measures of incubation success (r^2 0.64, 0.59 and 0.65 respectively). However, site specificity in the performance of the indices was observed, raising concerns regarding the application of simple statistical measures of incubation success. Furthermore, it was recognised that the indices of survival did not adequately describe temporally variable intragravel conditions, or respiratory responses to critical oxygen concentrations. In light of these concerns a deductive analysis of the causes of embryonic mortalities at each field site was undertaken. The results of the analysis suggested that the precise oxygen related causes of mortalities varied within and between the study sites. Three oxygen related causes of embryonic mortalities were identified: (i) critical oxygen concentrations, (ii) critical intragravel flow velocities, and (iii) critical oxygen fluxes -combinations of oxygen concentrations and intragravel flow velocities that were insufficient to support respiratory requirements.

Investigation of the impact of clay particles on exchange of oxygen across the membrane of Atlantic salmon eggs

Previous studies have commented on the impact of different sized sediment classes on incubation success, however, to date no study has attempted to quantify the impact of a given sediment size class on oxygen availability. Furthermore, it was recognised that cutaneous exchange of oxygen across the egg membrane could potentially be affected by the physical blocking of micro-pore canals on the egg surface. To investigate these factors, a laboratory study of the impact of clay particles on oxygen consumption was undertaken. The results of this study showed that relatively small accumulations of clay-sized materials can restrict the passage of oxygen to and/or across the chorion of incubating salmonid eggs (thin film of clay [<1mm] over the eggs resulted 96% reduction in recorded consumption). Furthermore, although it was not possible to delineate the impact of fine sediment on the availability of oxygen to the egg surface from its potential impact on the exchange of oxygen across the egg membrane, the evidence presented suggested that physical blocking of pore canals may contribute to asphyxiation of salmonid embryos.

Assessment of the influence of surface flow on subsurface flow patterns and intragravel flow velocities

The literature review identified a number of field and flume studies reporting the influence of surface flow on subsurface flow paths and flow velocities. However, the field evidence supporting claims that surface flow influences subsurface flow conditions is largely anecdotal and the flume studies have only assessed flow over flatbeds across a limited range of surface flow conditions. To provide evidence of the influence of surface flow on subsurface flow paths and velocities, a flume study was undertaken to assess subsurface pressure differential and intragravel flow velocities across a flatbed and sinusoidal bed form. Intragravel flow velocities were assessed from Darcian principles and from estimates provided by the conductiometric standpipe. To provide corroborating evidence from a natural river environment, temperature profiling at the field sites was used to assess the influence of surface-subsurface flow interactions.

The flume study showed that increases in surface discharge resulted in a consequent increase in intragravel flow velocity. At maximum discharge (0.1 m^3s^{-1}) and across the flatbed, intragravel flow velocities estimated from Darcian principles were around three times lower than those estimated using the conductiometric standpipe. Across the sinusoidal bedform, intragravel flow velocities calculated from Darcian principles were six times lower than those estimated from the conductiometric standpipe. Similarly, surface flow conditions were also shown to influence hydraulic gradient and subsurface flow paths, with increasing discharges resulting in increased hydraulic gradients and deeper penetration of surface water into the porous gravel medium. Across the flat bed and sinusoidal bed form, increasing discharge in the range 0.01 to 0.1 m^3s^{-1} resulted in a five fold increase in hydraulic gradient. Observations from the field sites, which indicated reduced surface-subsurface temperature gradients during high flow events, supported the flume observations. With reference to previous investigations, it was suggested that flow in the upper bed layers is composed of both Darcian and non-Darcian flow, and that the depth of non-Darcian flow can increase as surface flow increases. Furthermore, observations of greater increases in intragravel flow velocity across the sinusoidal bedform suggest an interaction between Darcian and non-Darcian exchange of surface water with the riverbed. Turbulent momentum coupling of surface and subsurface water was proposed as a potential Non-Darcian factor influencing the exchange of surface water with gravel riverbeds.

Investigation of the impact of fine sediment on the flux of oxygen through spawning gravels.

Previous investigations into incubation success have emphasised the impact of fine sediment accumulation. However, much of this research has been based on defining simple empirical relationships between the granular character of the riverbed and incubation success. Within the context of oxygen availability, there are two mechanisms by which sediment accumulation influences oxygen fluxes: (i) restricting the passage of water by physical blocking pore spaces and (ii) depleting oxygen from intragravel water through oxidation processes that are associated with the infiltration of oxygen consuming materials. Based on this observation, a field investigation into the impact of fine sediment accumulation on oxygen flux was undertaken.

The results of this study showed that commonly reported granular descriptors of incubation gravels were poor statistical determinants of incubation success. Furthermore, in a number of instances, the direction of the correlations opposed those reported in other studies. It was conclude therefore, that simple measures of granular structure are inadequate for describing the interaction of factors influencing survival at the study sites.

With respect to the impact of fine sediment accumulation on intragravel flow velocities, a linear relationship between percent fine sediment and intragravel flow velocity was identified. However, although statistically significant (95% confidence limit), the relationship was shown to be spatially discrete. Differences in the granular character of the monitoring locations and variations in hydraulic gradient were identified as potential explanations for the limited transferability of these relationships. The influence of organic material on intragravel flow velocities was also discussed. It was noted that the field site that recorded the highest proportion of infiltrated organic material (River Test: 20% organic), also recorded the lowest intragravel flow velocities (mean across all redds at hatching <10cm h^{-1}). It was suggested that the impact of organic material on interstitial pore space can be underestimated by simple assessments of the inorganic fine sediment fractions.

With respect to oxygen concentration, the oxygen demand of infiltrated materials was assessed at each field site. Demands varied between sites, with the highest demands recorded in the River Ithon and River Aran (7.36 mg O_2 g $(\text{organic})^{-1}$ h^{-1} and 7.98 mg O_2 g $(\text{organic})^{-1}$ h^{-1} respectively). The magnitude of the oxygen demand in each system was shown to be concurrent with the relative scale of the recorded decline in intragravel oxygen concentration at each field site. However, high spatial and temporal variability was observed, and it was suggested that a more thorough examination of oxygen demands would be required to fully examine the oxygen dynamics with gravels riverbeds. It was concluded that oxygen demands influenced intragravel oxygen concentrations and incubation success, and inputs of agriculturally derived materials, for instance fertilisers and animal faeces, were proposed as a potential cause of high intragravel oxygen demands and depleted oxygen concentrations.

Development of a new method of assessing the quality of salmon spawning and incubation habitats.

In view of the limitations associated with current methods of assessing habitat quality, a new method of assessing potential incubation success was developed. The assessment was based on a mass transport model that has previously been used to quantify rates of embryonic consumption and embryonic oxygen requirements. The model allowed identification of combinations of oxygen concentration and intragravel flow velocity that were likely to result in embryonic mortalities. Synthesis of this model with the results of the field season allowed generation of three categories of habitat quality based on oxygen availability: high (>75% survival), intermediate (25-75% survival) and low (<25% survival) (Table 7.1).

7.3 Factors influencing survival at the study sites

Applying the findings of the field and laboratory studies, Table 7.1 identifies potential causes of embryonic mortalities and factors influencing oxygen availability at each field site. Based on the mass transport model proposed in Chapter 6.5, an assessment of habitat quality is also provided.

Site	Potential cause of mortality	Potential factors influencing oxygen availability	Habitat quality
River Test	(i) Oxygen deficiencies resulting from combination of lowered oxygen concentrations and intragravel flow velocities. (ii) Accumulation of metabolic waste resulting from low intragravel flow velocities.	(i) The accumulation of fine sediments and its impact on intragravel flow velocity. However, it should be noted that the amount of material < 1mm (10%) was lower than the levels recorded at the other field sites. (ii) High percentage organic material (20%) further reduced gravel permeability, resulting in low intragravel flow velocities. Additionally, the presence of high levels of organic material may have promoted the growth of biofilms further lowering intragravel flow velocities. (iii) Limited bed mobility, reducing the potential cleansing of fine material from redd gravels. (iv) Oxygen demands of materials deposited in the riverbed, potentially induced by high organic content,, lowered intragravel oxygen concentrations.	Low: 8 redds Intermediate: 2 redds
River Blackwater	High survival recorded. Note: Poor survival recorded at a single location that exhibited low oxygen concentrations and intragravel flow velocities.	(i) Infiltrated fine sediments were slightly coarser than at the other field sites. Therefore, the impact of fine sediment accumulation on gravel permeability was comparatively lower at this field site. (ii) Low levels of organic material, reducing the impact of the oxygen demand on interstitial water. (iii) Loose, openwork and mobile gravels, promoted the influx of oxygenated surface water into the riverbed. (iv) Location of poor survival influenced by of low intragravel flow velocity and oxygen demand of deposited material.	High: 4 redds Intermediate: 4 redds
River Ithon	(i) Oxygen deficiencies resulting from combination of lowered oxygen concentrations and intragravel flow velocities. (ii) Accumulation of metabolic waste resulting from low intragravel flow velocities. (iii) Lethal oxygen concentrations.	(i) High levels of total fine sediment (<1mm) accumulation (22%) and its subsequent impact on gravel permeability and intragravel flow velocity (ii) High oxygen demand of infiltrated materials resulted in reduced intragravel oxygen concentrations. (iii) Long periods of low flow resulting in reduced surface-subsurface exchange of oxygenated water with the riverbed.	Intermediate: 4 redds Low: 5 redds
River Aran	(i) Oxygen deficiencies resulting from combination of lowered oxygen concentrations and intragravel flow velocities. (ii) Accumulation of metabolic waste resulting from low intragravel flow velocities. (iii) Lethal oxygen concentrations.	(i) High levels of total fine sediment (<1mm) accumulation (15%) and its subsequent impact on gravel permeability and intragravel flow velocity. (ii) High oxygen demand of infiltrated materials reduced intragravel oxygen concentrations. Note: high temporal and spatial variability in the oxygen demand of infiltrated materials was recorded.	High: 2 redds Intermediate: 1 redd Low :7 redds

Table 7.1 Summary of pressures on oxygen availability at the field sites.

7.4 Overview of principal management and research implications

7.4.1 Management considerations

The work presented in this thesis has a number of implications for the management of rivers and the rehabilitation of salmonid spawning and incubation environments. The key management consideration emanating from this project is a requirement for greater appreciation of the complex interacting processes and factors influencing the quality of salmonid spawning and incubation environments. This observation can be divided into two practical management considerations: (i) a requirement for improved methods of assessing the quality of spawning and incubation gravels and (ii) a requirement for the development of targeted management strategies that address the precise causes of poor salmonid recruitment over the incubation period.

Current assessments of habitat and water quality undertaken by U.K environmental agencies are based on high spatial coverage, low sampling frequency and simplistic sampling protocols. Typically, assessments of water quality are based on monthly spot checks, and assessments of habitat quality are based on simple visual assessments, for instance the River Habitat Survey. The findings of this study have highlighted the complex interaction of factors affecting the quality of salmonid incubation environments. It is suggested that current assessments of water and habitat quality are unlikely to provide datasets that will support robust assessment of incubation habitat quality or identification of the causes of poor habitat quality. Although it is recognised that isolated in-house research projects are often commissioned to investigate systems experiencing acute pressures (Rowlatt *et al.,* 1998), the results of this project suggest that these studies, which have largely focused on rates of fine sediment accumulation, are of limited value, and unlikely to provide insights into the precise nature of the problem in individual systems.

Two approaches to improving the quality of datasets for assessing spawning and incubation habitats can be identified. First, DEFRA and associated environmental agencies must continue to commission research projects investigating channel and landscape processes that affect the physical quality and ecological functioning of gravel riverbeds. Whenever possible, these projects should be guided by overarching research objectives that are designed to promote awareness of existing, and potential, pressures on U.K. freshwater systems. The findings of these projects will provide improved awareness of key riverine processes, and hence promote identification of primary monitoring requirements. Second, environmental agencies must recognise the limitations of their existing monitoring strategies, and develop new targeted monitoring strategies that promote identification and quantification of pressures on both the quality of the water, hyporheic and terrestrial environment. These monitoring strategies should not only target commonly cited causes of poor habitat quality, for instance excess sedimentation, but they must also assimilate and apply the findings of recent and ongoing research. Based on the findings of this project, potential monitoring considerations should include:

1) Focusing sediment survey resources on assessing sediment particles in the clay (or clay and silt) size classes. Additionally, consideration should be given to quantifying the proportion of organic material contained in deposited sediments.

2) Assessing the magnitude of oxygen demands associated with materials deposited, or with the potential to be deposited, in riverbed gravels. This monitoring could take the form of sampling sediment extracted from gravel riverbeds, or sampling suspended sediments during high flow events. Subsequent laboratory assessments of BOD and NOD could be used to determine the potential impact of deposited materials on the quality of spawning and incubation gravels.

3) Quantifying intragravel flow velocities within salmon spawning gravels as a means of assessing habitat quality. Large sections of spawning gravels could be cleansed (jet washed) of fine sediments prior to spawning. Using standpipes and dilution techniques similar to those adopted in this study, assessments of intragravel flow velocities within this spawning reach could be undertaken over the incubation period. The results of this study suggest that velocities above 50 cmh^{-1} are likely to provide high quality incubation conditions across a range of intragravel dissolved oxygen concentrations. Similarly, adopting the same methodology, oxygen concentrations, or combinations of oxygen concentration and intragravel flow velocity, could be used to assess habitat quality. However, based on the results of this project, which indicated variable survival at high oxygen concentrations, caution is advised when applying oxygen concentration alone as measure of habitat quality.

With respect to developing management strategies that address problems relating to poor incubation survival, the findings of this project have identified a requirement to tailor management treatments to catchment, sub-catchment or reach scale pressures. It is likely that improved monitoring programmes, similar to those discussed above, would be required to identify specific management options, however, based on the findings of this study, some broad considerations can be identified:

1) Sedimentary oxygen demands were identified as a factor contributing to lowered oxygen availability at the study sites, particularly in the tributaries of the River Wye. It is suggested therefore, that when addressing issues pertaining to sedimentation of spawning gravels, consideration should also be given to identifying and addressing the sources and pathways of materials contributing to oxygen demands within spawning gravels. These considerations should include the magnitude and timing of fertiliser application, over-wintering cattle and sheep, and the storage and management of agricultural waste.

2) Low flows were shown to restrict the exchange of surface water with the upper riverbed gravel layers, thus potentially reducing the flux of oxygenated water. Similarly, in the presence of groundwater inputs, low flows have been shown to promote increased propagation of groundwater at typical incubation depths, potentially allowing the intrusion of low oxygen concentration water into incubation zones. Consequently, consideration should be given to the impacts of land drainage and abstraction on the hydrological response of rivers systems. Of particular relevance is increased 'flashiness' and enhanced rates of high flow recession. These flow trends may result in prolonged periods of low flow that are interrupted by short duration high flow events that are capable of mobilising large amounts of fine sedimentary material.

3) Fine sediments in the clay size range were shown to severely restrict oxygen availability. Furthermore, the field sites that recorded the highest proportion of fine sediment in the size class generally recognised as detrimental to incubation success (<1mm) did record the lowest rates of incubation success. It is suggested therefore, that remedial strategies should aim to address sediment inputs in the clay and silt size classes. For instance, special attention should be given to areas of bank erosion that have revealed clay deposits.

4) Organic detritus was identified as a factor potentially contributing to lowered intragravel flow velocities. Consideration should therefore be given to how macrophyte vegetation is managed, particularly in lowland chalk streams. For instance, as macrophyte vegetation dies back at the onset of winter it provides a large source of organic detritus. These inputs are coincident with salmonid spawning and incubation periods. One management option for reducing inputs of organic detritus is thinning out macrophyte vegetation prior to the spawning and incubation period.

7.4.2 Research considerations

This project has identified a requirement for further research in a number of key areas. To assist identification of primary research considerations, a research strategy for advancing awareness of factors and processes influencing the quality riverbed gravels is presented (Figure 7.1). Appendix 9.3 provides an overview of potential research projects emanating from this approach.

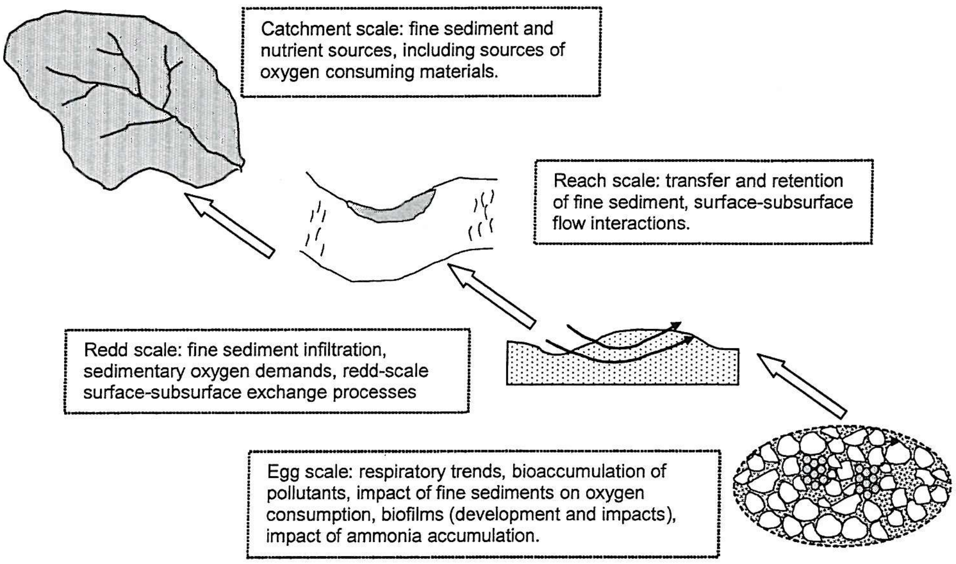

Figure 7.1 Overview of research considerations delineated at four spatial scales.

In summary, four key spatial units requiring further research attention have been identified. Synthesis of information across these spatial units will improve awareness of factors influencing incubation success and aid identification of appropriate management responses.

Egg-scale: Investigating egg-scale processes will improve our understanding of the interaction between eggs and the surrounding physical environment. Improved understanding of the impact of fine sediment (organic and inorganic) on the exchange of oxygen across the egg membrane of salmonid eggs will aid identification of important sedimentary features capable of degrading the quality of incubation environments. Similarly, the accumulation of excreted ammonia within the microenvironment surrounding incubating embryos has received only limited research attention. Awareness of the impact of ammonia accumulation on incubating embryos will aid identification of the potential importance of intragravel flow as a mechanism for cleansing the incubation environment of harmful metabolic waste.

Redd-scale: To date, only limited work has been carried out on the quality of sediments/materials deposited in non-urban river environments. This study has highlighted the potential importance of sediment oxygen demands, however, the accumulation of toxins, for instance agrochemicals, and nutrients are also of concern. There is a requirement therefore to improve our understanding of processes and factors degrading the biochemical, geochemical and hydrochemical quality of riverbed environments. With respect to sedimentary oxygen demands, a more detailed and extensive investigation of temporal and spatial variations in the magnitude and character of sediment oxygen demands would aid identification of its potential significance to intragravel oxygen fluxes and incubation success.

Reach-scale: The river reach is one of key morphological units used to characterise river environments. This study has highlighted a lack of information regarding interactions between surface and subsurface flow across riverbed morphological features, for instance pool-riffles. The coupling of surface-subsurface flow is poorly modelled by Darcian theory. Recent studies, have demonstrated the existence of non-Darcian driven flow in the upper layers of gravel riverbeds. Further investigation into the linkages between surface and subsurface flow may provide evidence of the impact long-term changes in hydrology on the hydrodynamic functioning of gravel riverbeds.

Catchment-scale: In recent years there has been a move towards catchment based management of aquatic environments. The Water Framework Directive, which was recently transposed into U.K. legislation, will continue to advance this trend. From a management perspective, there is a requirement to link *egg-scale*, *redd-scale* and *reach-scale* deteriorations in habitat quality to wider catchment scale processes. Of particular relevance is identification of sources and pathways of fine sediments, particularly in clay and silt size fractions. Similarly, identifying sources of materials contributing to sedimentary oxygen demands would aid managerial decisions regarding appropriate remedial responses to poor incubation success.

7.5 A critique of the adopted research approach

Specific limitations associated with the monitoring strategy and protocols adopted in this project have been discussed at appropriate junctures within the thesis. Furthermore, the potential limitations associated with the adopted research approach have been identified (Section 2.3). However, in light of the complex nature of the investigative approach utilised in this thesis, a critical re-examination of its strengths and weaknesses is required.

This thesis has provided an examination of the multiple interacting processes and factors influencing the availability of oxygen to incubating salmonid embryos. Investigation into these complex interacting processes required the development of a research project capable of assessing multiple processes across a variety of spatial and temporal scales. Furthermore, identification of research objectives, and interpretation of the research findings required assimilation of information from a variety of research fields.

The adoption of this research approach has provided insights into the interaction of factors and processes influencing the quality of salmonid spawning and incubation environments. Furthermore, this research approach has promoted awareness of processes and factors that have previously not been considered within the context of salmonid incubation habitat quality, and as such, will hopefully provide a catalyst for further research within these areas. Finally, adopting a multifaceted, research approach has allowed identification of practicable management considerations that address a variety of pressures on incubation habitats.

However, investigating an array of interacting processes and factors has restricted that depth of investigation within individual areas. Consequently, although the project has identified important processes and detailed their relevance to incubation success, it has not generated datasets of an appropriate quality to allow closer examination of the mechanistic principles underpinning these processes. For instance, although a simple analysis of the importance of sedimentary oxygen demands was undertaken, sampling and resource limitations restricted the scale and scope of this important element of the project. A more thorough field examination of sedimentary oxygen demands, which includes multiple sites and greater sample replication, would be required to elucidate the temporal and spatial dynamics of oxygen fluxes within hyporheic gravels.

Similarly, time constraints, which resulted from the scale and scope of the investigative approach, restricted the delivery of a detailed investigation into surface-subsurface flow interactions. Additional considerations that would have enhanced this project include greater emphasis on ensuring that the flume set-up (granular character, relative discharge range) was representative of field conditions, and closer examination of the hydro-dynamic processes underpinning the observed trends in flow interaction.

In reflection, although this study has not provided a panacea to the problem of poor incubation survival, it has helped redefine the nature and extent of the problem, and identified important areas for further research. It is hoped that this information will help inform future management decisions and research considerations.

8. References

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9. Appendices

Three appendices are included. The first details the refinement and recalibration of Carling and Booles' (1986) conductiometric standpipe method of estimating intragravel flow velocities. The second describes the two egg deployment techniques developed for the field monitoring programme. The third identifies a series of potential research projects designed to advance the key findings of this project.

9.1 Refinement and application of a conductiometric standpipe technique for measuring intragravel flow velocity

A refinement to the conductiometric standpipe method for determining intragravel flow velocities is described.

9.1.1 Introduction

Low ambient oxygen levels within the intragravel incubation environment of salmonid eggs and alevins can cause hypoxia and result in pre-emergent mortalities (Chapman, 1988; Chevalier and Carson, 1985; Crisp, 2000). Intragravel flow supplies oxygenated water to the incubation environment and removes harmful metabolic waste (Burkhalter and Kaya, 1975; Chapman, 1988; Bjorn and Reiser, 1991; Crisp, 2000). As such, intragravel flow is an important factor influencing pre-emergent salmonid survival (Daykin, 1965; Shumway; *et al.*, 1964). However, various attempts to quantify intragravel flow velocities have failed to produce an accurate or reliable field technique (Grost *et al.*, 1988).

In the absence of a reliable field technique, Darcy's Law is frequently applied to the problem of determining intragravel flow velocities. However, Darcy's law is typically applied to determine spatially averaged estimates of apparent velocity (bulk discharge through a volume of substrate and pore space), rather than point measurement of actual intragravel flow velocity. Although porosity values can be used to provide an improved estimate of intragravel flow, acquisition of reliable porosity values requires extraction of gravel samples from the sampling area, restricting the analysis of temporal trends. Additionally, concerns have been raised regarding the application of Darcy's law to estimate flow velocities within riverbed gravels. Based on the findings of a series of laboratory studies, two zones of flow within riverbed gravels can be delineated: a zone of non-Darcian flow towards the bed surface and a zone of slope driven Darcian flow at depth into the riverbed (Packman and Bencala, 2000). With respect to non-Darcian flow, it has been suggested that turbulent mixing, initiated by roughness at the bed surface, induces coupling of surface and subsurface flow, which results in surface driven velocity profiles in the bed (Shimizu *et al.,* 1990; Mendoza and Zhou, 1992; Zhou and Mendoza, 1993, 1995; Packman and Bencala, 2000). Although laboratory studies have only observed turbulent coupling at depths less than 0.1m, interactions between pressure driven and turbulent coupling have not been fully assessed (Packman and Bencala, 2000).

Among the field techniques developed to estimate intragravel flow velocity, the conductiometric standpipe method (Carling and Boole, 1986) was reported to provide data across a range of intragravel flow velocities found in salmon spawning gravels. However, field and flume tests of the conductiometric technique have highlighted poor performance in gravels of low permeability and at intragravel flow velocities less than 200 cm h^{-1}: conditions synonymous with poor salmonid incubation success (Cooper, 1965; Turnpenny and Williams, 1980).

A review of the original calibration data identified three concerns regarding the calibration procedure. First, the response of the probe varied when deployed in gravels of differing permeability, a factor that was not compensated for in the original calibration. Second, computational limitations at the time, restricted a detailed analysis of run time and its affect on the probe's ability to delineate low intragravel flow velocities. Finally, zero velocity runs were not included in the original calibration procedure. Instead, prototype zero velocity dilution runs were performed to determine the probe's lower response threshold, which was reported to be of the order of Fickian diffusion (0.5-1.0cm h^{-1}).

In reply to these limitations, three refinements to the original calibration were undertaken. First, an analysis of the probes response in gravels of varying permeability was carried out. Second, a detailed investigation into potential methods of improving the precision and accuracy of the probe was undertaken. This analysis focused primarily on assessing the influence of run time on probe response. Finally, zero velocity runs were added to the calibration procedure.

9.1.2 Description of conductiometric probe and sampling procedure

Detailed reviews of dilution theory can be found in Turnpenny and Williams (1982), and Carling and Boole (1986). In summary, the Carling and Boole (1986) technique is founded on the principles of Turnpenny and Williams' (1982) standpipe method for estimating intragravel flow velocities. Both techniques remotely record the rate of dilution of a known volume of saline solution within a standpipe deployed in a gravel substrate. The dilution rate, measured over a pre-determined time period, is compared with calibrated dilution curves to determine estimates of intragravel flow velocity.

The conductiometric probe employed in this study is the same probe used by Carling and Boole (1986). The instrument is composed of a small conductivity probe housed within the base of a section of plastic tubing. The instrument is inserted into riverbed gravels through a permeable standpipe. Standpipes are composed of a 100mm section of drilled stainless steel tubing welded to a conical drive point. The perforated tubing is sheathed in a section of retractable 260mm aluminium tube. The aluminium tube has two positions: (i) a sampling position where the tube is raised 50mm, allowing water to flow through the standpipe, and (ii) a non-sampling position where the aluminium tube is pushed to the base of the standpipe, thereby, protecting the standpipe from the intrusion of fine sediments. When not in use, tubes are sealed with a cylindrical piece of foam and a rubber bung, further restricting the influx of fine sediments that may interfere with monitoring equipment or obstruct access. An adaptor, which extends beyond the water surface, is attached to each standpipe prior to monitoring, thus creating a stable monitoring environment.

Once deployed, a small catheter allows the introduction of 10 ml of saline solution into the base of standpipe. The saline solution is composed of 50 g l^{-1} NaCl, diluted in a solution of 200ml ethanol (C_2H_5OH) and 800ml of distilled water. The ethanol is required to raise the specific gravity to 1000, thereby compensating for density differences between the solution and the external environment. As advised by Carling and Boole (1986), the electric stirrer has been removed, consequently, once the saline solution is injected, gentle agitation of the probe is required to initiate mixing. The original auxiliary logging equipment have been replaced by a Siemans™ conductivity meter linked to a Data Hog™ logging device that records the decline in conductivity at 10-second intervals.

All calibration runs were conducted in a 6.5m by 0.5m non-circulating hydraulic flume. A 6.0m test section was filled with three thoroughly sorted mixes of gravel, course sand, sand and silt that were designed to mimic potential variations in redd permeability over a typical incubation period (Table 9.1). The flume tailgate was set 0.03m below the height of the gravel and a tap maintained a constant head in the upstream tank. Altering the influent tap discharge and varying the channel slope controlled intragravel flow velocity through the gravel. Visible dye tracers were introduced through small plastic access pipes to determine the zone of disturbance induced by the tailgate. Three standpipes were deployed in the zone of minimum disturbance.

Gravel mix	% Fine sediment (<4mm)	Porosity w	Darcian permeability (cm h^{-1})	Intrinsic Permeability (cm^2)
1	0	0.35	14 247	5.17×10^{-5}
2	10	0.30	10 891	3.99×10^{-5}
3	30	0.22	6260	2.27×10^{-5}
4•	50	0.12	200	5.95×10^{-6}

• Gravel mix 4 used for zero velocity runs only

Table 9.1 Characteristics of calibration gravels.

For each run, the average intragravel flow velocity (V) across the wetted section was calculated from the relationship between discharge, cross-sectional area and porosity:

$$V = \frac{Q}{A} \times \lambda \qquad (9.1)$$

where Q is discharge, A is cross sectional area and λ is porosity. Finally, the Darcian permeability of the gravel was calculated using the standard pump test method (Terhune, 1958). As the standpipes were of similar design to those used in the original calibration procedure, the original permeability function was applied (Carling and Boole, 1986). In total, 140 runs were performed, with three replicates at each velocity and standpipe.

9.1.3 Results

For gravel mixes 1 and 2, which equate to Darcian permeabilities above 6260 cm h^{-1} and porosities greater than or equal to 0.3, there was no statistical difference in the probe's response (two-sample t-test, 5% significance level). However, for gravel mix 3, which equates to a permeability less than 6250 cm h^{-1} and a porosity less than or equal to 0.22, the probe's response differed significantly from the response recorded in gravel mixes 1 and 2 (two-sample t-test, 5% significance level). It was believed that the probe's response was transformed as a consequence of the lower porosity, which had resulted in reduction in natural dispersal of the saline solution through the available pore spaces. In view of this trend, two calibration curves were developed: (i) for describing gravels with permeabilities above 6260 cm h^{-1} and (ii) for describing gravels with permeabilities below 6260 cm h^{-1}.

A statistical analysis of the effect of run time on the probe's performance indicated that extending runs beyond ten minutes did not significantly alter the exponent of the decay curve (one-way ANNOVA, 5% significance level.). However, reducing the run time below 10 minutes significantly altered the exponent in over 50% of the runs (one-way ANNOVA, 5% significance level). Consequently, 10-minute runs were adopted as a practicable compromise between run time and probe response.

Finally, zero velocity runs were performed to determine the point at which diffusion significantly altered results based on flow dilution, thereby, allowing determination of the probe's lower threshold of response. On the assumption that static water would be uncommon in salmon spawning gravels with porosities greater than 0.22, zero velocity runs were carried in gravel mixes 3 and 4. Based on an average over three runs, the decay exponent for gravel mixes 3 and 4 were 0.0389 ± 0.0056 and 0.0315 ± 0.0094 respectively. Analysis of the flume data indicated that velocities less than 1 cm h^{-1} regularly generated similar exponent values; consequently, the lower limit of the probe's response was defined as 1 cm h^{-1}. Based on the 10-minute run period, and with incorporation of zero velocity run data, best-fit curves were fitted to the data sets (Figure 2). Prior to fitting best-fit curves, velocity runs less than 75 cm h^{-1} were removed from results obtained in gravel mixes 1 and 2. This was based on the observation that intragravel flow velocities less than 75 cm h^{-1} were difficult to attain in gravels with permeabilites greater than 6260 cm h^{-1}. Consequently, it was assumed that flow velocities below 75 cm h^{-1} would be uncommon in gravels with permeabilities less than 6260 cm h^{-1}. The calibration equations and curves are shown in Figure 9.1 and Table 9.2. Based on the standard deviation of the sampling distribution, the probes level of accuracy for calibration curve 1 (gravel permeabilities > 6260 cm h^{-1}) was calculated as 97 cm h^{-1} and for calibration curve 2 (gravel permeabilities > 6260 cm h^{-1}) the level of accuracy was defined as 18 cm h^{-1}.

y	x	*m*	*b*	r^2	*Equation No.*
Velocity*	Exponent	2647.5	-297.36	0.94	9.1
Velocity**	Exponent	854.94	-35	0.95	9.2

* Curve 1 (permeabilities > 6260)

** Curve 2 (Permeabilities < 6260)

Table 9.2 Summary of linear regressions relating the exponent of the conductiometric decay curve to intragravel flow velocities. Each equation is of the form y = $mx + b$, and r^2 = coefficient of variation.

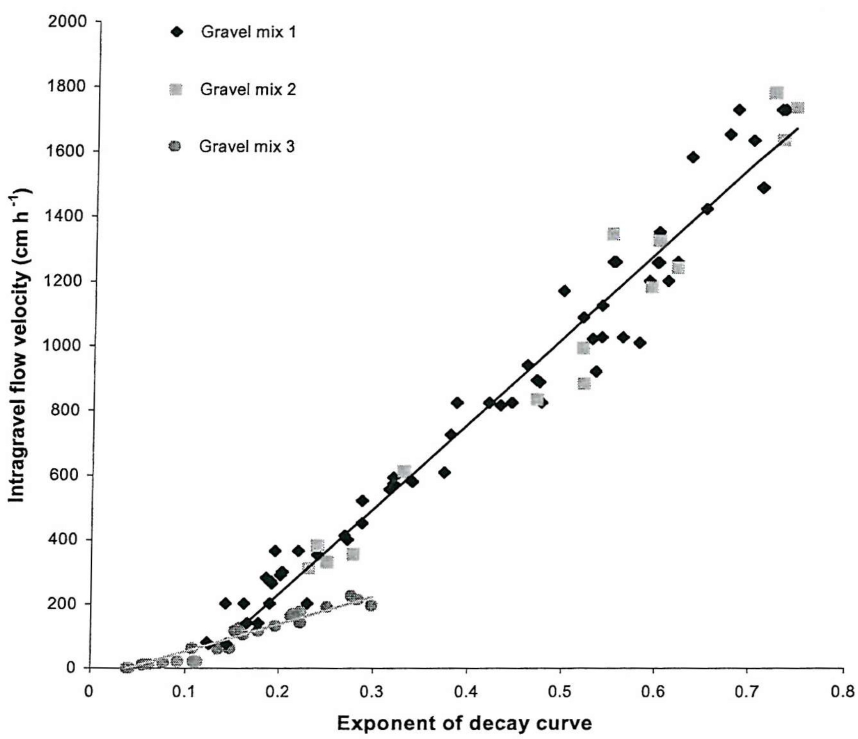

Figure 9.1 Calibration curves fitted using linear regression model: ——— permeabilities greater than 6260 cm h^{-1}; ------ permeabilities less than 6260 cm h^{-1}

With respect to the application of these calibration curves to the field study datasets, the pump test equipment required to assess gravel permeabilities was unavailable for the 2001-2002 field season. Therefore, for the purposes of estimating intragravel flow velocities, an exponent-decay-curve/intragravel-flow-velocity threshold was adopted to determine which calibration curve to apply. Both calibration curves were required to provide estimates of intragravel flow velocities across the range of intragravel flow velocities that were likely to be experienced in the field. A 0.28 exponent threshold, which relates to a 200cm h^{-1} velocity threshold, was defined. Above this threshold, calibration Equation 9.1 was applied and below the threshold Equation 9.2 was applied. This decay curve threshold was based on observations of the lower velocity limits of gravel mixtures 1 and 2. For the range of channel slopes recorded at the field sites (0.006-0.007), velocities below 200 cm h^{-1} were difficult to attain for gravel mixtures 1 and 2. However, it was recognised that in the field, surface flow and hydraulic gradient would influence the relationship between gravel permeability and intragravel flow velocity, potentially reducing the accuracy of the intragravel flow velocity estimates (Section 6.3). To allow cross-site comparisons of intragravel flow velocities, the approach was standardised, and the exponent-decay-curve/intragravel-flow-velocity threshold was also applied to the 2002-2003 datasets.

9.1.4 Field-testing of the conductiometric technique

In November 2001, two artificial redds were created in the River Test, England. The River Test is a groundwater-dominated chalk river with a catchment area of 1250 km^2 and mean annual discharge of 11.3 m^3 s^{-1}. In common with other chalk rivers, the River Test has a stable flow regime, which rarely exceeds 4-5 times minimum flow in any year (Acornley and Sear, 1998). Suspended sediments are composed of particles less than 250μm and bedload transport is uncommon (Acornley and Sear, 1999).

Each artificial redd contained a sediment pot, which could be removed and redeployed in its original location, and a standpipe (Figure 9.2). Intragravel flow velocities were estimated within each standpipe using the recalibrated conductiometric probe at seven-day intervals over a typical incubation period. Sediment pots were also removed at seven-day intervals. The contents were passed through a 4.0 mm sieve, and samples of fine sediment were retained for weight analysis. Once sieved, the pots were refilled with the sieved gravel (>4.0mm) and redeployed in their original location.

The average weekly intragravel velocities recorded across both redds using the recalibrated conductiometric standpipe are shown in Figure 3. Also shown in Figure 3 is river stage and average accumulation of fine sediments (<4.0 mm) across the two redds over the sampling period. Sediment accumulation was determined by cumulating the weekly rates of fine sediment deposition recorded in each pot. Total sediment accumulation based on the redeployed pot method was compared with freeze core data taken within the artificial redds at the end of the sampling programme. The results indicated that the total sediment accumulation determined using the pots was not statistically different from the total sediment accumulation in the undisturbed redd gravels (two-sample Mann Whitney, 10% significance level). The results of the field programme indicate that as sediments accumulated, intragravel flow velocities steadily declined. The velocities estimated using the recalibrated probe are comparable with velocities reported in other studies (Angradi and Hood, 1998; Clayton et al., 1996; Grost *et al.*, 1988).

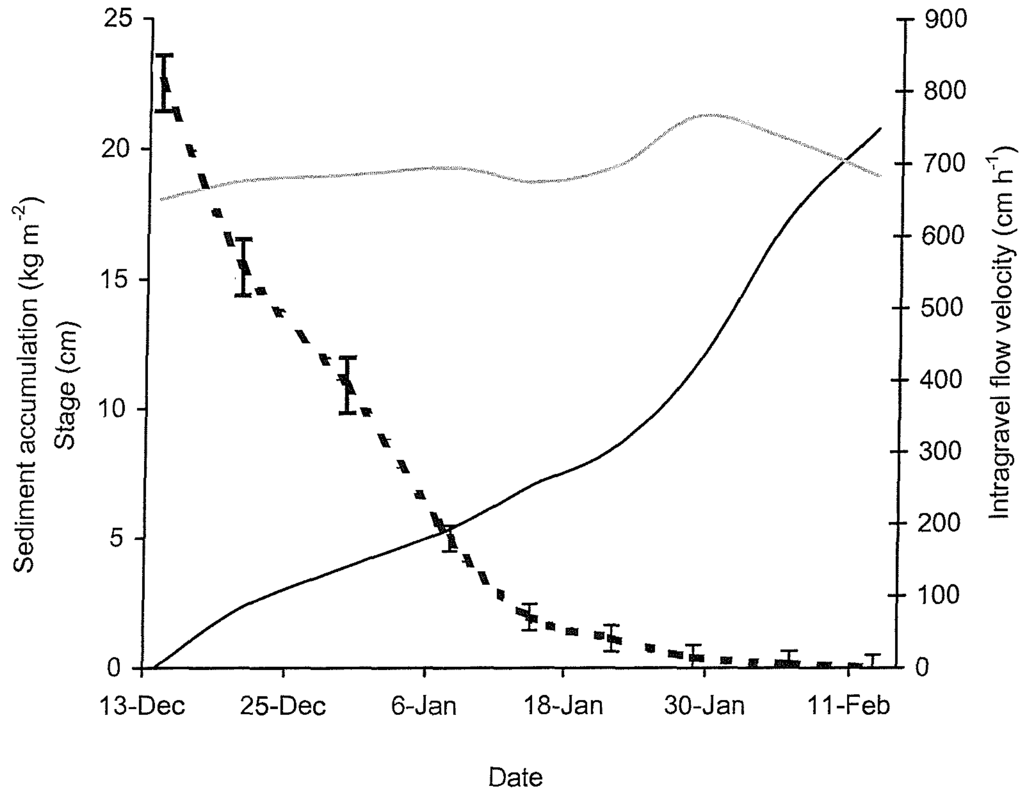

Figure 9.2 Fluctuations in intragravel flow velocity (▪▪▪▪) (including standard error bars), determined using the refined conductiometric standpipe technique. Also included is average rate of sediment accumulation, based on two sediment pots removed at weekly intervals (———), and stage (———).

9.1.5 Summary

The refinements to the Carling and Boole (1986) conductiometric standpipe technique have improved the accuracy and precision of the probe across a range of velocities reported in spawning gravels. Although concerns regarding the probes lower velocity threshold (1 cm h^{-1}) and the probes level of accuracy (18 cm h^{-1}) remain, the enhancement of the probes performance above these thresholds is a positive contribution to the problem of determining intragravel flow velocities in the field.

9.2 Two methods of deploying eyed eggs into artificially created salmonid redds

9.2.1 Introduction

Assessment of survival to emergence of salmonid progeny remains an important area of fishery research. In many instances, investigation of factors influencing survival requires the introduction of salmonid eggs into artificially constructed redds: details of important aspect of natural salmonid redds and methods of constructing artificial redds can be found in Peterson and Quinn (1996), and Chapman (1988). At present, eggs are typically introduced during redd creation. This dictates that either greened eggs are obtained and fertilised on site, or that redd construction is delayed until more robust eyed eggs are available for deployment. The principal benefit of using greened eggs over delaying redd creation, is that it allows studies to monitor the entire incubation period. However, stripping and fertilising eggs on site is a delicate operation that requires experienced handlers. Moreover, unpredictability exits in natural survival rates, and the deployment of a 'bad' batch of eggs may compromise recorded survival rates.

Delaying redd creation until eyed eggs are available, removes the difficult stripping operation and allows deployment of hatchery derived eggs that have been screened for mortalities and defects. Consequently, once deployed, one may be confident that recorded mortalities are a consequence of conditions within the incubation environment. However, by delaying the creation of redds, eggs are deployed into an unrepresentative incubation environment. Furthermore, the intragravel incubation period will be reduced, consequently, recorded survival rates may not be indicative of potential survival rates for that location.

The following short note describes two techniques that allow the introduction of eyed salmon eggs into pre-created artificial redds with minimal disturbance to the surrounding environment. By adopting this approach, the difficulties associated with stripping and handling greened eggs on site and the potential problems associated with deploying a 'bad' batch of eggs are removed. The first technique describes a method that allows deployment of eggs into pre-determined areas of the riverbed, including into sediment pots or similar monitoring equipment. The second technique, describes a method that allows direct insertion of eggs into the gravel substrate. Both methods are comparatively non-intrusive and are intended for integration into projects investigating factors influencing survival to hatch or emergence of salmonids.

9.2.2Technique one

The first technique is based on a simple nested insertion tube. The procedure minimises disturbance to the redd zone and allows deployment of eggs into a pre-determined area of the riverbed, or pre-deployed sediments pot or emergence traps. The deployment unit (Figure 1(a)) is composed of two cylindrical mesh tubes. The first tube acts as a small sediment pot and has a rigid based, open top and is enclosed in a small retractable elastic sock. The second tube, of slightly larger diameter, acts as a sump and provides an access and exit point.

The unit is designed to be inserted into an artificial redd during construction. Prior to deployment, the smaller inner tube should be filled with representative gravel from the artificial redd into which it will be deployed, and the elastic sock should be furled around the base of the pot. The smaller pot should be placed into the sump unit and the completed unit placed into the base of an artificially excavated egg pocket. A pre-prepared foam collar should then be inserted between the inner and outer tube to prevent the intrusion of fine sediments. Once deployed, construction of the redd can continue. Alternatively, the egg deployment unit can be placed within a sediment pot, which is subsequently deployed into an artificial redd.

This allows eggs to be deployed within an zone that can be monitored for sediment deposition and gravel composition.

When eyed eggs are available, the inner pot is removed from the sump (Figure 1(b)). At this time, care should be taken to carefully draw the sock up, thereby, retaining the fine sediment that has accumulated post redd construction. A length of hollow tube, of similar diameter to the inner pot and of adequate length to extend from the base of the redd beyond the water surface, is placed into the access point created by the sump. Small Harris baskets (suggested dimensions: diameter 50mm, height 70mm; suggested material: 4mm plastic mesh) are then filled with a mixture of eggs and gravel from the recovered pot. The Harris baskets is introduced to artificial redd through the insertion tube. A length of coloured nylon string tied to the top of the Harris basket allows the basket to be carefully lowered into the riverbed and acts as locator for subsequent recovery. Once the Harris basket is in place, the remaining gravel and fine sediment from the inner tube can be dropped through the insertion tube, covering the deployed eggss. Once the gravel/sediment mixture has settled, the insertion tube and outer mesh retaining tube can be carefully extracted. The dimensions of the pots and materials used should be tailored to suit budgetary requirements and project details, although suggested dimensions are included in figure 1. To reduce the potential introduction of harmful solutes, plastic coated wire mesh or stainless steel materials are advised.

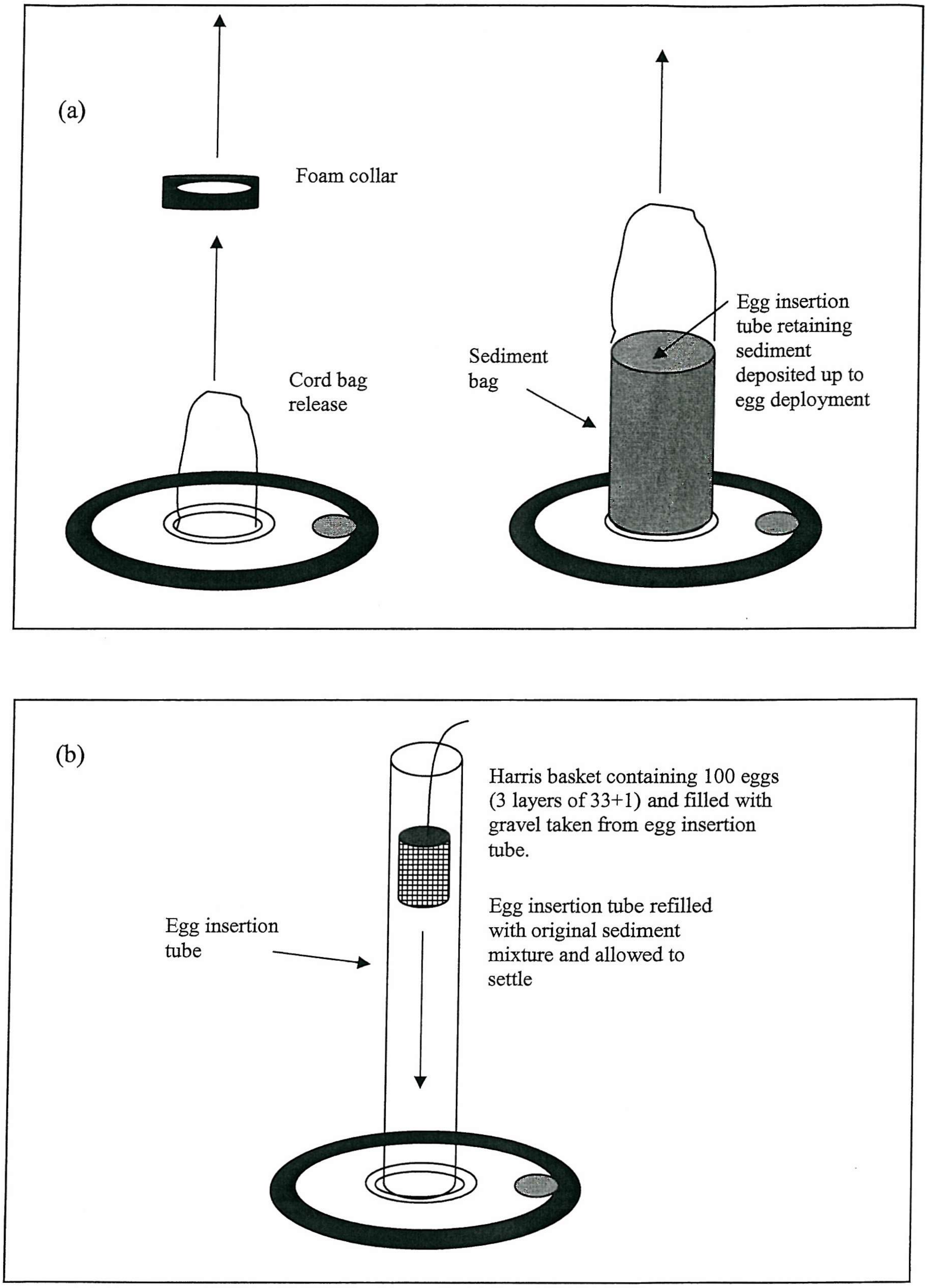

Figure 9.1 Overview of egg deployment technique one. (a) removal of insertion tube, (b) egg deployment.

9. 2.3 Technique two

The second technique allows deployment of eyed eggs into pre-created salmonid redds without a requirement for pre-prepared access points. However, the technique is unsuitable for deployment of eggs into sediment pots or other pieces of monitoring equipment. The technique is based on a twin-standpipe insertion unit as shown in figure 3. The unit is composed of two sections of stainless steel tubing. The inner tube has a drive point welded flush to its base and a driving pin welded to the opposite end. The driving pin is designed with a protruding lip that is extends beyond the edge of inner pipe and contains a small horizontal hole. The outer tube is constructed to fit over the inner tube, leaving a 1-2mm gap between the pipes. When fitted together, the top of the outer pipe should rest against the driving pin of the inner tube and the base should lie in line with the top of the driving point. The dimensions of the pipes should be customized for project requirements, although dimensions are suggested on figure 3.

When eyed eggs are available for deployment, the outer pipe is placed over the inner driving pipe and, using a driving tool, both units are driven into a pre-created artificial redd. Once inserted to the required depth, the inner driving tube is removed. If difficulties are encountered removing the inner tube, a rod may be inserted through the horizontal hole in the driving pin to ease removal. Once removed, the outer tube provides an access point to insert eyed eggs. It is suggested that the eggs are deployed within a Harris basket and that an insertion procedure similar to the one described in technique one is followed.

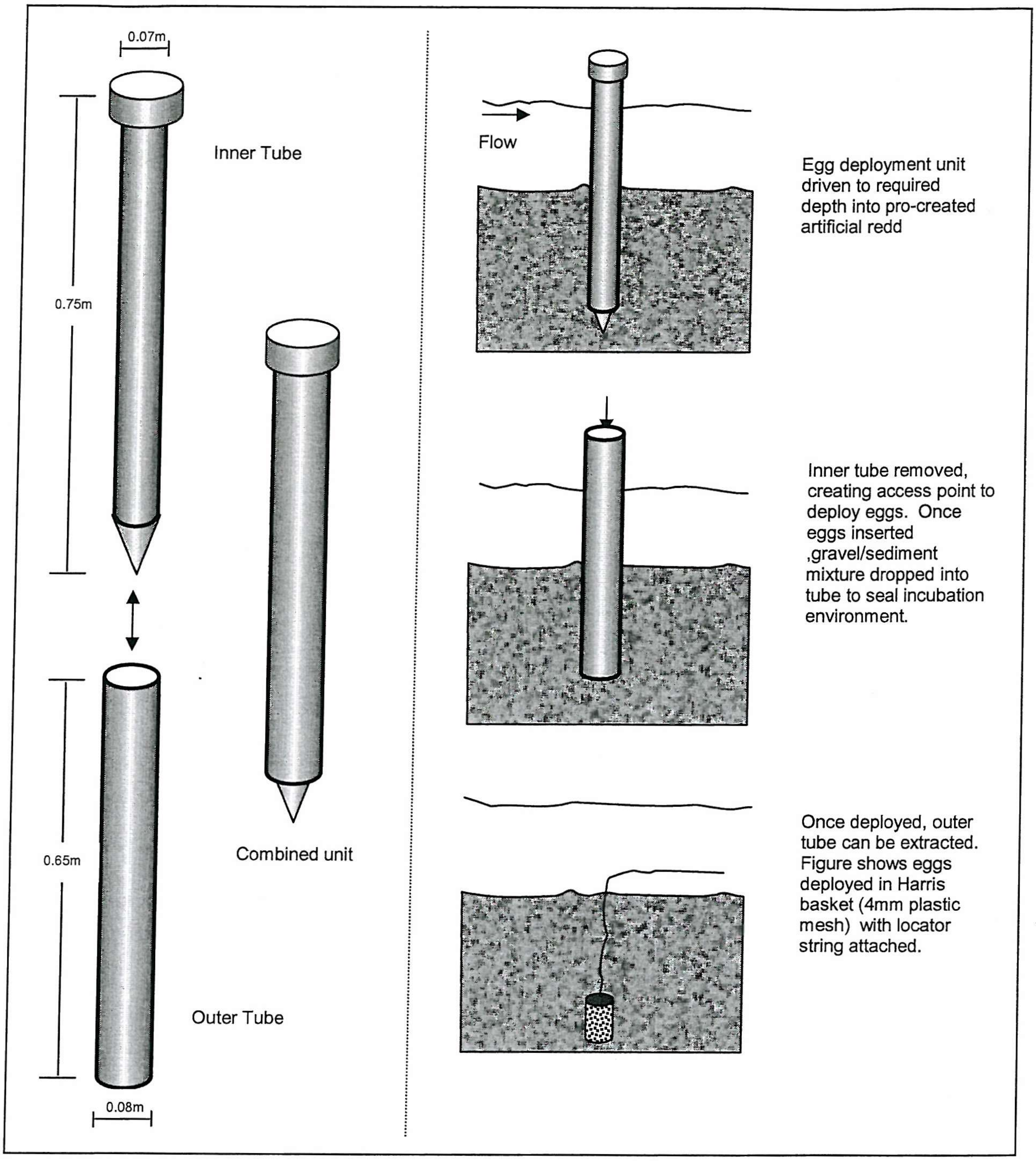

Figure 9.2 Overview of egg deployment technique two.

9.2.4 Field Tests

Field-testing of both techniques highlighted the potential benefits of adopting these approaches to deploying eggs. Five artificial redds were created in the River Aran, Wales. Egg insertion units, as described in technique one, were placed within a series of sediment pots that were deployed within the artificial redds. Each pot also contained a standpipe that provided access for a dissolved oxygen probe and conductiometric standpipe, which allows estimation of intragravel flow velocities (Carling and Boole 1986, Section X). Bi-weekly monitoring of conditions within the sediment pot provided data to determine oxygen fluxes through the redd zone:

$$O_{2(flux)} = C_o\,(v \times a_{egg})$$

Where C_o is the intragravel oxygen concentration within the egg pocket, **v** is the velocity determined with the conductiometric standpipe and a_{egg} is the cross section area of an incubating embryo.

Once eyed eggs were available for deployment, eggs were inserted into the sediment pots following the procedure outlined in technique one. Additional eggs were also deployed directly into the redds using the procedure described in technique two. Monitoring of conditions within the pots continued until hatching, at which time the Harris baskets were retrieved from the redds. A 100% recovery rate was recorded and survival was correlated with oxygen fluxes determined within the pots (Pearson correlation, $r^2 = 0.84$, significant at the 95% confidence limit). Additionally, comparisons of survival within each redd indicated no statistical difference in survival between the two deployment techniques (two-sample t-test, 95% confidence limit)

9.3 Summary of potential research projects

Based on the research consideration outlined in the main body of the thesis, a series of potential research projects aimed at advancing knowledge of factors and processes influencing incubation success are presented..

9.3.1 Introduction

Based on the research considerations outlined in Section 7.4.2, a series of potential research projects designed to advance knowledge of factors influencing the productivity of U.K. salmonid spawning and incubation environments are presented. These projects are divided into four categories: core science: strategic; core science: operational; management: strategic; and management: operational.

9.3.2 Core science: strategic

Assessment of the composition, sources and vectors of oxygen consuming materials deposited in salmon spawning gravels

The field-monitoring program highlighted the potential impact of oxygen consuming materials on the flux of oxygen through salmon spawning gravels. Oxygen consuming materials derive from both natural sources, for instance, terrestrial organic detritus and dissolved organic matter, and from non-natural sources, for instance, sewage, fertilisers, silage and agricultural waste. The impact of these oxygen demands (often referred to as Sediment oxygen demands [SOD]) is exacerbated when the flux of water through the riverbed is restricted, for instance, as a consequence of high levels of intragravel fines.

Typically, inputs of naturally derived materials have low oxygen demands and are an important component of a healthy functioning ecosystem. Non-natural consumers however, may impart a significant oxygen demand, potentially resulting in an oxygen deficient within the ecologically active upper layers of the riverbed.

The results of the field-monitoring program indicated that sediments deposited in the River Test contained high proportions of organic materials (>20% organic). However, the overall oxygen demand of these sediments was low. Consequently, although low intragravel flow velocities were recorded, the oxygen concentration of intragravel water remained above levels considered critical to salmonid incubation success. Conversely, in the River Ithon and River Aran the organic component of deposited sediments was low (<5%), however, the overall oxygen demand of the sediment was high (more than twice that of the River Test), potentially indicating the presence of agriculturally derived high oxygen demand materials (organic waste, fertilisers). When coupled with low intragravel flow velocity, this resulted in intragravel oxygen concentrations and fluxes below levels considered critical to incubation success.

In response to these observations, there is a requirement to ascertain the active components of infiltrated sediments across a range of catchments of varying land-use, and to identify the potential sources and vectors by which these materials enter freshwater systems. The proposed project would (i) establish the magnitude and active component of sedimentary oxygen demands within and between a range of UK catchments types, ranging from forested catchments to agriculturally intensive catchments and (ii) undertake a wider, catchment scale investigation of the potential sources and vectors of oxygen consuming materials. This knowledge would be used to define specific management strategies and treatments necessary to mitigate the impact of oxygen demands within spawning gravels on incubating embryos.

The role of stream hydrology on the supply of oxygen to incubating salmon progeny

The results of the monitoring program highlighted the influence of surface flow on the exchange and flux of oxygenated water through gravel streambeds. During high flows, oxygen rich water is forced into spawning gravels creating temporal (and spatial) changes in surface-subsurface exchanges and intragravel flow rates. During periods of low flow, rates of exchange are reduced, intragravel flow velocities are lowered and the flux of oxygen through the riverbed is restricted. Furthermore, the literature contains references to increased groundwater upwelling during periods of low flow. If the oxygen concentration of upwelling groundwater is distinct from the concentration of surface derived water, variable surface and subsurface inputs of oxygenated water will influence the oxygen concentration of hyporheic water (Malcolm *et al.*, 2003).

Many upland catchments have hydrological regimes modified by land use management, for example field drainage or forestry. These modifications may have a detrimental impact on salmon incubation success. This project would seek to establish (i) the connectivity between stream flow and intragravel flow within spawning gravel's and investigate how these processes vary over time according to the hydrological regime and the sedimentary composition of the riverbed, (ii) develop and validate a numerical model to represent this process and (iii) apply the model to simulate the variations in intragravel oxygen supply arising from modifications to hydrology resulting from land use and climate change. The investigation would focus on a vareity of catchments, ranging from groundwater dominated to upland freshet.

Turbulent driven exchange of surface water with gravel riverbeds

The influence of turbulent driven momentum exchange of surface water with the riverbed has been identified in a number of flume studies, and the results of this investigation has provided further evidence of this process. Delineation of the influence of this surface flow on the exchange of oxygenated water with gravels riverbed has important implications for systems experiencing concurrent problems of excess sedimentation and prolonged periods of low flow. Under these circumstances, the decoupling of surface water could exacerbate problems of low oxygen fluxes through spawning and incubation gravels.

A detailed flume investigation of surface and subsurface flow characteristics could be used to assess the mechanisms influencing surface exchange processes. The application of Acoustic Doppler Velocimeter (ADV) technology to assess 3-D turbulent flow fields over flatbed and sinusoidal wave forms could be coupled with detailed assessments of flow patterns above and below the riverbed. The application of passive tracer techniques would allow the development of detailed three-dimensional maps of surface and subsurface flow patterns.

Embryonic oxygen consumption and the impact of ammonia accumulation

As detailed in section 3.2 and 6.2, a variety of rates of embryonic consumption have been reported in the literature. Consequently, there is a requirement to produce detailed and reliable estimates of Atlantic salmon embryonic consumption rates. Furthermore, there is also a requirement for information pertaining to critical ammonia concentrations and critical dilution velocities. A simple laboratory study using an open flow system could be used to assess oxygen consumption and ammonia accumulation across a range of oxygen concentrations and flow velocities.

Impact of fine sediment on embryonic oxygen consumption

Section 6.2 detailed the impacts of clay particles on oxygen consumption, however, the scale and scope of the study was limited by resource constraints. Micro-electrode technology could be used to provide a more comprehensive assessment of conditions within the micro-environment surrounding an incubating egg capsule. Furthermore, a variety of sediment size classes, and mixtures of sediment size classes, could be introduced to the incubation environment to assess the direct influence of fine sediments on oxygen consumption.

9.3.3 Core Science: operational

Development of an oxygen flux probe for direct determination of spawning habitat suitability

At present, oxygen concentration is the most commonly adopted singular determinant of habitat quality. However, oxygen concentration alone provides limited information on intragravel flow velocities and, therefore, the flux of oxygen through the incubation environment.

A new approach to determining the quality of salmonid incubation environments, based on the ratio of oxygen supply to oxygen consumption by incubating salmonid progeny, is proposed. In essence, if the ratio attains 1.0 or less, then the incubation environment is of poor quality. Above this ratio, the environment is defined as marginal or good.

The development of an instrument of this type would require a pilot (feasibility) study assessing potential development avenues, available technology and costs. This project would assess (i) the potential application of current technology (microprobes, chemical reactions), (ii) investigate the areas where technology transfer might be of greatest value and (iii) propose a potential design template and budget.

9.3.4 Management: strategic

An appraisal of variations in the oxygen demand of materials infiltrating UK riverbeds

The sedimentary oxygen demand of materials infiltrating the incubation environment has been shown to influence the availability of oxygen to incubating salmon embryos and alevins (Section 6.4)s. At present, the oxygen demand of materials infiltrating riverbed gravels is not included in assessments of freshwater habitat quality; therefore, there is limited information on the variability of the oxygen demand of infiltrated material for U.K. river systems.

This project proposes to assess the spatial and temporal variability in oxygen demand of infiltrated materials across a range of U.K. salmon rivers of contrasting geology, hydrology and land use. Different approaches to sampling infiltrated materials for oxygen demands would be evaluated to determine appropriate sampling protocols. These approaches would include assessments based on sediment pots and suspended sediment sampling. Detailed laboratory processing techniques would be used to determine the potential source of oxygen demands (for example nitrogenous fertilisers, silage, terrestrial and instream organic matter). It is envisaged that the project would be run in conjunction with sediment fingerprinting to establish the source of both fine inorganic and organic sediment fractions. The project could be organised along similar lines to the national sedimentation survey.

Development of improved tool for assessing incubation habitat quality

As detailed in Section 6.5, the theories of mass transport can be used to determine thresholds of survival based on oxygen concentrations and intragravel flow velocities. However, the principal drawback of this approach is the lack of information it provides concerning factors resulting in reduced oxygen concentrations. The expansion of the approach outlined in Section 6.5 to include mechanisms to assess factors influencing oxygen concentration and intragravel flow could potentially provide managers with a powerful tool for assessing habitat quality.

Potential research routes include (i) the development of oxygen supply models (Alonso *et al.*, 1996) that relate sediment delivery and deposition to oxygen flux through riverbed gravels and (ii) the development of semi-empirical models of oxygen flux based on the relationships described in Section 6.4.

9.3.5 Management: operational

Multi-factor assessment of salmon spawning habitat quality in degraded streams

This thesis has developed an integrated approach to monitoring the quality of salmonid incubation environments. The methodology and techniques could be adapted for application by agencies responsible for freshwater salmonid habitats, including the Environment Agency, English Nature, and Scottish Fishery Boards.

This project would aim to (i) rationalise the methodology and techniques necessary for assessing incubation habitat quality and (ii) develop a field and technical support manual for use by practitioners engaged in monitoring and remediation. Consideration would be given to establishing reference targets for good quality incubation environment in groundwater dominated and freshet streams.