A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos

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Abstract:

Previous investigations into factors influencing incubation success of salmonid progeny have largely been limited to the development of empirical relationships between characteristics of the incubation environment and survival to emergence. It is suggested that adopting a process-based approach to assessing incubation success aids identification of the precise causes of embryonic mortalities, and provides a robust framework for developing and implementing managerial responses.

Identifying oxygen availability within the incubation environment as a limiting factor, a comprehensive review of trends in embryonic respiration, and processes influencing the flux of oxygenated water through gravel riverbeds is provided. The availability of oxygen to incubating salmonid embryos is dependent 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. Embryonic respiratory trends indicate that oxygen consumption varies with stage of development, ambient water temperature and oxygen availability. The flux of oxygenated water through the incubation environment is controlled by a complex interaction of intragravel and extragravel processes and factors. The processes driving the exchange of channel water with gravel riverbeds include bed topography, bed permeability, and surface roughness effects. The flux of oxygenated water through riverbed gravels is controlled by gravel permeability, coupling of surface–subsurface flow and oxygen demands imposed by materials infiltrating riverbed gravels. Temporally and spatially variable inputs of groundwater can also influence the oxygen concentration of interstitial water. Copyright © 2006 John Wiley & Sons, Ltd.

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INTRODUCTION

Global concern regarding declining effectiveness of salmonid incubation has produced a voluminous body of information on potential causes of poor pre-emergence survival. Among a composite of factors, the availability of oxygen within the gravel bed has been identified as an important factor restricting embryonic survival (Harvey, 1928; Turnpenny and Williams, 1980; Maret *et al*., 1993; 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 about the relationship between oxygen availability and embryonic survival. Furthermore, investigation into factors influencing oxygen availability to incubating salmonid progeny has largely been limited to studies of individual factors within singular systems, e.g. intragravel oxygen concentration and measures of granular properties of the incubation environment (McNeil and Ahnell, 1964; Koski, 1966, 1975; Phillips *et al*., 1975; McCuddin, 1977; Platts *et al*., 1989; Lotspeich and Everest, 1981; Tappel and

Bjornn, 1983; McCrimmon and Gots, 1986; Chapman, 1988; Young *et al*., 1991). This contrasts recent evidence, which indicates that the flux of oxygen through riverbed gravels is influenced by a complex interaction of intragravel and extragravel 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 improved awareness of factors potentially influencing the flux of oxygen through salmonid spawning gravels.

This review synthesizes information on trends in embryonic respiration and processes influencing the flux of oxygenated water through gravel riverbeds. The purpose of the review is to promote appreciation of the complex process governing oxygen fluxes within salmonid spawning gravels and to relate these processes to oxygen deficiency pre-emergence mortalities. Based on the work presented by previous investigators, a simple conceptual model of oxygen availability within salmonid spawning gravels is proposed (Figure 1). To summarize, the availability of oxygen to incubating salmonid embryos is dependent on the exchange of oxygenated water with the riverbed and the ability of the riverbed gravel to transport this water at a rate and concentration that meets embryonic respiratory requirements. Therefore, the review is organized into four sections: (i) an overview of the respiratory requirements and characteristics of incubating salmonid embryos and alevins; (ii) a summary of factors

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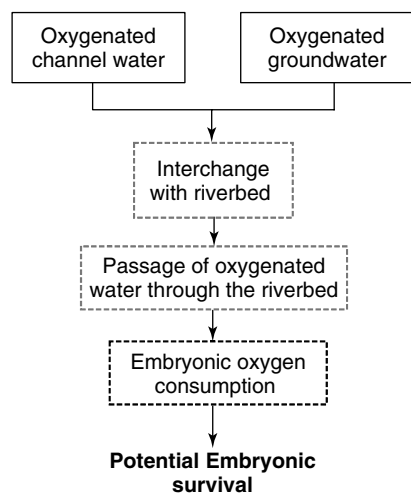
Figure 1. Summary of the dominant factors (solid boxes) and processes (dotted boxes) controlling the availability of oxygen to respiring salmonid embryos

influencing the exchange of oxygenated water with the riverbed; (iii) an examination of intragravel and extra-gravel factors influencing the passage of oxygenated water through riverbed gravels; (iv) the development of a holistic model of factors influencing the availability of oxygen to incubating salmonid progeny. An important aspect of the review is the dominance of literature from northwest America, and it should be recognized from the outset that there may be biological differences between different species of salmonid (Crisp, personal communication).

PRE-EMERGENT OXYGEN CONSUMPTION

Basic processes

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). Oxygen is transported from the boundary layer across the egg membrane by diffusion. If the oxygen concentration in the boundary layer drops, then the concentration gradient is reduced, potentially resulting in restricted consumption and growth deficiencies (Silver *et al*., 1963; Cooper, 1965; Garside, 1966; Mason, 1969). If the concentration in the boundary layer drops below a critical threshold, then the concentration gradient will be insufficient to support metabolic activity, and mortalities will occur (Daykin, 1965; Rombough, 1988).

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; Rombough, 1988). If incubating embryos consume oxygen at a greater rate than can be supported by the macroenvironment, then oxygen concentrations within the boundary layer will

decline, influencing the availability of oxygen to incubating embryos. Oxygen concentrations in the macroenvironment that result in restricted consumption are termed 'oxygen limiting', and if mortalities occur they are termed 'critical' (Davis, 1975). Post-hatching, embryos become mobile, allowing them the potential to migrate from areas of low oxygen availability. Therefore, alevins may be less susceptible to mortalities resulting from oxygen deficiencies.

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 (Silver *et al*., 1963; Cooper, 1965; Wickett, 1975; Hamor and Garside, 1977, 1979; Rombough, 1988). Stage of development is the factor most commonly associated with changes in oxygen consumption (Wickett, 1954; Hamor and Garside, 1977) (Figure 2). In broad terms, prior to hatching, consumption increases with development (Crisp, 1981). 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, 1977). The second peak occurs at hatching and has been ascribed to the exertion of breaking free from the egg capsule, which must be supported by increased oxygen uptake (Hamor and Garside, 1979).

Intragravel water temperature influences the rate of development of salmonid embryos and alevins (Alderdice *et al*., 1958; Combs, 1965; Garside, 1966; Hamor and Garside, 1976, 1977, 1979; Crisp, 1981) (Figure 2). As water temperature increases, metabolic activities increase and, as a result, consumption increases. Consequently, all other factors being equal, the development rate and the rate of oxygen consumption are directly related at any given temperature. Few studies have directly investigated the influence of temperature on oxygen consumption. However, results presented by Garside (1966) and Hamor and Garside, (1977) indicate that a twofold increase in temperature halves the development time of Atlantic salmon embryos. Assuming a direct relationship between
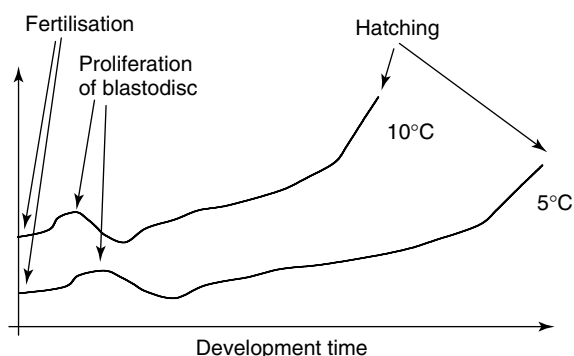

Figure 2. Summary of the influence of temperature and stage of development on rates of oxygen consumption

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

Temperature (°C)	Development stage	Oxygen consumption per egg (mg h^{-1})	Reference
10	Early	0·0013	Hamor and Garside (1979)
10	Eyed	0·02	Hamor and Garside (1979)
10	Eyed	0·001 04	Hayes *et al.* (1951)
5·5	'Domed' eyed	0·0014	Lindroth (1942) in Harmor and Garside (1979)
4·4	Well eyed	0·0012	Einum *et al.* (2002)
10	Hatch	0·048	Hamor and Garside (1979)
10	Hatch	0·0048	Hayes *et al.* (1951)
17	Hatch	0·0067	Lindroth (1942) in Harmor and Garside (1979)

temperature and development, this would result in a twofold increase in oxygen consumption.

Finally, embryonic oxygen consumption is also a function of oxygen availability (Alderdice *et al.*, 1958; Silver *et al.*, 1963; Garside, 1966; Hamor and Garside, 1977; Rombough, 1988). Hayes *et al.* (1951), in a laboratory study investigating the influence of oxygen supply on consumption for Atlantic salmon eggs, concluded that, at low levels of oxygen supply, consumption was dependent upon supply; however, at higher levels, consumption was independent of supply. Silver *et al.* (1963), Garside (1966; Hamor and Garside, 1977), and Rombough (1988) support this observation.

Rates of oxygen consumption

Research generally concurs on the factors influencing oxygen consumption; however, disparity exists regarding precise rates of consumption (Table I). 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 (Hamor and Garside, 1979; Chevalier *et al.*, 1984). Without further details on the experimental procedures of previous researchers, it is difficult to provide a comprehensive assessment of the accuracy and precision of reported rates of oxygen consumption.

Modelling consumption

Early attempts to assess embryonic oxygen consumption theoretically utilized simple models of oxygen diffusion across cell membranes (Harvey, 1928; Hayes *et al.*, 1951; Wickett, 1954). These early models were superseded with the application of the theory of mass transport, an established and tested theoretical model of solute and heat transfer (Daykin, 1965). The original model proposed by Daykin was refined by Wickett (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 (1984), who modified the model to assess consumption under varying internal egg conditions, and by Alonso *et al.* (1996), who added a function describing the influence of natural convection.

Although based on recognized theories of molecular transport, and integrating multiple aspects of oxygen supply and consumption, the theory of mass transport has received only limited application to the problem of estimating incubation success and habitat quality (Chevalier and Carson, 1984; Alonso *et al.*, 1996). Consequently, little is known about the ability of this theory to define oxygen consumption or habitat suitability accurately. One concern regarding the application of the theory of mass transfer is a lack of reliable information on important parameters used by the model. For instance, the oxygen diffusion coefficient of the egg capsule and the oxygen concentration of the perivitelline fluid are not well defined.

EXCHANGE OF OXYGENATED WATER WITH GRAVEL RIVERBEDS

Identification of hyporheic zone

The intragravel incubation environment of salmonid ova is contained within an ecotone referred to as the hyporheic zone. 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). For 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.

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 (Brunke and Grosner, 1997; Boulton *et al.*, 1998; Edwards, 1998; Malard and Hervant, 1999). In complex landscapes, hyporheic exchanges are typically composed of localized hyporheic processes embedded within larger hillslope groundwater systems (Harvey and Bencala, 1993; Malard and Hervant, 1999). 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 (Brunke and Grosner, 1997; Malard and Hervant, 1999; Sophocleous, 2002).

Groundwater inputs

In channels flowing above a sediment layer overlying an impermeable stratum, water within the hyporheic zone will be composed mainly of surface-derived water

(Sophocleous, 2002). However, groundwater may contribute to the hyporheic zone if the riverbed is composed of an extended sediment layer overlying a zone of permeable substratum. Based on the regularity of groundwater inputs, groundwater-fed streams are defined as perennial, intermittent or ephemeral.

Groundwater moves within three-dimensional flow fields that are controlled by gradients in hydraulic head and by hydraulic conductivity (Winter *et al*., 1998). 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. 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 (Fraser and Williams, 1998; Winter *et al*., 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.

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 localized geologic features and topographic characteristics (Dole-Olivier, 1998; Winter *et al*., 1998). Enhanced areas of upwelling may occur within subsurface geologic units of increased permeability, e.g. in ancient channels below the hyporheic zone (Brunke and Grosner, 1997). Similarly, localized 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).

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, salmonid populations have also been shown to display preferences for spawning in zones of groundwater upwelling (Lister *et al*., 1980; Sowden and Power, 1985; Curry and Noakes, 1995; Geist *et al*., 2002). Therefore, it seems appropriate to consider the influence of groundwater incubation success on a system-to-system basis.

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 Grosner, 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). 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 of 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 the Frissell *et al*. (1986) 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).

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 Grosner, 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. Downwelling is associated with
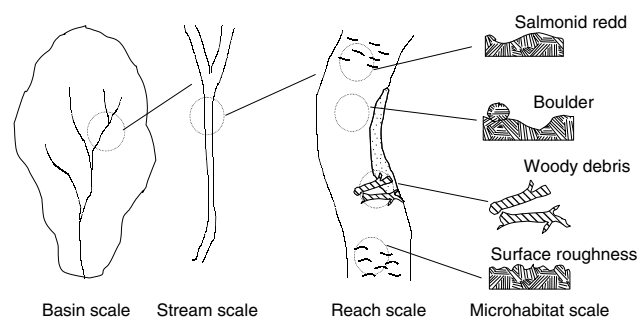

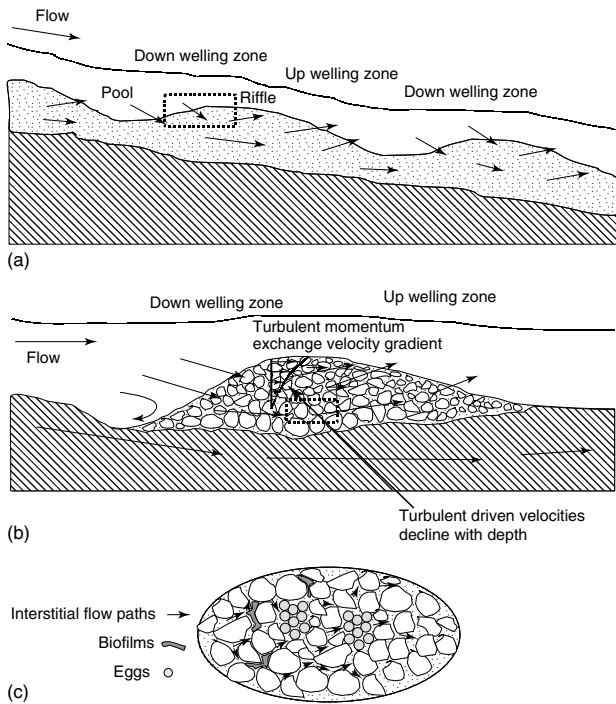Figure 3. Spatial hierarchy adopted to describe exchange processes (modified from Frissell *et al*. (1986))

Figure 4. (a) Reach-scale surface subsurface exchange flows. (b) Microscale exchange flows (redd). (c) Interstitial flow paths within the egg pocket (see below)

local areas of high to low pressure change, e.g. the interface between a pool and a riffle, and upwelling is associated with local areas of low to high pressure gradients, e.g. at the interface between a riffle and pool (Figure 4a). Reach-scale changes in substrate permeability also create areas of upwelling and downwelling, with downwelling occurring in areas of decreasing permeability and upwelling occurring 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 scales (Brunke and Grosner 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 localized 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 and Hervant, 1999). Obstacles in the streambed, e.g. 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 4b) (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 (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 (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 4b) (Mendoza and Zhou, 1992; Zhou and Mendoza, 1995; Packman and Bencala, 2000). Finally, the infiltration of fines and growth of biofilms influences the porosity of the gravel matrix (Figure 4c).

Under laboratory conditions, surface flow has been shown to influence the upper 0·1 m of the gravel substratum (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; Vervier et al., 1992; Panek, 1994; Brunke and Grosner, 1997; Angradi and Hood, 1998; Soulsby et al., 2001; Malcolm et al., 2003). Using hydrochemical indicators, Malcolm et al. (2003) showed that, during high flows, the relative contribution of surface water over groundwater increased, indicating deeper penetration of surface water. Similar results were reported by Fraser and Williams (1998), who observed a seasonally variable influence of groundwater within the hyporheic zone. They concluded that the downwelling of surface water during high flow events lowered the hyporheic–groundwater interface.

HYPORHEIC CONTROLS ON THE FLUX OF OXYGENATED WATER

Intragravel flow velocity

Once water has entered the hyporheic zone, its oxygen content and progress through the riverbed are 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 by 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, substratum permeability and surface-driven turbulent momentum exchange. 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 negative effect on permeability and intragravel flow increases (Chevalier and Carson, 1984).

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, 1984), local hydraulics (Einstein, 1968; Carling, 1992; Sear, 1993), the relationship between particle size and surface and subsurface interstitial pore spaces (Beschta and Jackson, 1979; Frostick et al., 1984), scour and fill sequences during floods (Lisle, 1989), and reach morphology (Diplas and Parker, 1985). For the purposes of this review, a précis of infiltration characteristics of relevance to intragravel flow velocities is provided. Infiltration is largely controlled by the relationships between sediment size and available pore space. 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 gravel layers, but are too large to pass through the sublayer gravels, become trapped near the surface of the riverbed (Beschta 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 sediment particles (Beschta and Jackson, 1979). Conversely, fine sediments that are smaller than the interstitial gaps in the surface and subsurface gravels will pass through the riverbed gravels and settle at the base of the permeable gravel layer (Einstein, 1968) (Figure 5a). Infiltration of this nature is often referred to as 'bottom-up' sediment accumulation. As the formation of 'seals' at the bed surface can inhibit deeper deposition of finer material, the mixture of fine sediment size classes exerts an important control over the amount of fine sediment that accumulates in riverbed gravels (Figure 5b).

The granular and morphological character of the salmonid redd may influence infiltration of fine sediments. First, an important control over the depth and rate of fine sediment deposition is the overlap of substratum 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. Second, 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. If the subsurface gravel is coarser than the surface layer gravel, then fine sediment intrusion is increased (Frostick et al., 1984). Third, by loosening the gravel substratum, 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 result in increased intrusion of fine sediments. 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 and Wolman, 1993).

The implications of these observations on intragravel flow velocities can be summarized as: (i) fine sediments that penetrate deep into the riverbed will reduce gravel permeability and intragravel flow velocity; (ii) the accumulation of coarser particle 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; (iii) although initially cleansed of fine sediments, owing to the granular and morphological properties of salmonid redds they may be susceptible to enhanced infiltration of fine sediments and the associated impacts on intragravel flow velocities (Greig et al., 2005).

In addition to inorganic substances, the infiltration of organic detritus into riverbed gravels must also be considered. The infiltration of organic material will also
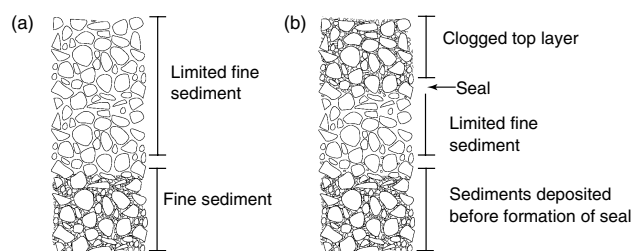

Figure 5. Trends in fine sediment accumulation: (a) 'bottom-up' sediment deposition; (b) formation of a seal near the bed surface (after Alonso et al. (1996))

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).

Intragravel oxygen concentration

The oxygen concentration of subsurface water is controlled by the oxygen content of surface and groundwater inputs (as described above) and by the contact time of water with oxygen-consuming materials within the hyporheic zone (Whitman and Clark, 1982; Chevalier *et al.*, 1984; Greig *et al.*, 2005). Oxygen demands within riverbeds, which are commonly referred to as either sediment oxygen demands (SODs) or sedimentary respiration, develop as microbial communities break down the organic and inorganic materials deposited in the riverbed. Based on the cycle driving oxygen consumption, the total SOD can be divided into biological oxygen demands (BODs) and nitrogen oxygen demands (NODs). A third component, referred to as the chemical oxygen demands, is more commonly associated with anaerobic conditions and is, therefore, not thought to influence the availability of oxygen significantly within zones of salmonid incubation (Chevalier *et al.*, 1984; Greig *et al.*, 2005).

In many river systems, BODs are the primary driving force for oxygen consumption. BODs 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. NODs are similar to BODs, except that the driver for the oxygen demand is a nitrogen oxidation process. Nitrogen sources are typically inorganic, e.g. fertilizers, 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 6) (Chevalier *et al.*, 1984). These time trends are provided as general markers; in reality, oxygen-demand curves are composed of multiple overlapping consumption cycles that are controlled by the specific chemical compositions of the materials being oxidized.

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 POM can

be described as autochthonous (in-stream source) and allochthonous (terrestrial source). Typical autochthonous material includes dead and necrotic macrophyte vegetation and small macroinvertebrate faeces. Typical allochthonous material includes leaf litter, cattle faeces, agricultural waste and effluent discharges (Jones *et al.*, 1994). 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, e.g. fertilizers, 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, when inputs of leaf litter and other naturally occurring allochthonous organic detritus are high, e.g. in autumn or during periods of clear-cutting (Cederholm *et al.*, 1981), and when localized sources of organic material are washed into the river, e.g. during periods of overland flow across arable land. Two mechanisms have been reported to control the influx of POM into the hyporheic zone (Jones *et al.*, 1994). 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).
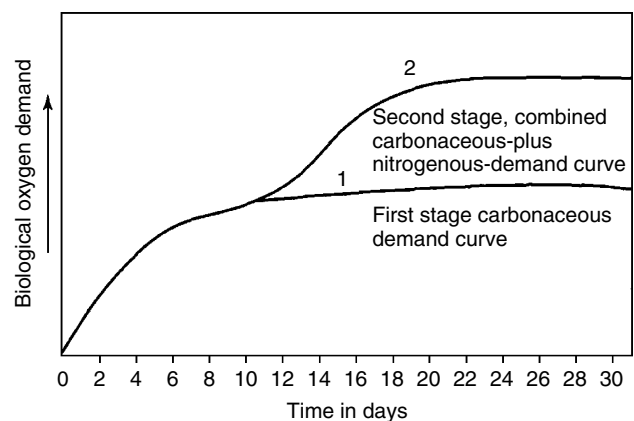

Figure 6. Typical oxygen demand response curve: (1) first stage BOD curve for oxidation of organic matter; (2) second stage NOD, influence of nitrification after Delzer and Mckenzie (2003)

Table II. Review of reported SODs (Chevalier *et al.* (1984))

Substratum	SOD (mg g^{-1} h^{-1})
Sand	0·0055
Lake mud	0·74
Detritus	0·33
Organic muck (30% organic)	2·45
Silt loam (9% organic)	0·0054
Gravel loam with wood fragments (17% organic)	0·31
Pasture loam with dead grass (20% organic)	12·08

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 *et al.*, 1984). At present, there are limited data sets on the oxygen demands associated with materials deposited in spawning gravels (Greig *et al.*, 2005). Typical SOD rates are reported in Table II. There are limited data on SODs and 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 and methodology of farming practices, e.g. the application of fertilizer and silage, may provide a source of nutrient-rich organic and inorganic material.

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 reduced 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). Oxygen concentration gradients exist between the zones of downwelling at the heads of riffles and subsequent zones of upwelling (Findlay, 1995; Franken *et al.*, 2001). Based on the mosaic of hyporheic flow paths discussed above, it is possible to conceptualize a hyporheic zone that is characterized by oxygen gradients that are spatially defined by distinct flow systems or interactions between flow systems (Figure 7).
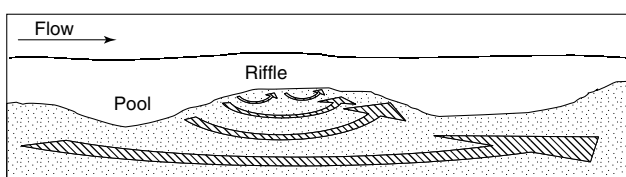

Figure 7. Summary of hyporheic flow paths. The thickness of the lines schematically represents the potential depletion in oxygen concentration of water within that flow path

HOLISTIC DESCRIPTION OF FACTORS INFLUENCING OXYGEN AVAILABILITY

Based on the information presented in the preceding sections, Figure 8 provides an overview of factors influencing the availability of oxygen to incubating embryos. This model does not include the build-up of toxic levels of ammonia that occur when rates of removal of metabolic waste decrease in response to falling rates of interstitial flow. A build-up of ammonia within the eggs may confound attempts to relate intragravel mortality to oxygen supply, since both processes are flow-rate dependent. This is an area requiring further investigation.

To summarize, 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 and mobility of alevins may also influence 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 a 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 throughflow of oxygenated water. For post-hatching oxygen-deficiency-related mortalities, observations of respiratory requirements indicate that peak metabolism occurs during hatching and that oxygen consumption declines post-hatching (Rombough, 1988). Furthermore, alevins are mobile and may migrate towards areas of higher oxygen availability. Therefore, it is probable that oxygen-deficiency-related mortalities are reduced post-hatching.

Factors influencing oxygen availability 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 the 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 overwinter grazing or poorly timed application of fertilizers or silage.
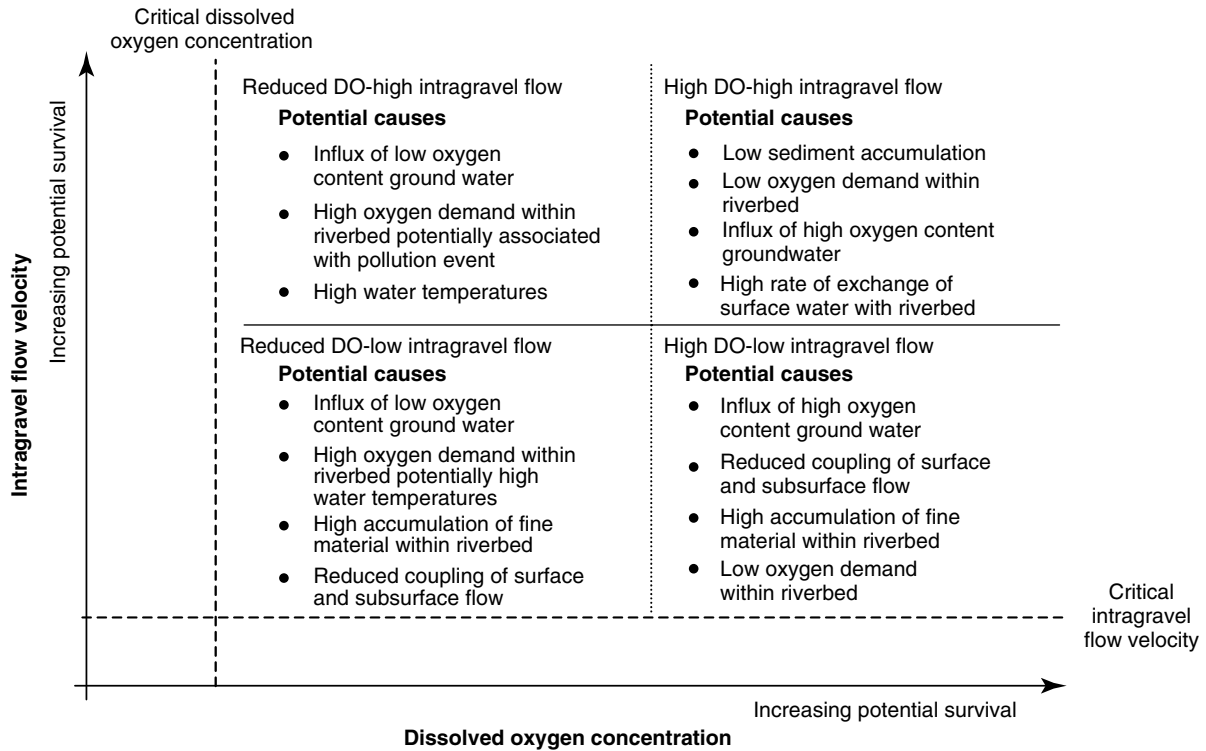
Figure 8. Overview of factors influencing the availability of oxygen to incubating salmonid embryos
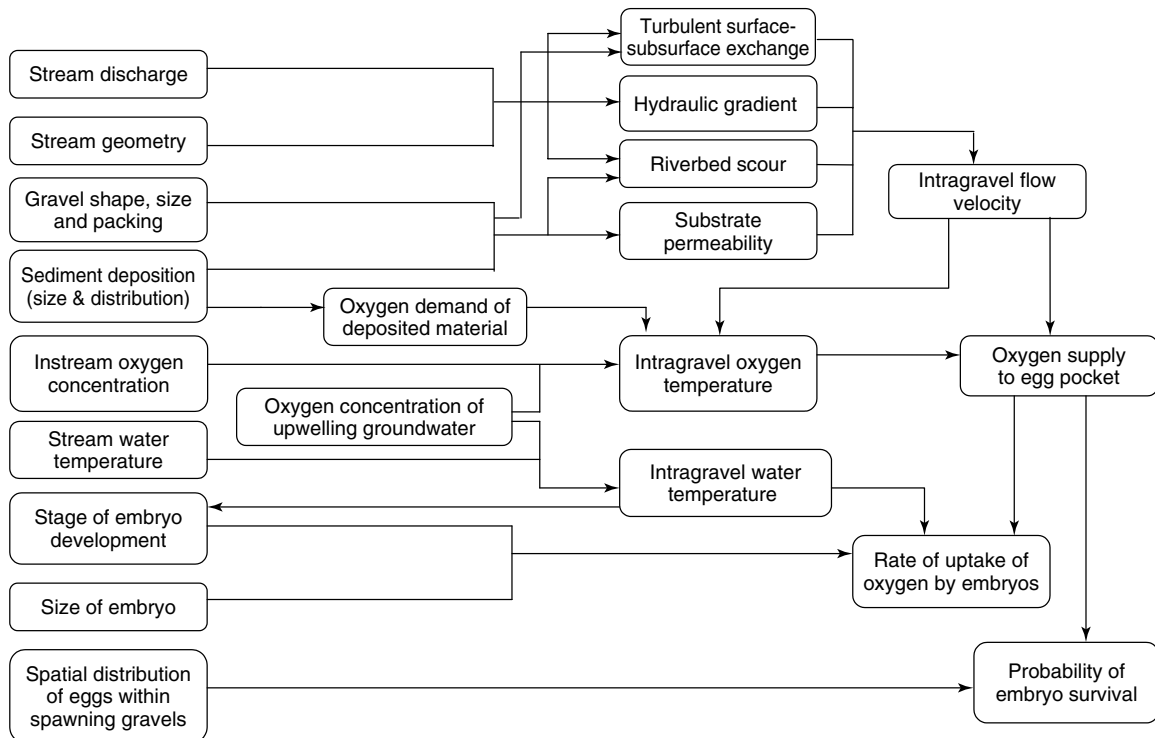

Figure 9. Conceptual model of the relationship between oxygen supply (flux) and embryonic survival. Also detailed are hypothetical scenarios potentially influencing oxygen fluxes

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 overmanaged 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 9 indicates the complexity associated with delineating the causes of oxygen-deficiency-related mortalities. Four oxygen availability scenarios are detailed: low dissolved oxygen concentration and low intragravel flow velocity, low dissolved oxygen concentration and high intragravel flow velocity, high dissolved oxygen concentration and low intragravel flow velocity, and high dissolved oxygen concentration and high intragravel flow velocity (Greig *et al.*, 2005).

In light of the observations presented in this review, it is proposed that there is a requirement to replace simple empirically defined measures of the ability of spawning and incubation habitats to support salmonid pollutions with more comprehensive measures of the riverbed environment that appreciate the complex and dynamic processes that influence oxygen availability. Although it is beyond the scope of this review to provide a detailed examination of potential methods and strategies for assessing the quality of spawning gravels, the key observation detailed in this review can be used to define a set of potential considerations for assessing the quality of spawning and incubation gravels (Table III).

CONCLUSIONS

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 the 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 synthesized to produce a holistic overview of the processes and factors influencing the availability of oxygen to incubating embryos.

Table III. Summary of key factors and processes that should be considered when assessing spawning and incubation habitat quality

Key considerations for defining spawning and incubation habitat quality

Simple empirical metrics of incubation success may not represent the range of processes and factors influencing oxygen availability and embryonic survival

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, must consider the range of 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, on 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 percentage below an arbitrary threshold

Clay particles can severely reduce the supply of oxygen to, and 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

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 a 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 additional 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 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

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