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

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Abstract

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

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

1. Introduction

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

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

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

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

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

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

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

2. Field sites and methods

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

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

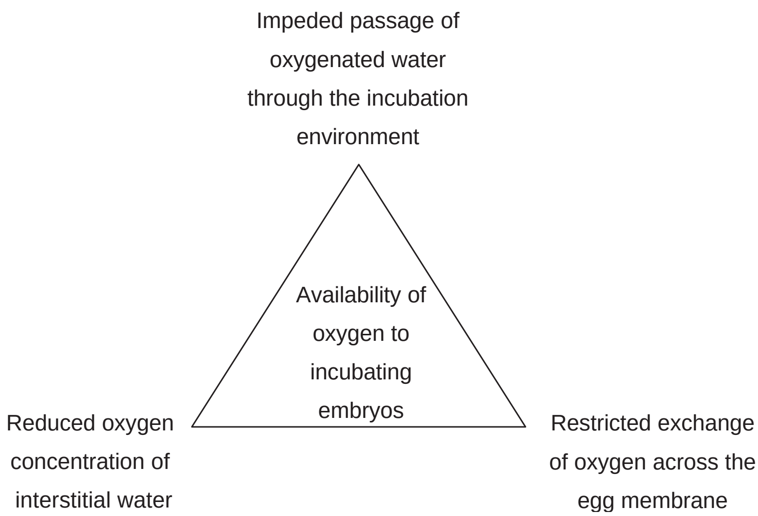

Fig. 1. Summary of factors influencing the availability of oxygen to incubating embryos.

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

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

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

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

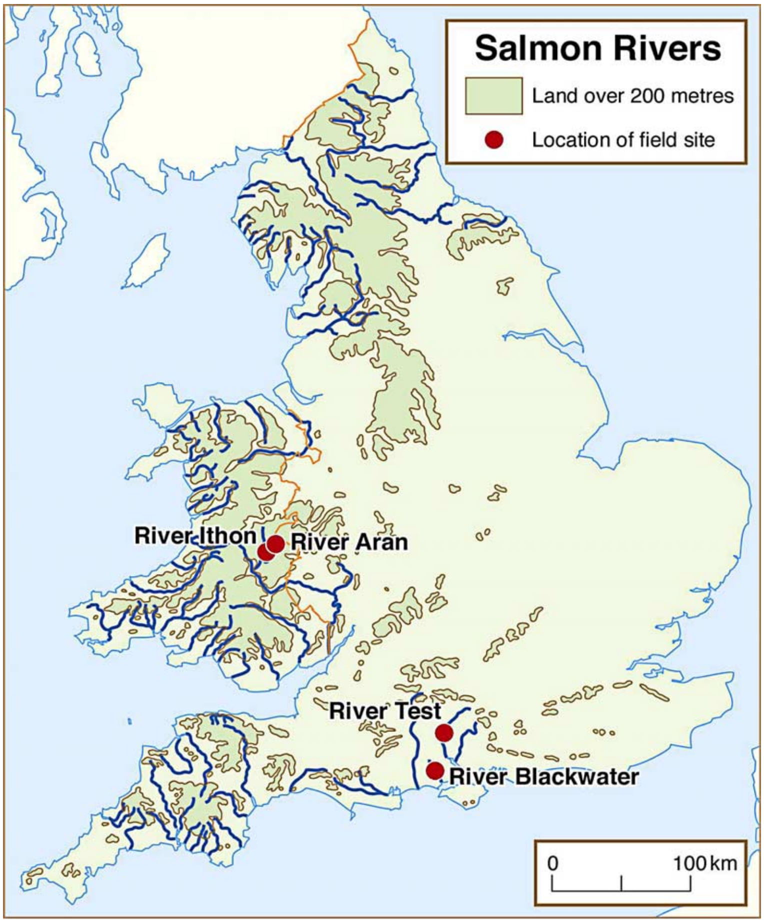

Fig. 2. Location of the four field sites and source of eggs used in this study.

Table 1
Summary of conditions represented at each field site

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

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

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

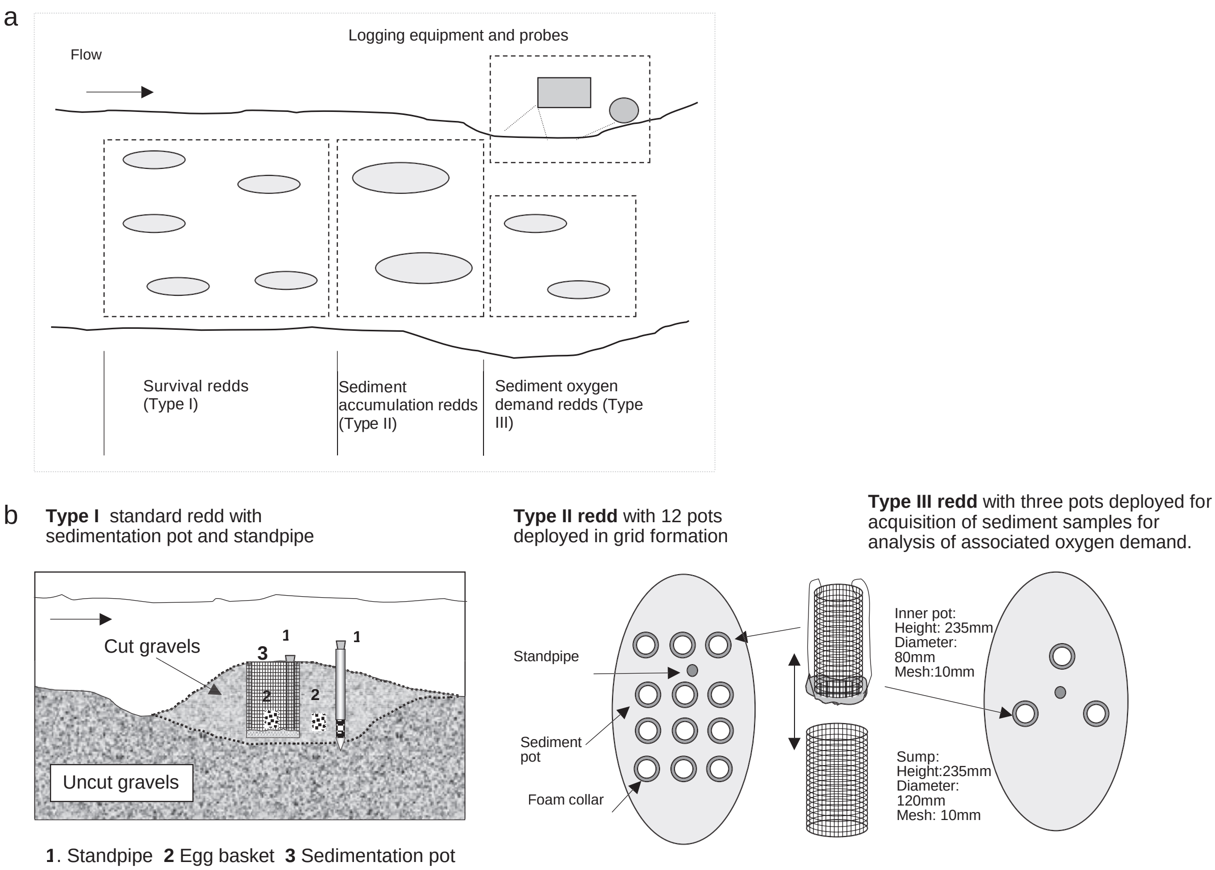

Fig. 3. (a) Schematic of monitoring set-up deployed at each field site. (b) Schematic of the different artificial redd experiments deployed at each field site.

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

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

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

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

3. Results

3.1. Physical conditions during the field season

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

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

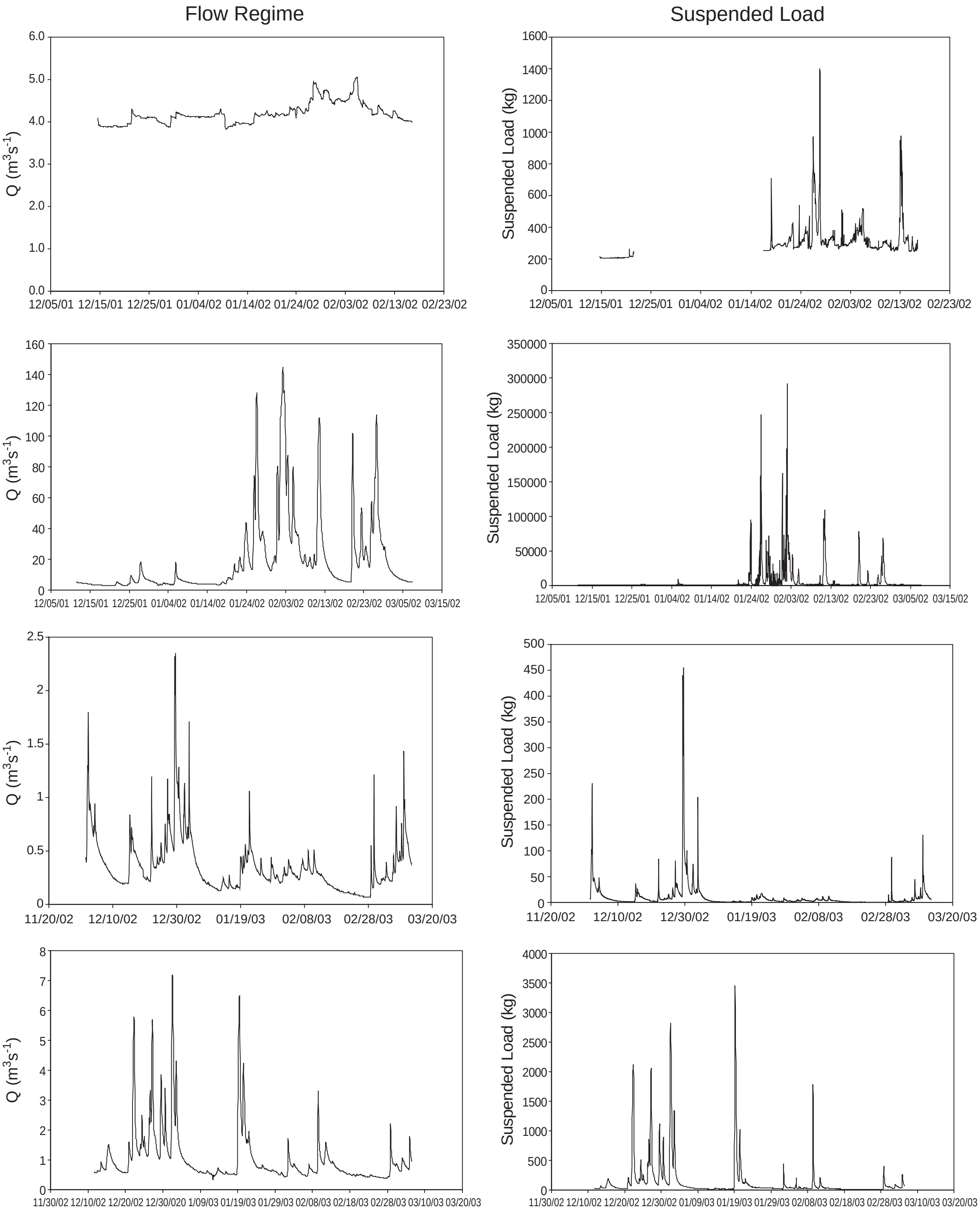

Fig. 4. Flow (Q) and suspended sediment transport conditions recorded over the incubation period at the four field sites.

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

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

3.2. Egg survival and oxygen supply

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

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

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

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

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

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

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

Table 4
Rates of survival recorded within artificial redds

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

Data omissions result from problems encountered during sampling.

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

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

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

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

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

[a] Significant at the 5% confidence limit.

3.4. Impact of fine sediment on interstitial flow velocity

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

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

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

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

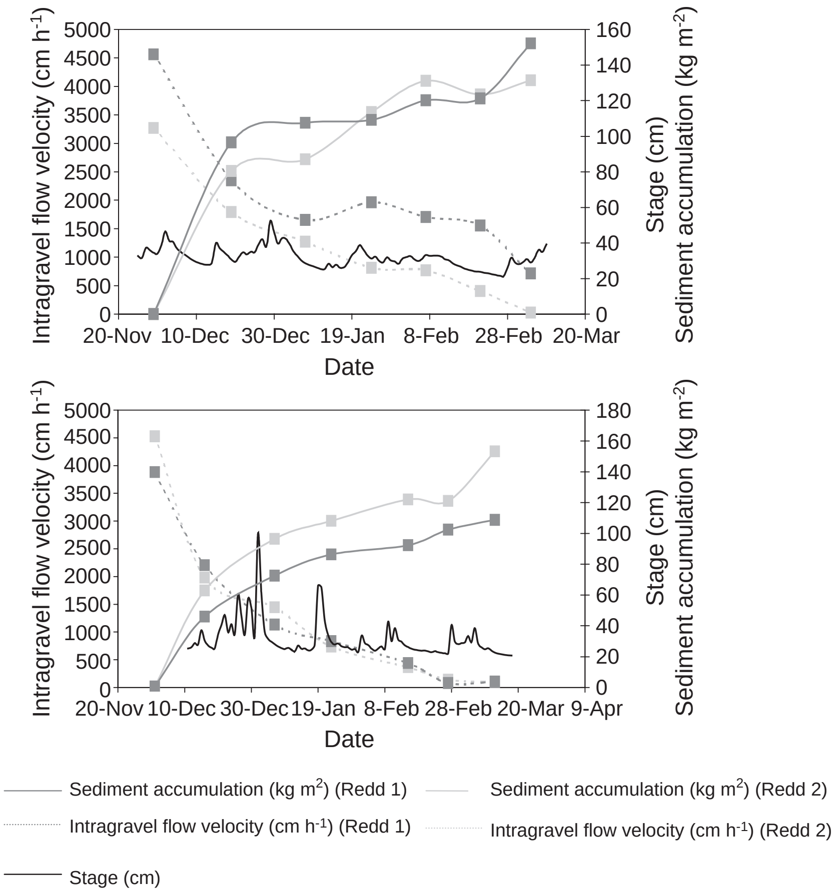

Fig. 5. Relationship between flow, fine sediment (<2 mm) accumulation and interstitial flow velocity at (a) River Blackwater and (b) River Aran.

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

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

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

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

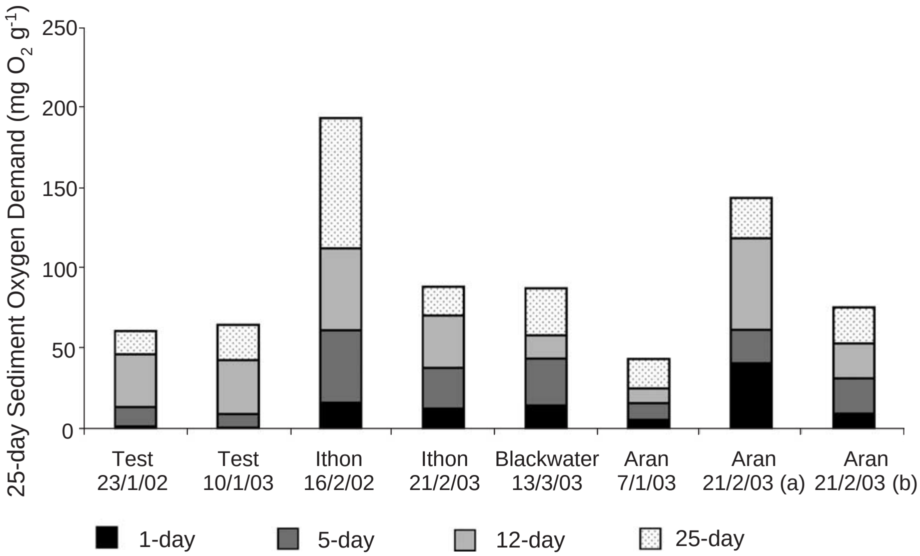

Fig. 6. Stacked column chart outlining temporal trends in oxygen demand for infiltrated fine sediments (<710 μm) recovered from the four field sites.

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

3.6. Impact of clay particles on oxygen consumption

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

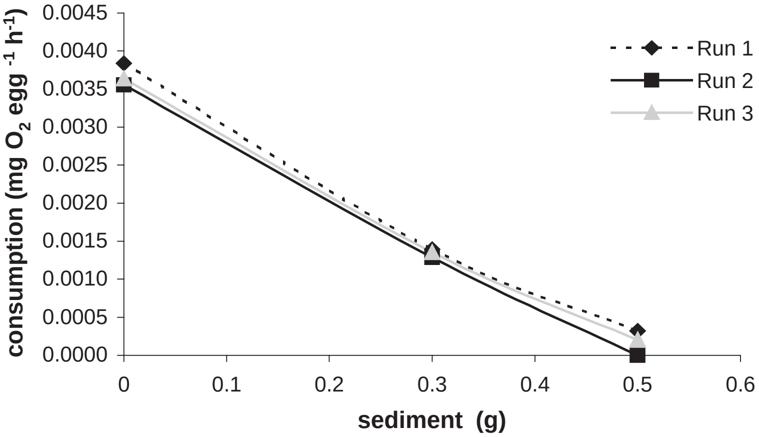

Fig. 7. Decline in egg oxygen consumption with the addition of inert clay particles. Volume of sample was 50 ml in all cases.

rate than under conditions of complete surface coverage.

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

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

3.7. Relationship between suspended sediment and infiltration

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

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

4. Discussion

4.1. Relationship between oxygen availability and embryonic survival

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

4.2. Impact of fine sediment accumulation on oxygen availability

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

4.3. Management implications

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

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

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

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

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

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

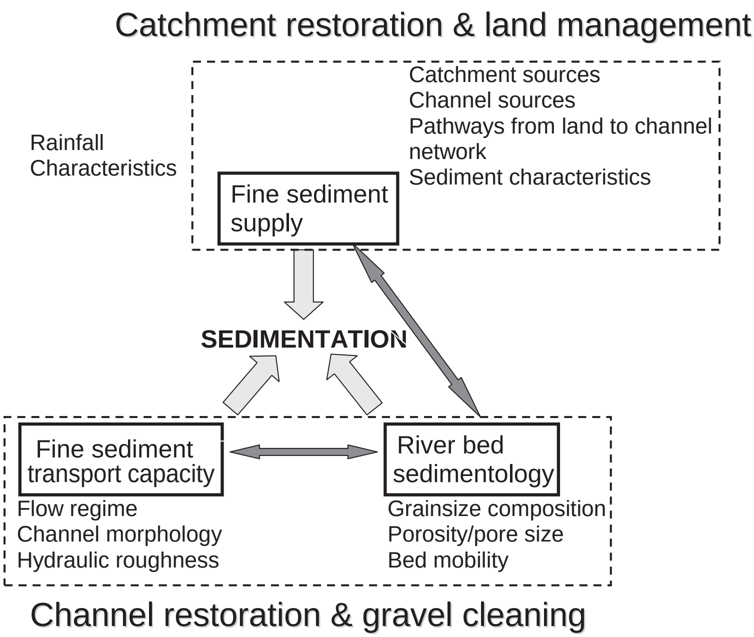

Fig. 8. Conceptual diagram of the fine sediment system of a river emphasizing the need to manage both source and storage elements on the catchment land surface as well as within the river network and spawning beds.

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

5. Conclusion

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

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

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The Biological Sediment Tolerance Index: Assessing fine sediments conditions in Oregon streams using macroinvertebrates

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ABSTRACT

Fine sediments in excess of natural background conditions are one of most globally common causes of stream degradation, with well documented impacts on aquatic communities. The lack of agreement on methods for monitoring fine sediments makes it difficult to share data, limiting assessments of stream conditions across jurisdictions. We present a model that circumvents these limitations by inferring fine sediments in Oregon streams through sampling of macroinvertebrates. Tolerances to fine sediments (<0.06 mm diameter) were calculated for 240 macroinvertebrate taxa, from a calibration dataset of 446 sites across Oregon, as well as an independent validation dataset of 50 samples. Weighted averaging methods were used to infer fine sediment levels in streams by weighting the tolerances of modeled taxa observed in a sample by their abundances. The final model, the Biological Sediment Tolerance Index (BSTI), showed a strong relationship to measured fine sediments (calibration $r^2 = 0.49$, validation $r^2 = 0.58$). Root-mean-squared-error was small in the calibration dataset (2% fines), but larger in the validation dataset (14% fines). Repeatability was assessed by examining variability in BSTI at 14 sites across Oregon. Because field methods for sampling macroinvertebrates are standardized across resource agencies in Oregon and the responses of macroinvertebrates represent the actual effects of fine sediments on stream ecosystems, the BSTI may offer water resource managers' a cost-effective method for assessing fine sediment conditions in their ongoing efforts to improve water quality across the state.

1. Introduction

Excess fine sediments are a leading cause of stream impairments across the world, frequently associated with biological impairments of stream ecosystems (Chutter, 1969; Ryan, 1991; Fossati et al., 2001; Paulsen et al., 2008). Effects from excess sedimentation are known to result in impairments to all levels of stream communities (Wood and Armitage, 1997; Suttle et al., 2004; Jensen et al., 2009; Jones et al., 2012). In the Pacific Northwest (PNW) region of the United States, these impairments have been directly related to declines in culturally and economically important salmon populations. For example, altered sediment regimes were identified as a high stress factor in 31 out of 40 Southern Oregon/Northern California coho salmon populations (NMFS, 2014), with impacts most frequently greater on the earliest life stages (Suttle et al., 2004; Jensen et al., 2009). While it is generally accepted that excess fine sediments may alter ecosystem function, based on both field (Von Bertrab et al., 2013) and experimental studies (Mathers et al., 2014; Jones et al., 2015), agreement on how to measure fine sediments and what levels are protective of aquatic life remains elusive.

Many resource management agencies in Oregon have broad-scale monitoring programs in place to measure and quantify stream substrate composition, however, the ability to easily utilize that information across programs is limited due to differences in field protocols (Roper et al., 2010). Additionally, Oregon's water quality standards for sedimentation provide no guidance on monitoring sediment conditions, nor at what levels may produce impairments: "*The formation of appreciable bottom or sludge deposits or the formation of any organic or inorganic deposits deleterious to fish or other aquatic life or injurious to public health, recreation, or industry may not be allowed (Oregon Administrative Rule 340-041-0007-11).*" This lack of clarity from resource management agencies, in addition to

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complicated field methods, causes confusion in the public—making it difficult to engage citizen-based groups in monitoring sediment conditions. In periods of reduced monitoring budgets, the ability to combine data across resource management agencies or to boost sampling efforts through volunteer monitoring organizations would greatly improve our understanding of the impacts of fine sediments on Oregon's streams.

Biomonitoring of benthic macroinvertebrates offers a potential solution to these problems through stressor-response modeling of macroinvertebrates to fine sediments. Macroinvertebrates are the most widely used indicators of stream biological conditions (Rosenburg and Resh, 1993; Hering et al., 2004) and are commonly used to assess stream conditions at regional (Hawkins et al., 2000; Hargett et al., 2007), state (Ode et al., 2008) and national scales (Wright et al., 1993; Smith et al., 1999; Paulsen et al., 2008). Due to their high taxonomic diversity, central position in stream ecosystem food-webs, and varied feeding strategies and habitat requirements, macroinvertebrates are effective indicators of biological conditions. Furthermore, the relatively longer life-cycles (from several months to several years) of macroinvertebrates integrate stream conditions through time (Hawkes, 1979; Cairns and Pratt, 1993; Hodkinson and Jackson, 2005).

Macroinvertebrate monitoring offers several advantages to monitoring fine sediments alone. First, macroinvertebrate field sampling methods have been standardized among the major PNW monitoring programs since the early 2000s (Hayslip, 2007), allowing for ease of transfer of comparable data among programs. Second, macroinvertebrate taxonomists in the PNW routinely work collaboratively to increase similarity in taxonomic information across laboratories (PNAMP, 2015). Another advantage provided by macroinvertebrate monitoring is public engagement. Macroinvertebrate field collection methods are relatively simple and easy to train to novices, and as long as taxonomic identification is standardized can show a high degree of similarity between professional and non-professional samples (Fore et al., 2001; Engel and Voshell, 2002). Finally, macroinvertebrate sampling offers a more cost-effective way of assessing stream ecological conditions than by monitoring for a single stressor. While monitoring for instream fine sediments alone may indicate a potentially impaired system, it is particularly useful to understand whether or not excess fine sediments are resulting in actual impairments to the community of organisms that we are trying to protect. Macroinvertebrate diagnostic indices have been developed for temperature (Yuan, 2007), stream acidity (Hamalainen and Huttunen, 1996; Larsen et al., 1996), and fine sediments (Extence et al., 2013; Relyea et al., 2012). Thus, the true cost-effective nature of biomonitoring can be realized when we integrate a suite of diagnostic indexes capable of identifying multiple potential causes of biological impairments, while requiring a single sample (e.g., Chessman and McEvoy, 1998). This last step requires thorough knowledge of individual taxonomic responses to a given stressor, such as we present here with fine sediments.

Macroinvertebrates may be strongly influenced by excess fine sediments (McClelland and Brusven, 1980; Lemly, 1982; Wood and Armitage, 1997). Responses to fine sediments are often taxon-specific, with effects observed on survival (Strand and Merritt, 1997), burial (Wood et al., 2005), egg hatching success (Kefford et al., 2010), growth (Kent and Stelzer, 2008), feeding (Hornig and Brusven, 1986), and relative abundance and richness (Angradi, 1999; Kaller and Hartman, 2004). Analyzing taxon-specific responses, or tolerances, to fine sediments allows for the creation of a diagnostic index to identify for a specific cause of impairment.

In the field of bioassessment, the term tolerance is often used to reflect taxon-specific responses to environmental gradients potentially altered by human activities (Yuan, 2004). There has been a recent movement to develop more rigorous and quantitative tolerance designations for individual taxa at various spatial scales. Carlisle et al. (2007) examined macroinvertebrate genera and families throughout the United States (US), developing tolerances to ions, nutrients, temperature, and both suspended and bedded fine sediments. Yuan (2004) determined tolerances to pH, nutrients, sulfate, and stream habitat within the Mid-Atlantic region of the US. Tolerances for land-cover (e.g., % forested) were developed for macroinvertebrates in the PNW (Black et al., 2004). Relyea et al. (2012) quantified macroinvertebrate taxa responses to fine sediments, then developed an index based on classification of those tolerances into discrete classes. Taken further, tolerances (i.e., optima) across taxa can be adapted into an assemblage-level index to infer stressor levels.

There are various approaches used in modeling tolerances to environmental gradients from biological samples. The need for transparent and quantifiable methods in setting management goals has moved the science away from the long-time standard of expert opinion. A frequently used approach is to rank tolerances into discrete classes. For example Extence et al. (2013) used a traits-based approach to model linkages between fine sediments and morphological or physiological adaptations in macroinvertebrates. Relyea et al. ranked macroinvertebrate tolerances based on abundance percentiles across a fine sediment gradient. Multivariate ordination, followed by ranked tolerances was used by Murphy et al. (2015) for fine sediments and Carlisle et al. (2007) for multiple stressors. But for developing continuous tolerances, which arguably is a more objective approach, weighted averaging (WA) (ter Braak and Barendregt, 1986) is perhaps the most commonly used technique.

WA has been frequently used to make inferences of historical environmental gradients for diatoms in lentic systems (Ter Braak and van Dam, 1989; Birks et al., 1990; Hall and Smol, 1992). More recently, WA has been used to infer environmental gradients in streams for diatoms (Pan et al., 1996; Ponader et al., 2007) and macroinvertebrates (Hamalainen and Huttunen, 1996; Larsen et al., 1996; Yuan, 2007). Performance and bias in WA models are susceptible to the range and evenness of sampling along the environmental gradient (ter Braak and Looman, 1986; Yuan, 2005) and to covarying factors (Yuan, 2007). WA may be considered less rigorous than other methods of inferring environmental gradients, such as maximum likelihood (ML) (Ter Braak and van Dam, 1989; Yuan, 2007), WA partial-least-squares regression (WA-PLS) (Ter Braak and van Dam, 1989; Larsen et al., 1996; Birks, 1998), or Boosted Regression Trees (Juggins et al., 2015). However, WA frequently performs as well as other methods and offers a suitable alternative to more complex methods (Ter Braak and van Dam, 1989; Birks et al., 1990; Birks, 1998; Juggins et al., 2015).

Our primary objective was to develop a biological index for inferring fine sediment conditions in streams across Oregon. We expanded on prior studies by modeling macroinvertebrate tolerances to smaller substrate particle sizes (<0.06 mm) than were previously examined (<2 mm; Yuan, 2007; Relyea et al., 2012). First, we quantitatively defined taxon-specific responses of macroinvertebrates to fine sediments. Second, we used these taxa responses to infer fine sediment levels, based exclusively on a macroinvertebrate sample. Our goal is to generate an index, the Biological Sediment Tolerance Index (BSTI) which may be used as a cost-effective method for assessing fine sediment conditions in Oregon streams. We intend for the index to be used by a broad range of resource managers, such as government agencies with well-developed biological monitoring programs to citizen-based monitoring organizations with relatively minimal resources and experience.

2. Methods

2.1. Study sites

We sampled 496 unique sites across Oregon for which we had paired macroinvertebrate assemblage and substrate composition data (Fig. 1). Most sites were selected randomly as part of spatially balanced surveys intended to make unbiased estimates of stream conditions across various spatial scales (Herlihy et al., 2000; Olsen and Peck, 2008), although a smaller proportion of sites were hand-selected based on various study designs. All sites were sampled during summer low-flow conditions (June–September), from 1999 to 2004. Study reaches ranged from 150 to 800 m in length, and consisted entirely of wadeable streams and rivers that allowed surveyors to safely wade across the width and along the thalweg. We used a calibration dataset of 446 sites (CAL) to build our models, randomly setting aside 50 sites as an independent validation dataset (VAL).

2.2. Macroinvertebrate data

Macroinvertebrate assemblages were sampled from riffle habitat with a D-frame kicknet. Eight individual 0.09 m^2 kicks were distributed randomly across the reach and composited into a single sample (Peck et al., 2006). Samples were preserved in the field with 95% ethanol. Macroinvertebrates were randomly sorted in the laboratory for a subsample target of 500 individuals (Caton, 1991). The sorted macroinvertebrates were identified to lowest-practical taxonomic level. Identifications were standardized to ensure consistent treatment across all samples, so that no ambiguous taxa were present in a sample (Cuffney et al., 2007). This procedure resulted in 240 operational taxonomic units (OTUs), of which 82% were at the genus to species level, 15% were at family to tribe, and 3% were at higher taxonomic levels.

2.3. Environmental data

To measure fine sediments throughout Oregon, stream substrates were surveyed over a reach length of 40-times the average wetted width, using protocols consistent with Kaufmann et al. (1999) and Peck et al. (2006). At each of 21 evenly spaced transects, five substrates were selected at distances of 0%, 25%, 50%, 75%, and 100% of the wetted width. A total of 105 particles per reach were visually assessed into one of 11 size classes, based on its median diameter. While visual estimates of substrate size are known to result in higher error and bias than measured values, the use of this approach provides a practical yet ecologically meaningful measure of sediment conditions (Faustini and Kaufmann, 2007; Glendell et al., 2014). To identify individual particles, the sampler's index finger was slid down a stadia rod to identify the particle size at each substrate sampling location. Fine sediments were the smallest of the 11 size classes and defined as silt or clay particles with a median diameter less than 0.06 mm. At this size, it was not possible to identify individual fines particles, but rather flocs of fines were distinguished from sand as not gritty when rolled between the fingers, similar to Glendell et al. (2014). Fine sediments were further defined as actual deposits and accumulations, not simply thin layers of fine sediment deposits over larger substrates (e.g., cobbles and boulders).

We calculated additional environmental and habitat characteristics to examine the similarities between the CAL and VAL datasets. Mean width and percent canopy cover were calculated from the same habitat surveys as fine sediments (Stoddard et al., 2005; Peck et al., 2006). We used Geographic Information Systems (GIS) to calculate elevation at the bottom of the sampling reach, stream gradient (slope), catchment area, and two climate-related variables (precipitation and air temperature; PRISM, 2004). A Human Disturbance Index was calculated from three GIS coverages at the catchment-scale (forest fragmentation, road density, and percent urban and agricultural landuse) and a reach-scale assessment of all human activities (Drake, 2004).

2.4. Taxa tolerances and inference models for fine sediments

In this paper, we use the generalized term tolerance (Yuan, 2004) to describe a taxon's response to human caused increases in fine sediments. We distinguish the use of tolerance in a manner similar to that of the term optima in an ecological sense, used to define a taxon's maximum along an environmental gradient, and not in the WA modeling sense of tolerance as the width of the taxon response-curve. Accordingly, a taxon's tolerance for percent fine sediments (%FN) is the point along the fine sediment gradient where abundances are maximized. Then, if we have an understanding of each taxon's response to increasing fine sediments, we can use the tolerances of all taxa found in a sample to make inferences of the fine sediment conditions within a stream reach (ter Braak and Looman, 1986).

We selected WA as the "minimal adequate model" (e.g., Birks, 1998) for inferring fine sediments from the biota. We explored multiple modeling alternatives to WA (ML, WA-PLS, WA tolerance down-weighting), but found simple WA to provide models with equivalent or better performance (data not shown). We used WA in C2 software (Juggins, 2007) to compute macroinvertebrate fine sediment tolerances and inference models of %FN. According to Birks (1998), the best WA models are typically those that include all taxa, even those with few occurrences. Therefore, rare taxa were not removed from the dataset, and tolerances were calculated for all 240 OTUs.

A taxon's WA fine sediment tolerance is the average of all %FN for stream reaches in which the taxon was found, weighted by the taxon's abundance in each sample (WA regression) (Birks et al., 1990). Tolerances were then used to develop models (WA calibration) for inferring %FN using macroinvertebrate samples only. A stream reach's %FN was inferred as the average fine sediment tolerance of all taxa present in a sample, weighted by their respective abundances (Birks et al., 1990). Shrinkage of the range of inferred parameter values occurs in WA because averages are taken twice, once in the regression step and once in the calibration step (Birks et al., 1990). We used two methods to counteract for shrinkage and rescale the inferred values. With classical deshrinking, the initial inferred value ($\%FN_{init}$) is regressed on the observed (field measured) %FN of the calibration set. For inverse deshrinking, the observed %FN is regressed on the initial inferred ($\%FN_{init}$) (Ter Braak and van Dam, 1989). Models using both types of deshrinking were generated and evaluated (see below).

To meet WA assumptions of unimodal response-curves (ter Braak and Looman, 1986), biological and environmental data were transformed prior to WA regression and calibration. Macroinvertebrate abundances were log transformed. Percent FN, which showed a highly left-skewed distribution (range = 0–98%, median = 7%), was transformed using the following equation:

$$\%FN_{trans} = \log 10\left(\left(\left(\arcsin\sqrt{\frac{\%FN}{100}}\right)\left(\frac{2}{\pi}\right)\right)+1\right) \quad (1)$$

Inference model performances were assessed by evaluating the root mean-squared error (RMSE) and coefficient of determination (r^2) of the observed versus inferred values for %FN. Because the inferred value of %FN for a site was included in the CAL dataset, the apparent r^2 for observed versus inferred values may not be realistic for assessing the predictive power of the models to novel datasets (Cumming et al., 1995; Reavie et al., 1995). Therefore, cross

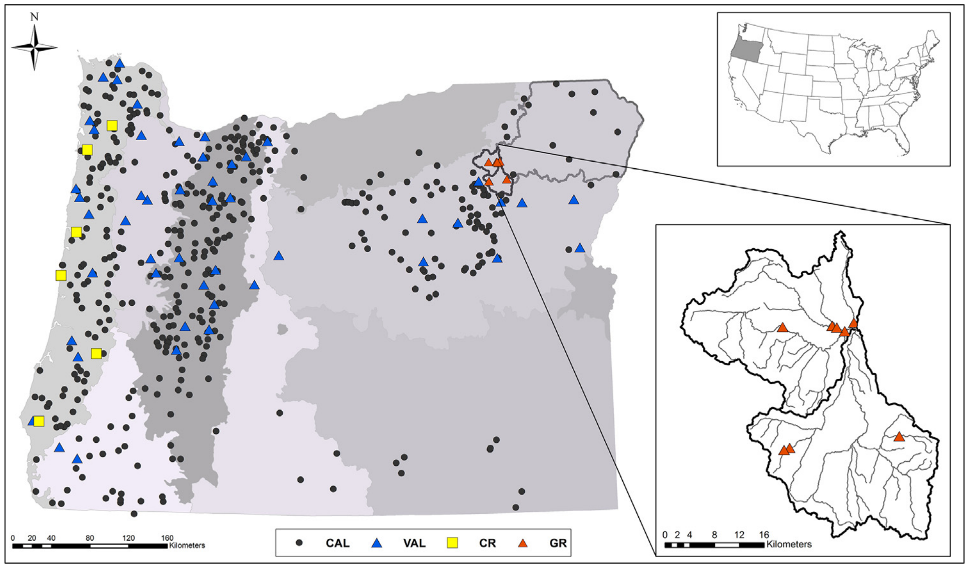

Fig. 1. Locations of 446 calibration (CAL) and 50 independent validation (VAL) sites throughout Oregon. Sites with repeat samples are shown in the Coast Range ecoregion (CR, $n = 6$) and Upper Grande Ronde Basin (GR, $n = 8$). Shaded areas represent Oregon's nine Level III ecoregions and the Grande Ronde Basin is outlined.

validation with leave-one-out jackknifing and independent validation (VAL) were used to confirm the apparent r^2 (ter Braak and Juggins, 1993). Jackknifing infers the environmental value for a site by using all the sites except the inferred site to derive an estimated value, thereby avoiding possible circularity in the model evaluations. Maximum bias, calculated as the largest absolute value of mean bias for 10 equal parts of the environmental sampling interval, was used to evaluate systematic model error (ter Braak and Juggins, 1993). Models that produced low RMSE, high r^2, and low maximum bias were considered better models, with the greatest emphasis placed on results of the VAL dataset.

Inferred fines were converted to the BSTI by back-transforming the final (post deshrinking) inferred values (%FN_{inf}):

$$\mathrm{BSTI} = \left[\mathrm{sine}\left(\frac{\pi(10^{(\%\mathrm{FN_{inf}})} - 1)}{2}\right)\right]^2 * 100 \qquad (2)$$

When untransformed in this manner, the BSTI is on the same scale as %FN.

2.5. Estimating variability with repeated sampling

We examined variability in BSTI from sites in Oregon's Coast Range Ecoregion (Omernik, 1987) and the upper Grande Ronde Basin (Fig. 1). These sites were chosen because they were sampled frequently across the years 1999–2009, as well as represented two different geographic regions and spatial scales. In the Coast Range, a total of 65 macroinvertebrate samples were collected across six sites. Sites in the Coast Range were part of a larger study with a random sampling design (ODEQ, 2005), with these annually repeated sites established for estimates of variability.

In the Grande Ronde, eight sites were sampled a total of 122 times. Sites in the Grande Ronde were selected as part of a long term study on the effectiveness of cattle exclusion and stream channel restoration (Whitney, 2007). In 1968 and 1977, McCoy Creek was relocated, straightened, and channelized to increase grazing capacity and production. Restoration activities began with cattle exclusion beginning in 1988, then in 1997 the stream was returned to its natural channel for a 0.8 km stretch (McCoy Creek-Lower). The other sites included here were selected as different types of controls. All Grande Ronde sites were located in the Blue Mountains Ecoregion (Omernik, 1987).

For both projects, not all sites were sampled in each year, with sample sizes ranging from 6 to 22 within a site. Samples represented a mixture of same-day duplicates, seasonal repeats, and inter-annual visits. We calculated BSTI summary statistics and 95% confidence intervals for each site, across all samples. In addition to natural gradients that are typically correlated with fine sediments, we also show quantified levels of human disturbances summed across the survey reach and at the watershed scale (Human Disturbance Index; Drake, 2004).

2.6. Example application of the BSTI in Oregon

To show the utility and cost-effective nature of the BSTI as a tool for assessing fine sediment conditions, we queried the Oregon Department of Environmental Quality (ODEQ) biomonitoring database for all records available to assess fine sediments across the state. Fine sediment conditions within 6th field hydrologic unit codes (HUCs) were determined by calculating averages for both field measured (%FN) and macroinvertebrate inferred (BSTI) fine sediments.

3. Results

3.1. Comparisons between the calibration and validation datasets

Overall, CAL and VAL datasets were similar for %FN and other habitat and environmental variables (Fig. 2). The distributions of %FN were similar between the CAL and VAL datasets, although minor differences were observed. VAL showed a slightly higher range (0–98%FN) compared to CAL (0–93%FN). VAL also showed slightly higher median (9%FN) compared to CAL (7%FN). Climate variables (precipitation and air temperature), canopy cover, and human disturbances were all quite similar between CAL and VAL.

From a stream size standpoint, the only substantial differences observed were due to one larger stream in the VAL, with a mean width two-times greater and a catchment area six-times greater than the maximum values represented in the CAL. The distributions of stream slopes were similar across the datasets, except for five samples in CAL that were beyond the maximum slope observed in VAL. Of all the variables examined between CAL and VAL, the greatest differences were observed in elevation. Median elevations

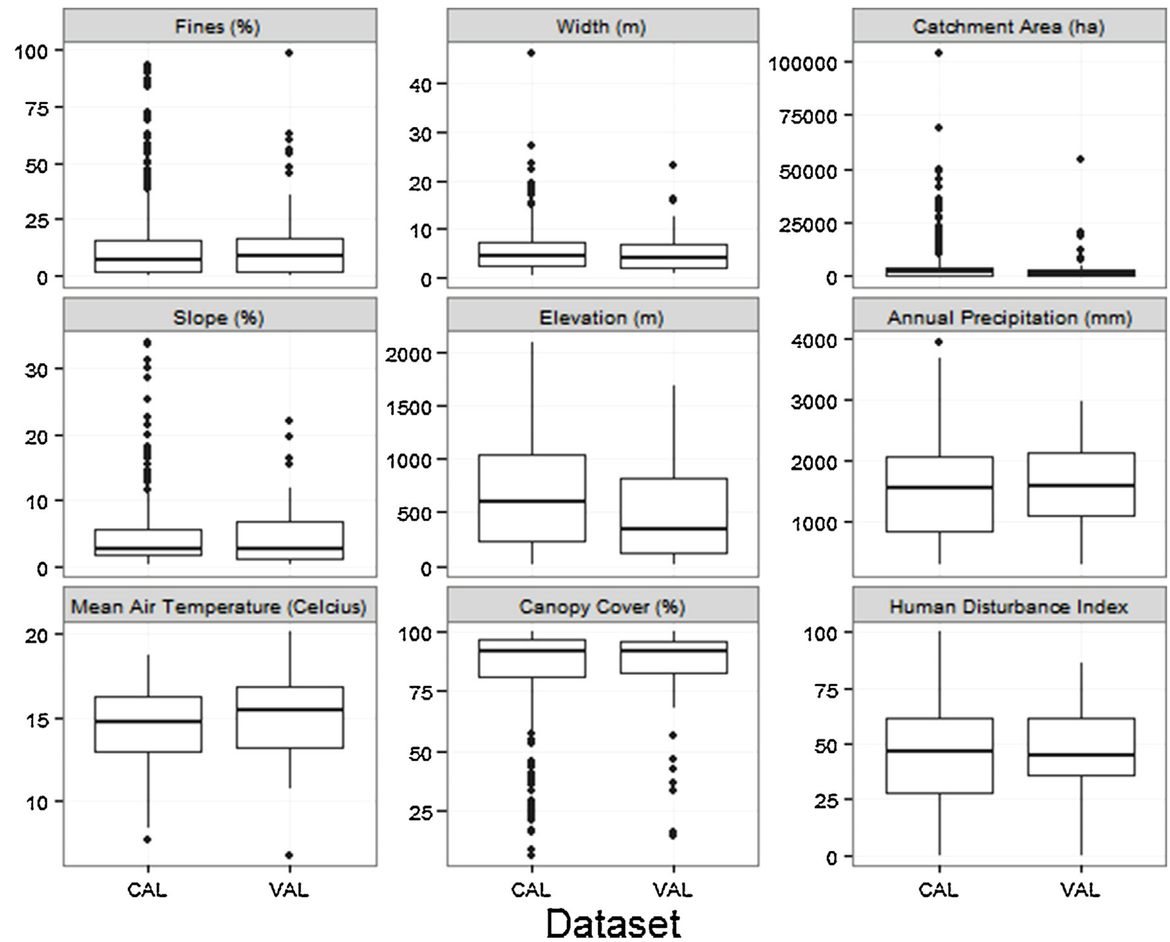

Fig. 2. Comparisons of fine sediments, habitat and environmental variables, and disturbance between the calibration (CAL) and validation (VAL) datasets. Fines are the percent of substrate <0.06 mm in diameter (%FN). A single outlier was removed from the VAL dataset in the Catchment Area plot (618,694 ha).

were almost two-times greater in CAL, with higher quartile and maximum values than observed in VAL; although CAL also showed a lower minimum elevation.

3.2. Tolerances across taxonomic groups

The greatest number of tolerances were calculated for Trichoptera taxa ($n = 69$), followed by Diptera ($n = 48$), Ephemeroptera ($n = 38$), and Plecoptera ($n = 36$). The fewest number of taxa were observed for the taxa categorized as Insect-Other ($n = 7$). Tolerances across all 240 taxa ranged from 0 to 73%FN, with an average tolerance of 10%FN. Taxa from the orders Ephemeroptera, Plecoptera, and Trichoptera (together: EPT) generally showed lower tolerances to fine sediments than taxa from other orders (Fig. 3). All three EPT orders had median tolerances of 6%FN, and relatively few taxa with tolerances above 10%FN. Non-Insect and Insect-Other (the latter comprised of taxa within the orders Odonata and Megaloptera) showed the highest tolerances to fine sediments, with median

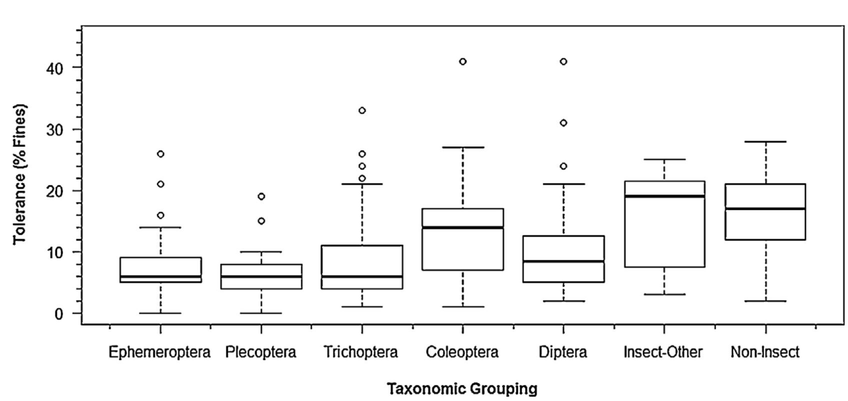

Fig. 3. Boxplots of fine sediment tolerances of 240 individual taxa, of various taxonomic resolution, organized by taxonomic groups. The dark horizontal bar represents the median, the lower and upper box limits represent the 25th and 75th percentiles, and the whiskers show the non-outlier range of tolerances. Open circles represent outliers. Two outliers were removed: Ephemeroptera (63%), Non-Insect (73%).

Table 1
Root mean squared errors (RMSE), coefficient of determination (r^2), bias estimates, and linear regression coefficients for inferred versus observed values across different sediment weighted averaging (WA) models. RMSE and bias units are in percent fine sediments (diameter < 0.06 mm). Maximum bias is a measure of systematic error in the inferences (ter Braak and Juggins, 1993).

	WA Inverse deshrinking	WA Classic deshrinking
Calibration RMSE	2	4
Jackknifed RMSE	3	5
Independent validation RMSE	14	19
Training r^2	0.49	0.49
Jackknifed r^2	0.41	0.42
Independent validation r^2	0.58	0.52
Training max bias	13	2
Jackknifed max bias	16	5
Independent validation max bias	19	22
Y-intercept	0.037	0.00
Slope	0.482	1.00

values of 17%FN and 19%FN, respectively. Across all groups, very few taxa had tolerances above 20%FN.

3.3. Weighted averaging model performance

Differences among the WA modeling options were minimal. WA with inverse deshrinking was chosen for the final BSTI because it showed the lowest RMSE (14% fines), highest r^2 (0.58), and lowest maximum bias (19%) in the VAL dataset (Table 1). Errors (RMSE) in VAL were substantially higher than observed in CAL (2%) and jackknifed (3%) datasets. Inferences of %FN tended to be overestimated when observed %FN were low, and underestimated when observed %FN were high (Fig. 4). This was true for both CAL and VAL, which had linear regressions with similar slopes.

The final inverse deshrinking equation was:

$$\%FN_{pred} = -0.312236 + 5.37189 * \%FN_{init} \quad (3)$$

3.4. Repeatability of the BSTI

Repeated measurements of the BSTI for six sites in the Coast Range Ecoregion and eight sites in the Grande Ronde Basin are shown in Table 2. Within the Coast Range, four of the six sites had median BSTIs of 10% or less and maximums less than 15%. The 95% confidence intervals for the five sites with low BSTIs ranged from 1–3%. Two of the sites (Montgomery and Tillamook) had median BSTIs near 30%, and maximums of 36–42%, respectively. These two sites also showed higher variability, with 95% confidence intervals approaching 8–9%.

In the Upper Grande Ronde Basin, median BSTI values ranged from 6–24%, with four of the eight sites showing a median BSTI below 10%. Maximum BSTIs in the Grande Ronde sites ranged from 9–29%. Variability in BSTI across all eight sites in the Grande Ronde was lower than that observed in the Coast Range, with 95% confidence intervals from 1–3%. We observed the highest BSTIs in the stream with active restoration (McCoy Creek-Lower), with a 57% increase in mean BSTI compared to the upstream control (McCoy Creek-Upper).

3.5. Estimating fine sediments using field observations and macroinvertebrate inferences

From ODEQ's biomonitoring database, we calculated average fine sediment conditions in 6th field hydrologic unit codes (HUCs) across Oregon. We observed a total of 803 sites with direct measurements of fine sediments, representing 407 HUCs, with an average sample size of 2.0 in each HUC (Fig. 5A). In contrast, assessing fines using macroinvertebrate tolerances tripled the total sample size (n = 2536), doubled the number of watersheds assessed (n = 817), and increased the average number of samples per watershed to 3.1 (Fig. 5B).

From a statewide perspective, the assessment of conditions between field measured and biologically inferred fine sediments was similar, although minor differences were observed. The BSTI showed a slightly compressed range (0–88%) compared to %FN (0–100%). Median BSTI (9%) was slightly higher than median %FN (7%), although means were nearly identical (13% and 14%, respectively). Comparisons among the condition bins in Fig. 5 also displayed minor differences. The BSTI showed a moderately lower percentage of watersheds in the 0–10% class (55%), compared to 64% for %FN. Conversely the BSTI had a moderately higher percentage of watersheds in the 11–20% class than %FN (26% and 15%, respectively) (Fig. 5). Results were similar at the upper end of percent fines, with the BSTI resulting in 10%

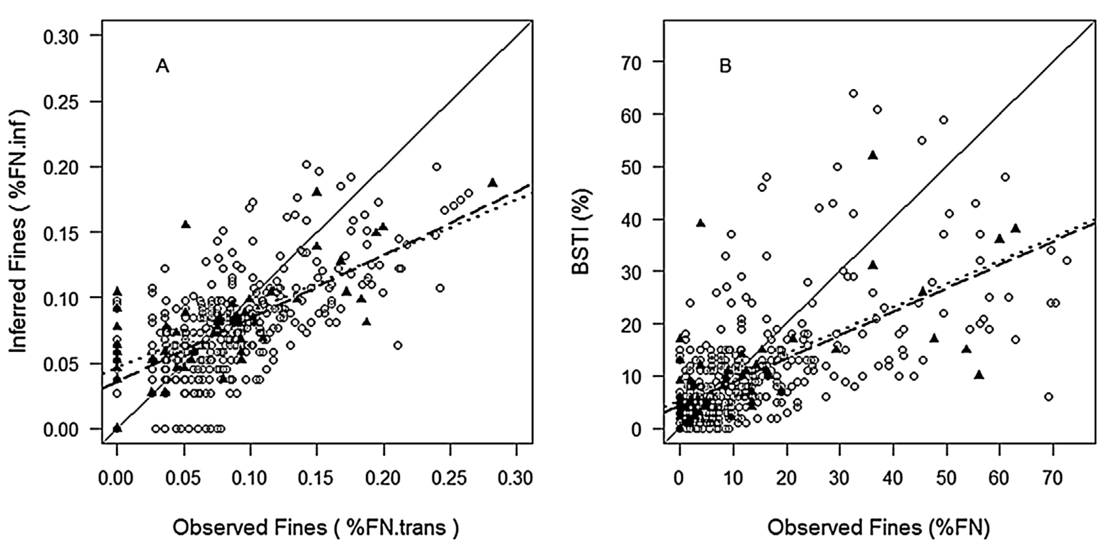

Fig. 4. Weighted averaging (WA) observed fine sediments versus inferred fine sediments. (A) Values on both axes are transformed percent fines, using Eq. (1). (B) Values on both axes are untransformed percent fines. White open circles: calibration sites (CAL, n = 446). Black triangles: independent validation sites (VAL, n = 50). Linear regression lines are shown for CAL (dashed) and VAL (dotted). The solid line is a 1:1 line.

Table 2
Natural gradients and summary statistics of sites used to assess the repeatability of the BSTI. The scale of BSTI is equivalent to percent fine sediments (%FN). 'HDI' = human disturbance index, '*n*' = sample size, 'CI' = confidence interval.

Stream name	Site type	Erodible lithology in watershed (%)	Slope (%)	HDI[a]	*n*	Median BSTI (range)	Mean BSTI (±95% CI)
Coast Range							
Ben Smith Creek	Random repeat	42	7.3	51	16	5% (3–8)	5% (± 1)
Big Creek	Random repeat	24	0.5	16	17	8% (4–12)	8% (± 1)
Montgomery Creek	Random repeat	93	3.0	75	6	31% (19–36)	29% (± 8)
Sixes River	Random repeat	98	0.3	43	10	10% (7–15)	11% (± 2)
Tillamook River	Random repeat	79	0.1	79	9	29% (6–42)	27% (± 9)
Wolf Creek	Random repeat	97	0.8	64	7	10% (9–12)	10% (± 1)
Grande Ronde Basin							
Dark Canyon Creek	Negative control	1	2.2	69	10	13% (8–21)	14% (± 3)
Limber Jim Creek—lower	Least disturbed	47	3.4	36	22	9% (5–12)	8% (± 1)
Limber Jim Creek—upper	Least disturbed	47	1.8	38	12	6% (3–14)	7% (± 2)
Lookout Creek	Least disturbed	47	1.8	37	12	8% (3–9)	7% (± 1)
McCoy Creek—lower	Treatment	1	0.9	69	17	24% (9–29)	22% (± 3)
McCoy Creek—upper	Upstream control	1	0.7	69	17	13% (8–21)	14% (± 2)
Meadow Creek—lower	Positive control	1	0.8	69	18	11% (3–19)	11% (± 2)
Meadow Creek—upper	Positive control	1	1.0	n/a	14	9% (6–12)	9% (± 1)

[a] Higher values (unitless) represent increased human disturbances in the study reach and watershed (Drake, 2004).

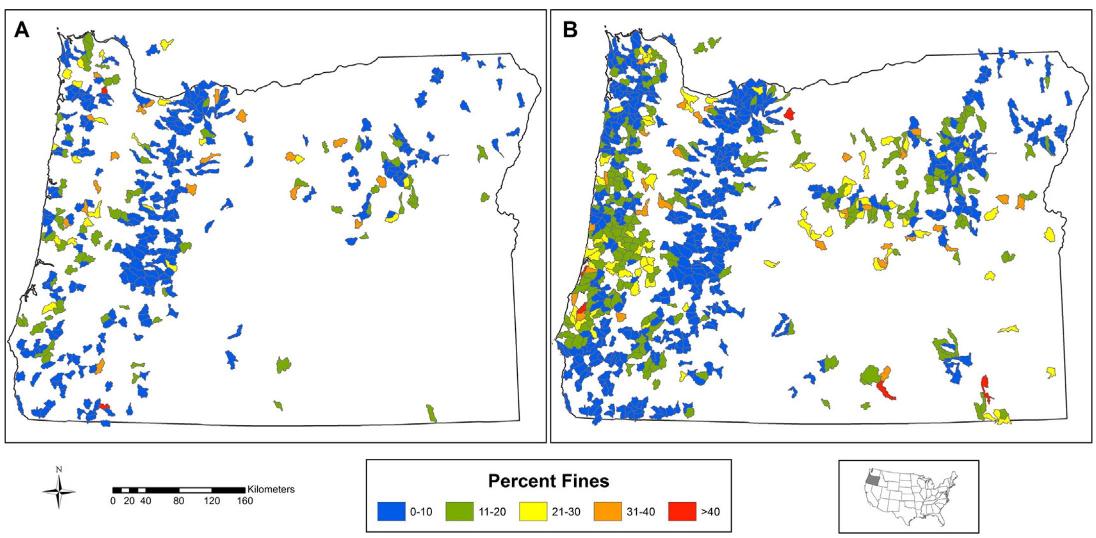

Fig. 5. Assessment of fine sediment conditions across Oregon using direct measurements of substrate composition (%FN; panel A), or inferred via macroinvertebrate tolerances (BSTI; panel B). Each watershed is a 12-digit Hydrologic Unit Code (6th field). Condition bins represent averages of all samples in a watershed.

of watersheds and %FN with 15% of watersheds above the 30% category.

4. Discussion

4.1. Fine sediment particle sizes

To our knowledge, our study represents the first efforts to infer fine sediment conditions in streams based on macroinvertebrate tolerances to the smallest bedded substrate particle sizes (silt and clay; median diameter < 0.06 mm). It should be noted that given the visual nature of our field methods it was not possible to verify the size of particles classified as fines. As such, the actual particle sizes used in estimating %FN are likely to include larger sizes. The substrate utilized by stream invertebrates includes both surface and subsurface habitat, thus the lack of information about subsurface sediment size classes presents an important limitation of this study. However, vertical stratification of the substrate typically results with finer sediment in the subsurface than the surface (Bunte and Abt, 2001), therefore surface estimates may be an underestimate of subsurface fines.

Yuan (2007), Relyea et al. (2012), and Murphy et al. (2015) each developed similar models or indices of macroinvertebrate tolerances to fine sediments, but all of these indices were calibrated on larger particles sizes (<2 mm; %SAFN). There is evidence that the smallest particles sizes, such as %FN in this study, show as much or perhaps more of an effect on macroinvertebrates than the larger particles sizes used in similar models (Runde and Hellenthal, 2000; Kaller and Hartman, 2004; Wood et al., 2005). Given that across Oregon we routinely observe a higher extent of wadeable streams exceeding thresholds for %FN compared to %SAFN (Hubler, 2007; Mulvey et al., 2009), we feel it is important to have a tool that addresses the most common and most likely stressor.

But, that is not to say that fine sediment sizes greater than modeled in our study may not impact macroinvertebrates. What becomes clear when reviewing the literature is that responses across varying size classes of fine sediments are taxon specific (Wood et al., 2005; Cover et al., 2008; Jones et al., 2012). Indices such as the BSTI that integrate taxon-specific responses to a stressor across the entire assemblage (Extence et al., 2013; Murphy et al., 2015) thus may offer increased sensitivity over the more traditional approaches, such as richness or relative abundances of indicator taxa.

4.2. BSTI model performance

The performance of the BSTI compares favorably to similar inference models for stream macroinvertebrates. The jackknife estimated r^2 of the BSTI (0.41, Table 1) was at the low end of that reported for macroinvertebrate WA pH models in Northern European streams (r^2 = 0.47–0.71) (Hamalainen and Huttunen, 1996; Larsen et al., 1996). The most direct comparisons are to fine sediment inference models for streams across the Western U.S. (Yuan, 2007). Yuan reported a WA r^2 of 0.41 and a ML r^2 of 0.42 for observed versus inferred fine sediments in the calibration set, while in our study the BSTI showed a CAL r^2 of 0.49. However, Yuan defined fine sediments as those particles with intermediate diameters less than 2 mm (%SAFN). One possible explanation for this modest improvement of the BSTI over Yuan's models could be higher precision estimates in field measurements for %FN, compared to %SAFN (Kaufmann et al., 1999; Stoddard et al., 2005). The correlative abilities of two macroinvertebrate fine sediment diagnostic indices developed for Europe (Turley et al., 2014; Murphy et al., 2015) were similar to the predictive abilities of the BSTI.

The majority of environmental inference models assess model performance from the calibration dataset itself and some form of cross-validation (e.g., leave-one-out jackknifing or bootstrapping). Few studies have examined model performance using independent validation datasets (Ter Braak and van Dam, 1989; Birks et al., 1990; Telford et al., 2004; Telford and Birks, 2011). Similar to our results, in each of these studies estimates of model errors (RMSE) based on the calibration datasets were consistently lower than observed in independent datasets. Birks et al. (1990) split their original calibration dataset into different calibration and independent validation datasets of varying sample sizes. They observed an increase in RMSE in the independent validation datasets for six models, and a decrease in validation RMSE for four models. This would indicate that final estimates of model performance can be influenced by the composition of the individual sites selected for any independent validation dataset. The multiple-trials approach used by Birks et al. (1990) and Telford et al. (2004) may provide a more accurate assessment of model performance than relying on a single validation dataset. However, this would require multiple versions of the inference model, which could make implementation within a management setting more complicated.

An additional consideration for future improvements of the BSTI centers on taxonomic resolution. Currently, 18% of taxa used in construction of the BSTI were identified to higher levels (less resolution) than genus or species. Turley et al. (2014) showed taxonomic resolution can have minor to modest effects on relationships between a biological index and the stressor of interest. However, typically improvements are observed. While it is unlikely to see taxonomic advances in groups of taxa routinely left at less resolved levels (e.g., Order, Class, etc.), there are already substantial advances within certain groups. Most specifically, the Chironomidae are widely recognized as a highly diverse family. Since the early to mid-2000s, standardized taxonomy in the PNW now routinely identifies the Chironomids to genus or species. These efforts, as well as efforts to standardize taxonomic levels for all taxa across PNW monitoring programs (PNAMP, 2015) should work to improve future versions of the BSTI. On the other hand, Juggins et al. (2015) showed inference model improvements when non-informative taxa were excluded. Incorporating methods to determine non-informative taxa may lead to model improvements.

4.3. Repeatability of the BSTI

Few studies have examined the repeatability of biological inference models of environmental gradients, such as the BSTI. Hamalainen and Huttunen (1996) calibrated their macroinvertebrate—pH inference models with 64 sites, sampled three times in a single year. Ponader et al. (2007) included repeated samples in the development of diatom-based nutrient inference models for New Jersey streams, finding that exclusion of the repeat samples did not significantly decrease model performance. However, neither of these studies examined the repeatability of the models across sites.

Our examination of repeat data shows the BSTI can make precise inferences for a site, with a degree of independence from natural gradients that may influence fine sediments levels in streams. These results may give an indication of the suitability of the BSTI as a bioassessment tool for detecting human disturbances at a site, when placed in context with these natural gradients (see management discussion, below). For example, in the Coast Range we observed the highest BSTI values and variability for Montgomery Creek and Tillamook River (Table 2). Both sites contain high percentages of erodible lithology in their watersheds, which would be expected to increase fine sediments. But Montgomery Creek had the second highest stream gradient in the Coast Range, which would be expected to decrease sedimentation by increased stream power (Wood and Armitage, 1997). On the other hand, these two sites had the highest human disturbance values of all 14 repeat sites. Conversely, the Sixes River site had two natural gradients typically associated with higher sedimentation (high erodibility and low slope) and one gradient associated with lower sedimentation (high rainfall = increased stream power); yet the Sixes showed moderate BSTIs (11 ± 2%; Table 2). In the Grande Ronde, we observed the lowest BSTIs for the three sites (both Limber Jim Creek sites and Lookout Creek) with the highest potential source material (high erodibility); but these three sites conversely had the highest slopes and precipitation. Incidentally, these sites also showed the lowest degrees of human disturbance across the study area. The highest fine sediment inferences in the Grande Ronde were observed in the restoration site, McCoy Creek-Lower. This result is unsurprising, given that the restoration action was to return the creek from a heavily channelized section back into the previously abandoned natural channel which had a lower slope, higher sinuosity, and had accumulated fine sediments over the years. Similar to observations in the Coast Range, the two sites with the greatest degree of human disturbances in the Grande Ronde (Dark Canyon and McCoy-Lower), showed increased variability (although minor) in BSTI.

4.4. Management implications

Clearly, excess sedimentation is a global issue (Chutter, 1969; Ryan, 1991; Wood and Armitage, 1997; Paulsen et al., 2008); but resource management efforts to address the impacts caused by fine sediments above natural background levels must be dealt with at local scales. Larger, regional scale biotic-fine sediment indexes have been developed for the Western United States (Yuan, 2007) and the PNW (Relyea et al., 2012), but these indexes lack the density of sampling locations necessary to adequately represent a management area as environmentally heterogeneous as Oregon (Omernik, 1987). Thus, we focused on development of an index with the greatest utility in identifying potential stream impairments in Oregon.

The BSTI provides an alternative, robust, and cost-effective approach to monitoring fine sediment conditions across Oregon. The shared macroinvertebrate field methods across resource agencies in the PNW and the increased ability to engage citizen-based monitoring groups provides an opportunity to substantially increase our assessments of fine sediment conditions. As an example of the cost-effective nature of the BSTI, we queried the Oregon Department of Environmental Quality (ODEQ) biomonitoring database for all records available to assess fine sediments across the state (Fig. 5). While direct comparisons between the two datasets are not possible (due to spatial and temporal differences in monitoring), similar overall patterns are presented. However, the BSTI offers a clear advantage due to increased sample size, filling in gaps in the Coast Range (far left), Northeastern Oregon, and (to a lesser extent) Southeastern Oregon. Most importantly, approximately 43% of the BSTI scores were obtained from data sources outside of ODEQ. These partners represented nearly all monitoring organization types, from local citizen-based monitoring groups operating at watershed or basin scales, up to a broad-scale and long-term federal program that spanned multiple PNW states. All of these external datasets were capable of integration within ODEQ's program due to the foresight of resource managers to align sampling and laboratory methods for macroinvertebrate monitoring (Hayslip, 2007). Unfortunately, similar efforts to align physical habitat protocols have had minimal traction.

While the BSTI demonstrated a good ability to infer instream fine sediment conditions with high repeatability, we feel the greatest stream management utility would be within a reference condition approach (Bailey et al., 1998, 2004; Reynoldson and Wright, 2000). Reference expectations for BSTI scores at any study site would be based on the distribution of BSTI scores observed at a population of least disturbed (Stoddard et al., 2006) reference sites. Here, standard biointegrity indices like Observed/Expected taxa (O/E; Wright et al., 1993; Hawkins et al., 2000) or Indices of Biotic Integrity (Karr, 1981; Karr, 1991; Rehn et al., 2007) could be used to identify biological impairment, and then the BSTI could be used to identify excess fine sediments as a likely cause of the biological impairment. While reference expectations are built into O/E and IBI indexes, they are not integrated into WA inferences of environmental gradients, such as the BSTI. (The rationale for this is that not all taxa are observed at reference sites, especially the most tolerant taxa.) As shown in the sites with repeat sampling, BSTI values can show a complex relationship between natural environmental gradients and human disturbances. Future efforts to integrate the use of the BSTI into a reference condition approach should therefore address the need to factor out natural gradients from reference expectations. Until that time, the bins shown in Fig. 5 may provide interim guidelines for assessing conditions, with BSTIs less than 10% indicating little to no fine sediment impairment and BSTIs greater than 30 indicating moderate to severe impairment.

There is a wide range of possibilities in how the BSTI, or similar indexes that explicitly infer stressor gradients using biota, could be used in a stream management setting. Anyone wishing to calculate the BSTI for their own data simply need to apply macroinvertebrate abundances and the tolerances in Appendix to the weighted averaging and inverse deshrinking formulas presented by Ter Braak and van Dam (1989) and Birks et al. (1990), followed by the back-transformation step provided in Eq. (2). Sites lacking measured fine sediment data and high BSTI values (on the scale of % fine sediments) could be prioritized within monitoring plans for more technical sediment field studies to confirm whether or not the instream conditions match those inferred by the macroinvertebrate assemblage (e.g., Turley et al., 2014). Or BSTI reference benchmarks could be used by resource managers as targets within total maximum daily loads (TMDLs) (Karr and Yoder, 2004; Yagow et al., 2006), representing desired shifts in the protected biological assemblage toward more natural conditions. Citizen-based monitoring groups could use expected BSTI scores to assess the effectiveness of restoration projects, such as additions of large woody debris or decommissioning of failing road networks to improve instream sediment conditions. In this example, a stream with a high degree of excess fine sediments could be monitored to see if the assemblage-level tolerance to fine sediments decreased following implementation of the restoration actions.

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Appendix A. Tolerances of macroinvertebrate taxa to percent fine sediments (median diameter < 0.06 mm), as well as the number of occurrences ('*n*') in the calibration dataset. Tolerances are presented on two different scales, the first on the scale of percent fines, and the second on the transformed scale as presented in Eq. (2). 'Type' refers to the taxonomic groupings used in Fig. 2.

Taxon	Type	Level	Count	Tolerance (% FN)	Tolerance (transformed)
Heptagenia	Ephemeroptera	Genus	1	0	0
Prostoia	Plecoptera	Genus	1	0	0
Neophylax occidentalis	Trichoptera	Species	5	1	0.0214
Ordobrevia	Coleoptera	Genus	37	1	0.0309
Plumiperla	Plecoptera	Genus	8	2	0.0336
Pilaria	Diptera	Genus	5	2	0.0344
Sierraperla	Plecoptera	Genus	2	2	0.0348
Diamesinae	Diptera	Sub-Family	1	2	0.0359
Podmosta	Plecoptera	Genus	1	2	0.0359
Rhyacophila Oreta Gr.	Trichoptera	Species group	1	2	0.0359
Soyedina	Plecoptera	Genus	1	2	0.0359
Valvata	Non-Insect	Genus	1	2	0.0367
Oligophlebodes	Trichoptera	Genus	31	2	0.0383
Arctopsyche	Trichoptera	Genus	72	2	0.0396
Cryptochia	Trichoptera	Genus	24	2	0.0396
Agraylea	Trichoptera	Genus	7	2	0.0397
Allocosmoecus	Trichoptera	Genus	4	2	0.0407
Ochrotrichia	Trichoptera	Genus	14	2	0.041
Epeorus grandis	Ephemeroptera	Species	90	2	0.0415
Acneus	Coleoptera	Genus	10	2	0.0416
Kathroperla	Plecoptera	Genus	26	3	0.0419
Blephariceridae	Diptera	Family	19	3	0.0423
Epeorus deceptivus	Ephemeroptera	Species	11	3	0.0428
Soliperla	Plecoptera	Genus	33	3	0.043

Taxon	Type	Level	Count	Tolerance (% FN)	Tolerance (transformed)
Rhyacophila Hyalinata Gr.	Trichoptera	Species group	136	3	0.0434
Rhyacophila Iranda Gr.	Trichoptera	Species group	11	3	0.0435
Ampumixis	Coleoptera	Genus	59	3	0.0442
Petrophila	Insect-Other	Genus	5	3	0.0447
Hesperoconopa	Diptera	Genus	21	3	0.0451
Eubrianax edwardsi	Coleoptera	Species	36	3	0.0454
Oreogeton	Diptera	Genus	36	3	0.0464
Rhyacophila Nevadensis Gr.	Trichoptera	Species group	4	3	0.0464
Drunella doddsi	Ephemeroptera	Species	83	3	0.0471
Rhyacophila Angelita Gr.	Trichoptera	Species group	74	3	0.0472
Ecclisomyia	Trichoptera	Genus	19	3	0.0475
Philocasca	Trichoptera	Genus	2	3	0.0479
Drunella grandis	Ephemeroptera	Species	240	3	0.048
Polycentropodidae	Trichoptera	Family	18	3	0.049
Visoka	Plecoptera	Genus	109	4	0.0494
Nemoura	Plecoptera	Genus	3	4	0.0495
Anagapetus	Trichoptera	Genus	31	4	0.0498
Pteronarcys	Plecoptera	Genus	112	4	0.0498
Caudatella	Ephemeroptera	Genus	90	4	0.0502
Epeorus longimanus	Ephemeroptera	Species	92	4	0.0504
Wiedemannia	Diptera	Genus	10	4	0.0512
Megarcys	Plecoptera	Genus	70	4	0.0513
Parapsyche elsis	Trichoptera	Species	82	4	0.0514
Zapada frigida	Plecoptera	Species	27	4	0.0514
Leucotrichia	Trichoptera	Genus	4	4	0.0524
Rhyacophila Vagrita Gr.	Trichoptera	Species group	14	4	0.0525
Neotrichia	Trichoptera	Genus	6	4	0.0526
Rhyacophila Brunnea Gr.	Trichoptera	Species group	221	4	0.053
Agapetus	Trichoptera	Genus	51	4	0.0534
Pseudolimnophila	Diptera	Genus	2	4	0.0536
Rhyacophila Vofixa Gr.	Trichoptera	Species group	30	4	0.054
Drunella coloradensis/flavilinea	Ephemeroptera	Species	134	4	0.0541
Acentrella insignificans	Ephemeroptera	Species	9	4	0.055
Procloeon	Ephemeroptera	Genus	2	5	0.0556
Rhithrogena	Ephemeroptera	Genus	253	5	0.0556
Clinocera	Diptera	Genus	73	5	0.0557
Zapada columbiana	Plecoptera	Species	104	5	0.0557
Atherix	Diptera	Genus	28	5	0.0558
Neophylax splendens	Trichoptera	Species	67	5	0.0561
Perlinodes	Plecoptera	Genus	15	5	0.0564
Rhyacophila Betteni Gr.	Trichoptera	Species group	272	5	0.0566
Acentrella turbida	Ephemeroptera	Species	36	5	0.0567
Pedomoecus	Trichoptera	Genus	6	5	0.057
Pseudochironomini	Diptera	Tribe	2	5	0.0572
Antocha	Diptera	Genus	187	5	0.0575
Thaumalea	Diptera	Genus	28	5	0.0588
Brachycentrus	Trichoptera	Genus	40	5	0.0589
Claassenia sabulosa	Plecoptera	Species	4	5	0.0591
Neophylax rickeri	Trichoptera	Species	72	5	0.0591
Serratella tibialis	Ephemeroptera	Species	170	5	0.0593
Cultus	Plecoptera	Genus	18	5	0.0595
Drunella pelosa	Ephemeroptera	Species	25	5	0.06
Rhyacophila Verrula Gr.	Trichoptera	Species group	17	5	0.0603
Glossosoma	Trichoptera	Genus	270	5	0.0604
Deuterophlebia	Diptera	Genus	112	5	0.0605
Suwallia	Plecoptera	Genus	25	5	0.0606
Apatania	Trichoptera	Genus	71	6	0.0611
Calineuria	Plecoptera	Genus	254	6	0.0612
Doroneuria	Plecoptera	Genus	35	6	0.0616
Cordulegastridae	Insect-Other	Family	1	6	0.0621
Neothremma	Trichoptera	Genus	39	6	0.0622
Rhyacophila narvae	Trichoptera	Species	132	6	0.0626
Baetis bicaudatus	Ephemeroptera	Species	17	6	0.0632
Hydatophylax	Trichoptera	Genus	10	6	0.0633
Rhyacophila Grandis Gr.	Trichoptera	Species group	19	6	0.0636
Psephenus	Coleoptera	Genus	22	6	0.0637
Baetis tricaudatus	Ephemeroptera	Species	398	6	0.0641
Amiocentrus	Trichoptera	Genus	56	6	0.0643
Maruina	Diptera	Genus	52	6	0.0645
Timpanoga hecuba	Ephemeroptera	Species	14	6	0.0645
Ironodes	Ephemeroptera	Genus	176	6	0.0646
Ameletus	Ephemeroptera	Genus	184	6	0.0647
Dicosmoecus gilvipes	Trichoptera	Species	14	6	0.0647
Cinygmula	Ephemeroptera	Genus	244	6	0.065
Hydropsyche	Trichoptera	Genus	248	6	0.065
Baetis flavistriga	Ephemeroptera	Species	17	6	0.0651
Drunella spinifera	Ephemeroptera	Species	65	6	0.0651
Goeracea	Trichoptera	Genus	1	6	0.0651

Taxon	Type	Level	Count	Tolerance (% FN)	Tolerance (transformed)
Forcipomyiinae	Diptera	Sub-Family	62	6	0.0652
Serratella teresa	Ephemeroptera	Species	20	6	0.0655
Rhyacophila pellisa/valuma	Trichoptera	Species	50	6	0.0658
Yoraperla	Plecoptera	Genus	190	6	0.0658
Rhabdomastix	Diptera	Genus	21	7	0.0661
Palaegapetus	Trichoptera	Genus	3	7	0.0662
Rhyacophila Alberta Gr.	Trichoptera	Species group	16	7	0.0664
Hesperoperla pacifica	Plecoptera	Species	176	7	0.0673
Heterlimnius	Coleoptera	Genus	259	7	0.0674
Despaxia	Plecoptera	Genus	4	7	0.0677
Kogotus/Rickera	Plecoptera	Genus	14	7	0.068
Zapada Oregonensis Gr.	Plecoptera	Species group	65	7	0.0681
Hemerodromia	Diptera	Genus	17	7	0.0686
Micrasema	Trichoptera	Genus	223	7	0.0688
Prosimulium	Diptera	Genus	35	7	0.0699
Lepidostoma	Trichoptera	Genus	195	7	0.07
Attenella	Ephemeroptera	Genus	49	7	0.0702
Taeniopterygidae	Plecoptera	Family	11	8	0.0707
Dicosmoecus atripes	Trichoptera	Species	162	8	0.0708
Turbellaria	Non-Insect	Class	158	8	0.071
Sweltsa	Plecoptera	Genus	312	8	0.0717
Hexatoma	Diptera	Genus	176	8	0.0721
Ecclisocosmoecus	Trichoptera	Genus	11	8	0.0724
Glutops	Diptera	Genus	124	8	0.0728
Tanytarsini	Diptera	Tribe	426	8	0.073
Moselia	Plecoptera	Genus	61	8	0.0733
Skwala	Plecoptera	Genus	75	8	0.074
Chelifera/Metachela	Diptera	Genus	165	8	0.0741
Simulium	Diptera	Genus	303	8	0.0745
Epeorus albertae	Ephemeroptera	Species	73	8	0.0746
Orthocladiinae	Diptera	Sub-Family	444	8	0.0746
Trombidiformes	Non-Insect	Order	383	9	0.075
Setvena	Plecoptera	Genus	6	9	0.0751
Wormaldia	Trichoptera	Genus	221	9	0.0755
Paraperla	Plecoptera	Genus	35	9	0.0757
Ephemerella	Ephemeroptera	Genus	97	9	0.076
Dicranota	Diptera	Genus	53	9	0.0761
Narpus	Coleoptera	Genus	109	9	0.0762
Zaitzevia	Coleoptera	Genus	274	9	0.0763
Limonia	Diptera	Genus	12	9	0.0766
Psychoda	Diptera	Genus	2	9	0.0766
Baetis alius	Ephemeroptera	Species	3	9	0.0784
Malenka	Plecoptera	Genus	203	9	0.0786
Diphetor hageni	Ephemeroptera	Species	250	9	0.0787
Gomphidae	Insect-Other	Family	65	9	0.0788
Nixe/Leucocruta	Ephemeroptera	Genus	55	10	0.079
Rhyacophila Rotunda Gr.	Trichoptera	Species group	2	10	0.079
Baetis notos	Ephemeroptera	Species	15	10	0.0791
Meringodixa	Diptera	Genus	26	10	0.0797
Pericoma/Telmatoscopus	Diptera	Genus	70	10	0.08
Chironomini	Diptera	Tribe	260	10	0.0803
Capniidae	Plecoptera	Family	33	10	0.0804
Leptoceridae	Trichoptera	Family	6	10	0.081
Oligochaeta	Non-Insect	Class	361	10	0.081
Gumaga	Trichoptera	Genus	18	10	0.0813
Zapada cinctipes	Plecoptera	Species	281	10	0.0817
Diura	Plecoptera	Genus	278	10	0.0819
Tricorythodes	Ephemeroptera	Genus	15	10	0.0823
Ephydridae	Diptera	Family	11	10	0.0825
Labiobaetis	Ephemeroptera	Genus	1	10	0.0827
Heteroplectron	Trichoptera	Genus	14	11	0.0832
Paraleptophlebia	Ephemeroptera	Genus	293	11	0.0836
Dixella	Diptera	Genus	122	11	0.0839
Ceratopogoninae	Diptera	Sub-Family	200	11	0.0842
Nematoda	Non-Insect	Phylum	231	11	0.0855
Lara	Coleoptera	Genus	105	11	0.0856
Odontoceridae	Trichoptera	Family	4	11	0.0857
Tanypodinae	Diptera	Sub-Family	279	12	0.0875
Optioservus	Coleoptera	Genus	236	12	0.0876
Pristinicola	Non-Insect	Genus	28	12	0.0877
Helicopsyche	Trichoptera	Genus	15	12	0.0881
Ormosia	Diptera	Genus	1	12	0.0895
Stratiomyidae	Diptera	Family	9	12	0.0897
Rhyacophila Lieftincki Gr.	Trichoptera	Species group	18	13	0.0909
Rhyacophila blarina	Trichoptera	Species	58	13	0.0918
Dixa	Diptera	Genus	5	13	0.0931
Podonominae	Diptera	Sub-Family	8	13	0.0932
Psychoglypha	Trichoptera	Genus	30	14	0.0936

Taxon	Type	Level	Count	Tolerance (% FN)	Tolerance (transformed)
Parapsyche almota	Trichoptera	Species	39	14	0.094
Prostoma	Non-Insect	Genus	6	14	0.0945
Limnophila	Diptera	Genus	42	14	0.0948
Desmona	Trichoptera	Genus	1	14	0.0949
Amphizoa	Coleoptera	Genus	3	14	0.0954
Cryptolabis	Diptera	Genus	9	14	0.0961
Psychomyia	Trichoptera	Genus	10	15	0.0968
Hirudinea	Non-Insect	Class	4	15	0.0973
Pteronarcella	Plecoptera	Genus	19	15	0.0973
Juga	Non-Insect	Genus	132	15	0.0986
Hydraena	Coleoptera	Genus	27	15	0.0991
Ochthebius	Coleoptera	Genus	5	15	0.0995
Fluminicola	Non-Insect	Genus	32	16	0.0999
Cinygma	Ephemeroptera	Genus	79	16	0.1
Cleptelmis	Coleoptera	Genus	76	16	0.101
Hydrophilidae	Coleoptera	Family	46	16	0.101
Rhyacophila Coloradensis Gr.	Trichoptera	Species group	5	16	0.101
Goera	Trichoptera	Genus	9	16	0.102
Metrichia	Trichoptera	Genus	1	16	0.102
Tabanidae	Diptera	Family	26	16	0.102
Ferrissia	Non-Insect	Genus	14	17	0.103
Margaritifera	Non-Insect	Genus	5	17	0.103
Ostracoda	Non-Insect	Class	93	17	0.103
Hydroptila	Trichoptera	Genus	43	17	0.104
Dytiscidae	Coleoptera	Family	64	17	0.105
Microcylloepus	Coleoptera	Genus	9	17	0.105
Lymnaeidae	Non-Insect	Family	11	18	0.106
Isoperla	Plecoptera	Genus	65	19	0.11
Planorbidae	Non-Insect	Family	17	19	0.11
Sialis	Insect-Other	Genus	25	19	0.11
Cheumatopsyche	Trichoptera	Genus	26	20	0.112
Dolichopodidae	Diptera	Family	10	20	0.112
Haliplidae	Coleoptera	Family	9	20	0.113
Asellidae	Non-Insect	Family	12	21	0.114
Sphaeriidae	Non-Insect	Family	176	21	0.114
Centroptilum	Ephemeroptera	Genus	6	21	0.115
Dolophilodes	Trichoptera	Genus	4	21	0.115
Libellulidae	Insect-Other	Family	2	21	0.115
Muscidae	Diptera	Family	10	21	0.116
Pedicia	Diptera	Genus	10	21	0.116
Physa	Non-Insect	Genus	28	21	0.116
Corydalidae	Insect-Other	Family	7	22	0.118
Farula	Trichoptera	Genus	2	22	0.118
Molophilus	Diptera	Genus	2	24	0.122
Onocosmoecus	Trichoptera	Genus	19	25	0.124
Tipula	Diptera	Genus	34	25	0.124
Coenagrionidae	Insect-Other	Family	25	25	0.125
Dubiraphia	Coleoptera	Genus	7	25	0.126
Corixidae	Insect-Other	Family	6	26	0.127
Protoptila	Trichoptera	Genus	2	26	0.128
Corbicula	Non-Insect	Genus	2	27	0.129
Hyalella	Non-Insect	Genus	15	27	0.13
Gammarus	Non-Insect	Genus	12	28	0.131
Helichus	Coleoptera	Family	8	28	0.131
Ptychopteridae	Diptera	Family	12	31	0.139
Pseudostenophylax	Trichoptera	Genus	3	34	0.144
Curculionidae	Coleoptera	Family	1	41	0.159
Prodiamesinae	Diptera	Sub-Family	8	41	0.16
Callibaetis	Ephemeroptera	Genus	2	63	0.199
Talitridae	Non-Insect	Family	1	72	0.217

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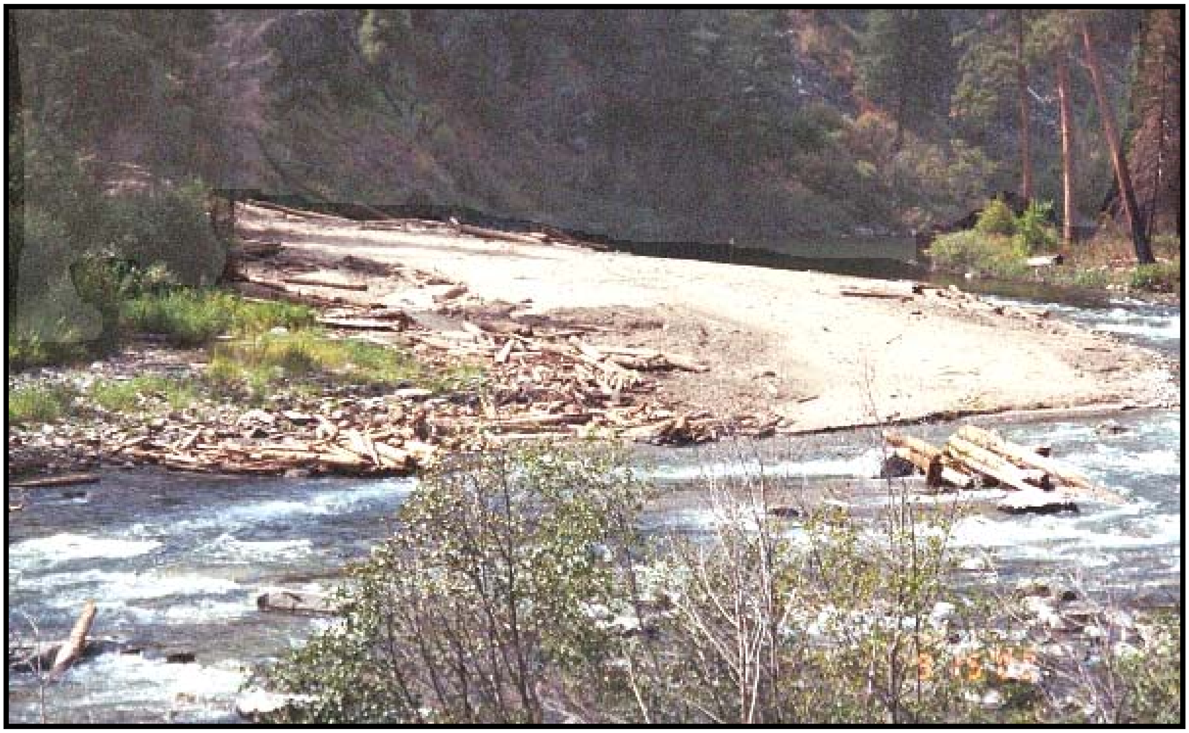
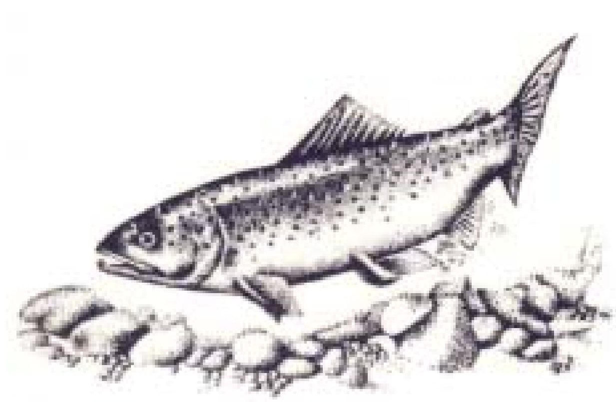
Guide to Selection of Sediment Targets for Use in Idaho TMDLs





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June, 2003

Guide to Selection of Sediment Targets for Use in Idaho TMDLs

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Executive Summary

Excessive fine sediment is the most common pollutant in impaired streams in Idaho. Total Maximum Daily Load (TMDL) plans prepared to address excessive fine sediment must comply with the existing narrative water quality standard for sediment, which states "*Sediment shall not exceed quantities ... which impair beneficial uses*" (IDAPA 58.01.02.200.08). While this aptly describes a goal, it does not describe objectives for TMDL plans and stream restorations. Through this report, the Idaho Department of Environmental Quality is suggesting appropriate water column and streambed measures for gauging attainment of the narrative sediment goal.

One of the important beneficial uses of Idaho streams is production of trout and salmon for ecological and recreational purposes. The effects of excessive fine sediment on the embryo, fry, juvenile and adult life stages of salmonids are well studied. Characteristics of the stream that change with increasing fine sediments and are known to affect salmonids and other aquatic biota are the best measures of sediment-caused impairment of beneficial uses. These characteristics and the threshold values that describe minimal degradation are the targets that are recommended in this report.

Water column and instream measures that were determined to be the best indicators of sediment related impairment of beneficial uses include light penetration, turbidity, total suspended solids and sediments, embeddedness, extent of streambed coverage by surface fines, percent subsurface fines in potential spawning gravels, riffle stability, and intergravel dissolved oxygen. The relationships between these measures and the aquatic biota are described in this paper, with special attention given to growth, survival, reproductive success, and habitat suitability of salmonids. Target levels for most measures are recommended based on generalized relationships found in the scientific literature and specific background conditions that exist in Idaho streams. The targets for turbidity and intergravel dissolved oxygen were established based on existing Idaho Water Quality Standards. Where data to describe sediment-biota relationships are lacking or highly variable or background conditions are highly variable, statewide numeric thresholds are inappropriate. For total suspended solids and sediments, embeddedness, and surface sediments, target levels should be established for each individual stream based on local reference sediment conditions. To provide a regional perspective of the recommended target levels, comparisons are made to standards adopted in neighboring states and provinces.

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1. Introduction

Sediment is the biggest water quality problem in Idaho streams. For over 90% of the streams on the state's 1998 303(d) list sediment was identified as a pollutant of concern. Between 1992 and 2003, 76% of the approved TMDLs in the state addressed sediments (DEQ 2003). Temperature is the second most frequently listed pollutant on the 303(d) list, at about half the frequency of sediment. Sediment can have direct effects on beneficial uses for salmonid spawning, cold and warm water aquatic life, and domestic, agricultural, and industrial water supplies. Water quality plans will be written to address these sediment concerns, including an estimation of a total maximum daily load (TMDL) for sediment. The TMDL is a limit on the quantity of sediment, which enters the stream from both natural and human-caused sources. This limit is to be set at a level such that water in the streams will meet state water quality standards. Idaho's water quality standard for sediment is narrative, "*Sediment shall not exceed quantities ... which impair beneficial uses*" (IDAPA 58.01.02.200.08). A narrative standard for sediment is necessary and desirable as it accommodates the vast range of sediment conditions that exist in nature. The primary beneficial use addressed in this paper is the propagation and maintenance of viable aquatic ecosystems, especially as they support salmonid fisheries.

With no fixed numeric criterion, a major challenge to preparing a TMDL for sediment is development of a numeric target that can be used to derive a load capacity. The target is a site-specific interpretation of the narrative sediment criterion based on an assessment of how sediment in a particular waterbody impairs beneficial use. The sediment targets are surrogate measures for beneficial use support. As such, they supplement a load or concentration goal used in a TMDL, providing a bridge over the uncertainty in the connection between sediment loading and support of beneficial uses.

The work of developing sediment criteria is ongoing. One of the first efforts by Idaho Department of Environmental Quality (DEQ) to address sediment concerns was Harvey's 1989 Technical Review of Sediment Criteria. He recommended four criteria as they relate to domestic water supply, salmonid spawning, and cold water aquatic life beneficial uses. Harvey's work was the basis for current state Water Quality Standards for intergravel dissolved oxygen for salmonid spawning and turbidity for both cold water aquatic life and domestic water supply.

Sediment-caused impairment can take many forms and be measured in a variety of ways. To assist planners responsible for writing TMDLs for Idaho streams, DEQ has explored measurements of sediment that may assist in setting targets and in gauging progress toward meeting water quality standards. Earlier recommendations (Harvey 1989) and the targets recommended in this document are site-specific and are not enforceable. The ultimate measure of sediment water quality standard attainment, and the only measure recognized in Idaho's water quality rules, is instream beneficial use support.

Sediments can be dichotomously classified in at least three overlapping ways - clean or contaminated, organic or inorganic, and suspended or bed material. This paper deals only with clean sediment, not sediment that is contaminated by toxic substances such as heavy metals. Organic solids are only a minor fraction of sediment in most Idaho streams, providing a vital source of food energy in many smaller streams. Organic matter can become abundant enough to cause water quality problems, typically below sewage outfalls where decay can depress dissolved oxygen levels. The distinction between inorganic and organic fractions is not always made in the monitoring or study of sediment. Inorganic sediment, the product of physical weathering of geologic materials, predominates as a water quality problem in Idaho and is the main focus of the studies referenced below. While we refer to both suspended solids and stream bed deposits collectively as sediment, clearly these solids act differently upon aquatic life depending on their location in the aquatic environment. This important distinction is affected by the balance between particle size and stream energy, and presents difficulty in both the measurement of sediment load and its relation to beneficial use support.

One of the fundamental questions regarding sediment in streams and its effect on biota is particle size. Particle size may be described as a fraction below some cutoff value, an average (median, mean, geometric mean) diameter, or most robustly as a frequency or cumulative frequency distribution. Chapman (1988) suggested, based on the work of Tappel and Bjornn (1983) and others, that two sizes of sediment be considered: fine sediment (< 0.85 mm) which is most responsible for suffocation and abrasion of salmonid eggs, and coarser sediment (< 9.5 mm) which can create a surficial barrier preventing salmonid fry emergence from the redd. Hunter (1973) reported a minimum substrate size of 6 mm for steelhead, rainbow trout, and cutthroat trout spawning areas. Particles less than 0.063 mm (silt and clay) remain suspended in flowing water and are largely the cause of turbidity and effects on visual feeding. Although it is often assumed that smaller substrates (e.g., fine sediment) are the overriding problem in streams, there are times when large size substrate (> 9.5 mm) can also be a problem (e.g. filling of pools with cobbles or deficit of spawning gravel). For most of the proposed streambed targets, sediment size of concern is fines less than 6.35 mm based on Burton and Harvey (1990). Fine sediments can cause impairment with either too much or too little in the system. The overwhelming problem in Idaho is excessive fine sediments.

In an ideal world, target levels to achieve sediment reduction would be developed for each stream. Not only will stream sediment conditions differ between, for example, ecoregions, conditions will also vary within reaches of the same stream, and over time. Sediment conditions, even in the absence of development (e.g., wilderness areas), are highly variable (Rosgen 1980, Nelson et al. 1997). It is important to remember that there is a range of conditions, a natural distribution, within a stream that is important to maintain (Russ Thurow, Forest Service, personal communication). Stochastic events (e.g., summer thunder storms) may create conditions in which sediment parameters exceed targets, even in pristine streams (Benda and Dunne 1997).

Nothing precludes the establishment of site-specific targets if enough information is available. Necessary information would include: sufficient sites throughout the stream drainage to ensure a representative sample; within year data covering both base flow, spring runoff, and episodic events; and between years data to cover a range of precipitation and spring runoff conditions. If site-specific data were not available, targets could be based on a relatively undisturbed stream similar to the study stream (i.e., a reference stream in a paired watershed). Sufficient data to establish site-specific sediment targets on individual Idaho streams seldom exist; however, there is enough similarity among Idaho streams that some statewide targets can be recommended.

Some authors would argue against establishment of any type of threshold, which, if not met, would be assumed to have certain and deleterious effects on aquatic biota. For example, Chapman and McLeod (1987) found no functional predictors for evaluating quantitative effects of sediment on the natural incubation, rearing, or wintering phases of salmonid life history in the northern Rocky Mountains. Chapman (1988) and Everest and others (1987) caution against applying results of laboratory studies to field conditions. These conclusions emphasize the need for writers of TMDLs to carefully consider available data when establishing sediment targets on streams.

Sediment targets for water column, streambed, and subsurface flow parameters are proposed. No targets are currently recommended for channel characteristics (e.g., residual pool volume, width/depth ratio). A brief summary of channel characteristics as they relate to sediment loading is presented in Appendix A.

Targets are considered for the following parameters:

Water Column parameters:
- Turbidity
- Light penetration
- Total suspended solids and suspended sediment

Streambed parameters:
- Embeddedness
- Surface sediment
- Subsurface sediment
- Riffle stability

Subsurface Flow parameter:
- Intergravel dissolved oxygen

The targets proposed for the above mentioned parameters are benchmarks, selected such that few, if any, deleterious effects are expected to occur. At levels beyond the target, there may or may not be deleterious effects depending on the parameter value and the particular site. The proposed targets should not be viewed as points to which streams with parameter levels better than the targets can be degraded. The State’s anti-degradation rule requires streams that presently have conditions better than the proposed targets are maintained at those above par conditions.

It is not expected that every stream needs targets for all the parameters listed. On the other hand, in most cases, due to the inherent variability in the relation of sediment loads to target parameters and lag times in response, more than one target could be useful. For example, Lloyd (1987) suggested reasonable turbidity criteria could protect aquatic habitats from decreased light penetration, suspended sediments, and possibly heavy metals. Separate settleable solids or streambed standards could then be applied to protect aquatic habitats from the impacts of heavier sediments on benthic substrates. The choice of targets should be appropriate to the stream under study, as some streams may not lend themselves to a particular target (e.g., Riffle Stability Index in southeast Idaho streams).

There are several definitions (below), which help to clarify subsequent recommendations. It should also be noted that where concentration ranges and resultant biological effects are discussed for parameters such as turbidity or suspended solids, the lower end of the range is presented as a conservative effect threshold for use in recommending a target.

- Baseline background - the biological, chemical, or physical condition of waters measured at a point immediately upstream (upgradient) of the influence of an individual point source discharge or nonpoint source input;

- Natural background - naturally occurring background (i.e., expected historic value of the parameter for a given site absent any impact from human activity); and,

- Base flow - the value of the parameter when flows are low and relatively stable (i.e., neither on the rising nor falling limb of an annual runoff or storm event hydrograph).

2. Water Column Measures

There are valid reasons for considering the water column measures both individually and in relation to each other. Turbidity is a measure of light dispersion caused by particles suspended in a water column. Light penetration, turbidity, and suspended solids are therefore correlated, though the characteristics of the particles in suspension can change the degree of light dispersion or penetration. Larger particles can increase total suspended solids (TSS) without refracting light as much as the same quantity of smaller particles would. Lloyd (1987) concluded that turbidities of 25 and 95 NTU could be expected to impact fish communities through indirect effects of light extinction and the accommodating decrease in the production of plants and fish food. While effects of light penetration are usually associated solely with primary production, turbidity is also associated with elevated stress in fish, predatory efficiency, inducement of invertebrate drift, and suffocation of incubating salmonid embryos. TSS is perhaps the most direct measurement of sediment loads in the stream, and is treated in this paper in terms of its effects on fish, macroinvertebrates, and the aquatic habitat.

As turbidity and suspended solids increase, benthic macroinvertebrates tend to drift. They are especially prone to drift as the duration of the sediment pulse is lengthened (Shaw and Richardson 2001) and when suspended particles are smaller (Runde and Hellenthal 2000). Net-spinning caddisflies have been observed drifting in highly turbid suspended solids, while they will remain to be buried alive by less turbid suspended sediments (Runde and Hellenthal 2000). In a turbid water column, macroinvertebrates will be less visible to salmonid predators and have a better chance of survival (Vogel and Beauchamp 1999, Sweka and Hartman 2001, Shaw and Richardson 2001) while survival is also probable when overlying sediments are large (Runde and Hellenthal 2000).

Attempts have been made to predict TSS from turbidity, thereby avoiding the greater time and expense of measuring TSS. However, predictive models can be so sensitive to location and time period (Mack 1988) that the application may be limited to the current year and waterbody for each calibration effort. TSS and turbidity showed a strong positive relationship in nine urban/suburban Puget lowland streams (Packman et al. 1999). After log transformation, the coefficient of determination was 0.96, but confidence intervals around predicted TSS were large after back-transforming. In New Mexico TMDLs (e.g., Canyon Creek, Whitewater Creek, and Cordova Creek), the turbidity standard is converted to TSS by calibrating with local data so that the TSS values in units of mg/L can be converted to sediment loads in lbs/day.

Turbidity units (NTU) have been calibrated to approximate TSS measures using 40 mg/L kaolin clay to set a standard of 40 NTU, which should result in a TSS to turbidity slope of about 1.0 (Keyes and Radcliffe 2002). However, the calibration is not reliable for application in natural streams because the composition of suspended particles in streams rarely resembles the kaolin clay standard. Larger particles contribute weight to a TSS measurement, but will not scatter light as much as a similar weight of smaller particles.

2.1 Light Penetration

2.1.1 Biological background

Inorganic suspended materials reduce light penetration in a waterbody. This decreases the depth of the photic zone and reduces primary production leading to a decrease in the primary consumers that form the basis of fish diets (U. S. EPA 1986, Lloyd et al. 1987, Kiffney and Bull 2000, Rosemond et al. 2000). Benthic herbivores are also responsive to sediment accumulation in algal mats (Kiffney and Bull 2000), further reducing the abundance of these important grazers. In addition to negative effects on primary production and grazer abundance, reduced light can affect salmonid visual acuity by diminishing reaction distances (Vogel and Beauchamp 1999) and changing predatory efficiency.

In slow moving waters, suspended materials decrease light penetration while increasing absorption of solar energy near the surface. The heated upper layers tend to stratify the water column (NAS and NAE 1973), reducing the dispersion of dissolved oxygen and nutrients to the lower depths of the waterbody. In a study of the effect of clay on a New Zealand stream, Davies-Colley et al. (1992) suggested that restriction in light penetration into water may be a generally important mechanism by which fine inorganic solids damage streams.

2.1.2 Other states

No northwestern state had a specific light penetration standard. British Columbia has a clarity standard based on Secchi disk readings (>= 1.5 m [average of at least 5 readings over 30 days]).

2.1.3 Recommendation

We recommend that settleable and suspended solids should not reduce the depth of the compensation point for photosynthetic activity by more than 10% from the seasonally established norm for aquatic life. This standard is the same as recommended in the U. S. Environmental Protection Agency "Gold Book" (1986).

2.2 Turbidity

2.2.1 Biological background

Increased levels of turbidity dramatically reduce light penetration in both lakes and streams and are associated with decreased production and abundance of plant material (primary production), decreased abundance of food organisms (secondary production), decreased production and abundance of fish (Lloyd et al. 1987), decreased growth of fish (Sigler et al. 1984), and decreased predatory efficiency (Sweka and Hartman 2001). Benthic invertebrates tend to drift as turbidity increases (Runde and Hellenthal 2000, Shaw and Richardson 2001). Predatory salmonids also avoid highly turbid waters (Servizi and Martens 1992) and they do not benefit from increased drift associated with turbidity (Shaw and Richardson 2001) because sight distances and capture rates are reduced (Vogel and Beauchamp 1999). Servizi and Martens (1992) showed that coho salmon were relatively tolerant of low-turbidity suspended solids, but that behavioral responses match other studies when turbidity levels were considered.

Turbidity includes both organic and inorganic particles. The inorganic component of turbidity may be comprised of clay, silt, or other finely divided inorganic matter of less than 2 mm diameter (APHA et al. 1995). Plankton, microscopic organisms, and finely divided organic matter make up the organic component of turbidity. Generally speaking, the component of concern as it relates to physiological effects on fish and macroinvertebrates is the inorganic component.

Work on the effects of turbidity to aquatic fauna, especially salmonids, is extensive. Effects range from relatively benign indicators of stress to reduced growth and mortality (Table 1). Behavioral modification and secondary stress indicators occur at relatively low turbidity levels. Servizi and Martens (1992) noticed that blood sugar levels (a secondary indicator of stress) increased with turbidity at all levels tested and coughing increased significantly between 3 and 30 NTUs. Altered behavior, avoidance, and reduced feeding rates are generally noticed between 10 and 30 NTUs over the course of 24 hours. Reduced reaction distances are observed at even lower turbidities. A decrease in growth has been found in turbidities of 22 NTUs and reduced survival rates were seen in turbidities as low as 15 NTUs. Many of these studies were conducted in laboratory settings and/or with artificially induced turbidity. They mostly represent continuous (chronic) exposures. A turbidity of 30 NTU has been described as having a clarity such that when viewing a newspaper through a 6 inch column of water, the lines of print would be visible, but not legible.

Turbidity can affect primary producers by reducing light penetration and thus photosynthesis (Waters 1995). Lloyd (1987) concluded that in Alaska turbidities of 25 NTU or more could cause light extinction at too shallow a depth with an associated decrease in plant production, fish food, and fish. Modeling of a clear, shallow stream indicated that an increase of 5 NTU would decrease gross primary production by 3-13% while a 25 NTU increase would result in a 13-50% reduction. He also postulated that these levels of turbidity could be expected to interfere with sight feeding of fish, angler success, and aerial escapement surveys.

Table 1. Summary of effects on fish, periphyton, and invertebrates noted for turbidity ranges. Units of Nephelometric (NTU) and Jackson (JTU) turbidity units are roughly equivalent (U. S. EPA 1983a).

Effect	Organism	Turbidity range	Reference
Increased blood sugar levels	Juvenile coho	Linear correlation	Sevizi and Martens 1992
Increased coughing	Juvenile coho	3 - 30 NTU for 24 hours	Sevizi and Martens 1992
Altered behavior	Juvenile coho	10-60 NTU	Berg 1982; Berg and Northcote 1985
	Largemouth bass and green sunfish	14-16 JTU	Heimstra et al. 1969
Emigration/avoidance	Steelhead and coho	11-51 NTU	Sigler et al. 1984
	Juvenile coho and steelhead	22-265 NTU	Sigler 1980
	Juvenile coho	>37 NTU	Sevizi and Martens 1992
Reduced feeding rate	Juvenile coho	10-60 NTU	Berg 1982; Berg and Northcote 1985
	Brown trout	7.5 NTU	Bachman 1984
	Lahontan cutthroat trout and Lahontan redside shiner	3.5-25 NTU	Vinyard and Yuan 1996
Reduced reaction distance	Lake trout, rainbow trout, cutthroat trout	3.2 – 7.4 NTU	Vogel and Beauchamp 1999
	Brook trout	0 – 43 NTU	Sweka and Hartman 2001
Reduced growth	Juvenile coho and steelhead	22-113 NTU	Sigler 1980
	Juvenile coho and steelhead	as low as 25 NTU	Sigler et al. 1984
Reduced survival	Juvenile coho	15 – 27 JTU	Smith and Sykora 1976
Reduced primary production	Algae/periphyton	3 – 25 NTU	Lloyd et al. 1987
Reduced density	Benthic invertebrates	8.4 – 161 NTU	Quinn et al. 1992
Reduced feeding rate, food assimilation, and reproductive potential	*Daphnia pulex*	10 NTU	McCabe and O'Brien 1983

Both pelagic and benthic invertebrates are affected by turbidity. A turbidity level of 10 NTU caused significant declines in feeding rate, food assimilation, and reproductive potential of *Daphnia pulex* (McCabe and O'Brien 1983). In a New Zealand stream subjected to clay discharges from alluvial gold mining (range in mean of NTU from 8.4-161 following addition of clay), Quinn et al. (1992) found invertebrate densities were significantly lower at all downstream sites ranging from 9-45% (median 26%) of densities at matched upstream sites.

In addition to the periphyton, macroinvertebrate, and salmonid effects, warmwater fish are also affected by turbidity. Work on largemouth bass and green sunfish showed altered behavior at 14-16 JTU (Heimstra et al. 1969). In Georgia, the highest fish Index of Biotic Integrity (IBI) values were found in streams with low-flow turbidity values less than 6 NTU (Walters et al. 2001). IBI values were consistently lower in streams with low-flow turbidity values exceeding 8 NTU.

It is not uncommon for increased turbidity levels resulting from human activity to affect downstream aquatic life. From the above, effects of chronic exposure to increased turbidity are evident - reduced feeding, resulting in reduced growth if prolonged, and eventual avoidance. On the other hand there is evidence that short exposures to very high turbidities (100,000 ppm), have no lasting effect (Wallen 1951). A lack of response to episodes of increased sediment loading is not contradictory as tolerance to brief periods of high sediment levels is a trait essential to survival in an environment of spring freshets and capricious floods (Gammon 1970). Instream construction activities generate sediments in an amount that is unlikely to meet reasonable criteria that have been set according to effects of upland activities (Reid and Anderson 1998). Downstream of culvert removal activities in Idaho, turbidity levels peaked at 92 NTU above background though levels recovered to background often at night following cessation of construction activity, and at completion of the project (Wegner 1998). While brief spikes in turbidity may be benign, frequent episodes are not (Shaw and Richardson 2001).

2.2.2 Other states

Turbidity in Idaho should not be greater than 50 NTU instantaneous or 25 NTU for more than 10 consecutive days above baseline background (Idaho Department of Environmental Quality n.d.a.). This standard is similar to other state and province standards (Table 2). Most of the other entities also relate their standard to a baseline background except for Montana which relates its standard to a naturally occurring (natural background) turbidity level. Wyoming tiers its turbidity criteria by ecoregion. The Washington Department of Ecology in its TMDL for the Yakima River (Joy and Patterson 1997) set a turbidity target of 25 NTU for irrigation return drains and tributaries. Alaska's applicable water quality criterion for propagation of aquatic wildlife states that turbidity may not exceed 25 NTU above natural conditions. Several TMDLs approved in California specify a target of <= 20% above naturally occurring background (see Appendix C).

Alberta's turbidity guidelines for freshwater aquatic life include targets for both low flow (clear) and high flows, and turbid waters. The guideline for clear flow is a maximum increase of 8 NTU above background levels for any short-term exposure (e.g., 24-hour) and maximum increase of 2 NTU above background for long-term exposure (e.g., 24 hours to 30 days). For high flow or turbid waters, instantaneous increases should not exceed 8 NTU when background is 8-80 NTU, and no more than 10% of background when background is > 80 NTU (Alberta Environment 1999).

Eastern U.S. states have established standards for controlling erosion and sedimentation that can occur during disturbance of uplands (Keyes and Radcliffe 2002) and instream crossings (Reid and Anderson 1998). Examples of criteria for upland disturbances include: Alabama -

Table 2. Water quality standards related to sediment for states and provinces surrounding Idaho. Note that background refers to baseline background except for Montana.

State/ Province	Turbidity	Total Suspended Solids Or Settleable Solids	Intergravel Dissolved Oxygen	Remarks
Colorado				For embeddedness, surface sediments and sub-surface sediments: Attainment when – > 73% of reference, or > 58% of reference and biology > 50% of reference
Montana	varies according to stream classification A - no increase above naturally occurring turbidity A1 - no increase above naturally occurring turbidity except under short-term authorization B1 - no more than 5 NTU (instantaneous) above naturally occurring turbidity B2 & B3 - no more than 10 NTU (instantaneous) above naturally occurring turbidity C1 - no more than 5 NTU (instantaneous) above naturally occurring turbidity C2 & C3 - no more than 10 NTU (instantaneous) above naturally occurring turbidity I - no increase in naturally occurring turbidity which will impair beneficial uses	narrative only - no change above background which will, or is likely to, impair uses	For A-1, B-1, B-2, C-1, and C-2 classified waters, 1-day minimum (instantaneous) of 5.0 mg/l, 7-day mean >= 6.5 mg/l	Class A streams are used for drinking water Class B streams are suitable for drinking water B1 streams are coldwater streams B2 streams are marginally coldwater streams B3 streams are predominantly warmwater streams Class C streams are marginal for drinking water C1 streams are coldwater streams C2 streams are marginally coldwater streams C3 streams are predominantly warmwater streams Class I streams are presently impaired with goal of improving water quality to support uses

Table 2 (cont'd). Water quality standards related to sediment for states and provinces surrounding Idaho. Note that background refers to baseline background except for Montana.

State/ Province	Turbidity	Total Suspended Solids Or Settleable Solids	Intergravel Dissolved Oxygen	Remarks
Oregon	no more than a 10% cumulative increase relative to an immediately upstream control point	sediment has a narrative standard - not to exceed deposits deleterious to fish or aquatic life or injurious to public health	minimum spatial median of 6.0 mg/l for salmonid spawning streams	
Nevada	site specific for major water bodies based on the most restrictive beneficial use of the water body	TSS - 25 - 80 mg/l (instantaneous), generally coldwater 25 mg/l and warmwater 80 mg/l		Settleable Solids - narrative only - waters must be free of substances from controllable sources which settle in sufficient amounts to interfere with any beneficial use
Utah	varies according to stream classification Class 2A, 2B, 3A, & 3B watersheds - not to exceed 10 NTU (instantaneous) above background Class 3C & 3D watersheds - not to exceed 15 NTU (instantaneous) above background	narrative only - unlawful for any person to discharge or place any substance which produces undesirable physiological responses in desirable resident fish or aquatic life		Class 2A waters - protected for primary Class 2B waters - protected for secondary contact recreation Class 3A waters - protected for coldwater species of game fish and other cold water aquatic life Class 3B waters - protected for warmwater species of game fish and other warm water aquatic life Class 3C waters - protected for nongame fish and other aquatic life Class 3D waters - protected for waterfowl, shore birds, and other water-oriented wildlife not included above

Table 2 (cont'd). Water quality standards related to sediment for states and provinces surrounding Idaho. Note that background refers to baseline background except for Montana.

State/ Province	Turbidity	Total Suspended Solids Or Settleable Solids	Intergravel Dissolved Oxygen	Remarks
Washington	varies according to class of water body Class A A & A - not to exceed 5 NTU (instantaneous) over background if background is 50 NTU or less; if background is greater than 50 NTU cannot exceed a 10% increase (instantaneous) Class B & C - not to exceed 10 NTU (instantaneous) over background if background is 50 NTU or less; if background is greater than 50 NTU cannot exceed a 20% increase (instantaneous)	narrative only - no degradation which would interfere with or become injurious to existing beneficial uses		Class AA - extraordinary waters Class A - excellent waters Class B - good waters Class C - fair waters
Wyoming	varies according to stream classification Class 1& 2 watersheds with coldwater fisheries - not to exceed 10 NTU (instantaneous) above background Class 1& 2 watersheds with warmwater fisheries & Class 3 watersheds - not to exceed 15 NTU (instantaneous) above background	narrative only - no human-induced quantities which could result in significant degradation of habitat for aquatic life	For class 1, 2, and 3 waters, 1-day minimum (instantaneous) of 5.0 mg/l, 7-day mean >= 6 5 mg/l	Class 1 watersheds - outstanding waters Class 2 watersheds - non-class 1 watersheds that support game fish Class 3 watersheds - non-class 1 watersheds that support non-game fish
British Columbia	varies according to water use aquatic life - not to exceed 5 NTU (instantaneous) over background if background is 50 NTU or less; if background is greater than 50 NTU, cannot exceed a 10% increase (instantaneous)	varies according to water use aquatic life - not to exceed 10 mg/l (instantaneous) if background is 100 mg/l or less; if background is greater than 100 mg/l, cannot exceed a 10% increase (instantaneous)	instantaneous minimum of 6	Light Penetration: average minimum Secchi disk >= 1.5 m, taken over 30-day period (at least 5 samples) Subsurface Sediments: No significant accumulation by weight of particles <3mm

background + 50 NTU; Georgia - background + 10 NTU for trout streams, background + 25 NTU for non-trout streams; Florida - background + 29 NTU; North Carolina - Background + 10 NTU for trout streams, background + 50 NTU for non-trout streams; South Carolina - background + 10%; Tennessee - background + 50 NTU; and, Vermont - background + 10 NTU. Separate criteria for permitted instream activities consider a mixing zone or time period which are exempt from turbidity limitations (Table 3).

Eastern states have established standards for controlling erosion and sedimentation (Table 3) that can occur during disturbance of uplands (Keyes and Radcliffe 2002) and instream crossings (Reid and Anderson 1998). The instream criteria for permitted activities consider a mixing zone or time period which are exempt from turbidity limitations.

Table 3. Examples of turbidity criteria that account for upland and instream disturbances.

State	Turbidity restriction
Alabama	Upland: Background + 50 NTU
Florida	Upland: Background + 29 NTU Instream: Not to exceed 29 NTUs outside the 800 meter downstream mixing zone. Within the mixing zone, not to exceed 1000 NTUs for 12 consecutive hours, or 3000 NTUs for 3 consecutive hours.
Georgia	Upland: Background + 10 NTU for trout streams, background + 25 NTU for non-trout streams Instream: Post construction levels are not to exceed 20 NTUs
New Hampshire	Instream: Not to exceed 10 NTUs above background outside of a mixing zone. For watercourses greater than 10 ft wide, the mixing zone is 1000 ft. For those less than 10 ft wide, it is 500 ft.
New York	Instream: Not to exceed 10 NTUs outside of a 300 ft mixing zone.
North Carolina	Upland: Background + 10 NTU for trout streams, background + 50 NTU for non-trout streams
South Carolina	Upland: Background + 10%;
Tennessee	Upland: Background + 50 NTU
Vermont	Upland: Background + 10 NTU

2.2.3 Recommendation

We affirm the current Idaho water quality standard (Water Quality Standards and Wastewater Treatment Requirements 58.01.02.250.02.e) to protect cold water aquatic life, turbidity below any applicable mixing zone should not be greater than 50 NTU instantaneous or 25 NTU for more than 10 consecutive days above baseline background (Idaho Department of Environmental Quality n.d.a.). We feel that this standard is most applicable to periods of high flow whether during the time of annual runoff (i.e., spring for most Idaho streams) or episodic storm events.

Some evidence suggests that detrimental effects to biota can occur with turbidity as low as 10 NTU. Therefore, we recommend that chronic turbidity not exceed 10 NTU at summer base flow.

2.3 Total Suspended Solids and Suspended Sediment

Total suspended solids (TSS) and suspended sediment are sampled and analyzed differently, and therefore often give different results for the same waterbody. The target addressed here regards TSS, not suspended sediment. Protocols for measuring TSS as recommended by the U.S. EPA are included in Appendix B, where a comparison to the suspended sediment analytical method (of the USGS) is also given. Direct measurement of TSS is limited by standard equipment to particle sizes of 2.0 mm or less. This is smaller than the range of fines considered in surface or subsurface sediments (up to 6.4 mm), but is more representative of the particles actually found in suspension. Larkin and Slaney (1996) found that deposition in sediment traps was highly correlated with suspended sediment, suggesting that total suspended solids could be related to surface and subsurface sedimentation measures.

2.3.1 Biological background

Much information is available on the effects of total suspended solids (TSS) and suspended sediment on aquatic fauna, particularly fish. Direct acute effects of suspended sediment on adult fish may not be observed until concentrations reach thousands to tens of thousands of mg/L (Waters 1995, Everest et al. 1987, Newport and Moyer 1974, Wallen 1951, Lake and Hinch 1999). However, the effects of sediment are dependent on the duration (Newcombe and MacDonald 1991) and frequency (Shaw and Richardson 2001) of exposure as much as concentration, so concentration measures must be considered over time to be meaningful. Most researchers report greater sensitivity of younger fish, particularly sac fry, with increased mortality evident at concentrations on the order of a thousand mg/L or less (Anderson et al. 1996, Newcombe and MacDonald 1991). Responses to lower concentrations are largely behavioral (avoidance, reduced feeding, coughing, seeking refuge) which can lead to reduced growth if exposure is frequent or persistent. As noted by Gammon (1970), loss of fisheries due to avoidance or failed reproduction is as real as direct mortality, the cause makes little difference to the fisherman (or the fish community).

A significant relationship has been documented between suspended sediment duration (concentration x days) and percent egg-to-fry survival of rainbow trout (Slaney et al. 1977). Survival dropped below 30% at about 1000 mg/L-day, and approached zero at about 2000 mg/L-day. The relationship between suspended sediment duration and percent fines by weight in the gravel of simulated redds was also found to be significant. Arctic grayling sac fry exposed to suspended sediment averaging 750 mg/L over a 96-hour period experienced nearly four times the mortality of a control group exposed to suspended sediment averaging 105 mg/L (Reynolds et al. 1989). Bachmann (1958) observed a cessation of feeding in cutthroat trout exposed to a suspended sediment concentration of 35 mg/L over a 2-hour period.

In a study of sub-lethal responses to low-turbidity (large particle) suspended sediments, blood sugar levels (a secondary indicator of stress) were found to increase at low levels of short duration (Servizi and Martens 1992). Coughing frequency increased significantly between 2 and 240 mg/L in a 24-hour exposure. Avoidance behavior climbed steadily with increasing TSS, but was inconsistent until levels reached more than 4000 mg/L in 96 hours. These relatively high levels of suspended solids may be attributed to the composition of the particles (240 mg/L was equivalent to approximately 30 NTU). Thus, higher concentrations of larger suspended sediments may not be as disruptive of normal salmonid behavior as are smaller suspended sediments associated with higher turbidities. Fish IBI values were consistently low in Georgia streams with low-flow TSS values exceeding 8 mg/L (Walters et al. 2001). The highest IBI values were found in streams with low-flow TSS values less than 6 mg/L.

Human activities in and around waterbodies often result in varied sediment input during the active phase of a project. Stream restoration activities in bull trout habitat of the Middle Kootenai River (MT) were monitored for TSS before, during, and after instream disturbances for culvert removals and road repair (Wegner 1998). Instream disturbance had an obvious effect on downstream TSS values. With pre-construction values below 20 mg/L, peak values during the construction phase reached as high as 1,574 mg/L. Return to pre-construction levels took two to three days after construction activity stopped. Another example described by Wegner (1998) showed that TSS values never peaked above 16 mg/L when measured 1000 feet below the construction activity. Incidentally, these instream activities were considered necessary for the long-term rehabilitation of bull trout habitat, which, from the perspective of USFS hydrologists, outweighed any short-term impacts. Wegner found that variability in sediment production could be partially attributed to the diligence of equipment operators in reducing sediment sources during disturbances.

Newcombe and Jensen (1996) developed concentration:duration charts based on the effects (e.g., behavioral, sublethal, para-lethal, lethal) of the two parameters on the life stages of various fish. Miller used the Newcombe and Jensen charts in his development of recommendations for suspended sediment targets in the lower Boise River (IDEQ 1998a). Miller's TSS targets of geometric means not to exceed a 60-day chronic exposure of 50 mg/L or 14-day acute exposure of 80 mg/L were adopted for the lower Boise River TMDL.

Discretion must be used when applying Newcombe and Jensen's models. For the models, Severity of Effect was categorized into nil (< behavioral or 0); nil or behavioral (< sublethal or 3); and nil, behavioral, or sublethal (< lethal or 8). The duration which met the Severity of Effect at various concentrations was then calculated using the model formulas. Table 4 shows durations for sub-lethal effects at various concentrations. Concentrations as low as 5 mg/L for only 1 day would have behavioral effects on all species and life stages according to the models. This result appears to be somewhat inconsistent with other work (e.g., EIFAC 1964).

Table 4. Duration (days) for a sub-lethal Severity of Effect for concentrations (mg/L) of suspended sediment based on models from Newcombe and Jensen (1996). Behavioral effects were predicted to occur in less than 1 day at all concentrations (not shown).

	Duration[1]				
Suspended Sediment Concentration	Salmonids			Salmonids & Non-salmonids	Non-salmonids
	Juveniles & Adults	Adults	Juveniles	Eggs & Larvae	Adults
5	541	1841	252	1	5
10	233	613	124	1	4
25	76	143	49	1	3
50	33	48	24	1	2
80	19	23	15	1	2
100	14	16	12	1	2

[1]Duration (days)=(EXP((Effect-a-(c*LN(SS))/b))/24

Information is not quite as abundant on the effects of suspended sediment on macroinvertebrates. Rosenberg and Wiens (1978) exposed benthic invertebrates to 8 mg/L of suspended sediment for 5 hours and observed increased rate of drift. They found that invertebrates most sensitive to sediment, i.e., those species which drifted almost immediately after the sediment addition, included important salmonid prey (Plecoptera and Ephemeroptera). Populations of Ephemeroptera disappeared when exposed to greater than 29 mg/L of suspended sediment for 30 days (M. P. Vivier, personal communication in Alabaster and Lloyd [1982]). Macroinvertebrate drift tends to increase with longer repeated pulses (Shaw and Richardson 2001) and with smaller particle sizes (Runde and Hellenthal 2000). The filter feeding zooplankton *Daphnia pulex* displayed a reduced capacity to assimilate food when exposed to 24 mg/L of suspended sediment for only 15 minutes (McCabe and O'Brien 1983).

Higher levels of total suspended solids affect primary production, not only by reducing light penetration but also through abrasion. Lewis (1973) observed severe abrasive damage to the leaves of the aquatic moss *Eurhynchium riparioides* after 3 weeks of exposure to 100 mg/L of coal-dust.

Several groups have categorized concentrations of total suspended solids based on their effect on the aquatic environment, primarily fish (Table 5). The European Inland Fisheries Advisory Commission (EIFAC 1964) in their review of suspended solids in relation to fisheries concluded that concentrations less than 25 ppm have no harmful effect on fisheries; concentrations of 25-80 ppm will have some effect but it is possible to maintain good to moderate fisheries; concentrations of 80-400 ppm are unlikely to support good fisheries; and, concentrations greater than 400 ppm will at best result in poor fisheries. Gammon (1970) felt that the suspended solids criteria proposed by EIFAC may be too liberal for fish populations in the U. S. (Lloyd 1987). Others who agreed with EIFAC proposed criteria for high (0-25 mg/L) and moderate (26-80 mg/L) protection include Alabaster (1972), NAS and NAE (1973), and Alabaster and Lloyd (1980). Newport and Moyer (1974) recommended high protection at 0-25 mg/L and moderate protection at 26-100 mg/L. Wilber (1969, 1983) was slightly more liberal on high protection at 0-30 mg/L and moderate protection at 30-85 mg/L. Hill (1974) was much more conservative recommending a high protection range of 0-10 mg/L as was DFO (1983) in their recommendation of 0 mg/L for high protection. DFO also proposed a limitation of 1-100 mg/L for moderate protection. The U. S. Environmental Protection Agency (Mills et al. 1985) has classified impairment of aquatic habitat or organisms by TSS as: concentrations less than 10 mg/L - improbable; concentrations greater than 10 mg/L and less than 100 mg/L - potential; and concentrations greater than 100 mg/L - probable. Suspended sediment effects linked with high, moderate, or low habitat conditions for endangered species were developed by Clearwater and Nez Perce National Forests and Cottonwood (Idaho) area BLM (Matrix 1998). High levels of habitat conditions on these federal lands were associated with suspended sediment levels >= 25 mg/L for up to 10 days and >= 80 mg/L for up to 5 days in a year. Habitat conditions were low with >= 25 mg/L for more than 31 days or >= 80 mg/L for more than 11 days in a year. Intermediate levels were considered moderate habitat conditions.

2.3.2 Other States

No state or province has a standard or target for suspended sediment but several address total suspended solids (Table 2). Nevada has a standard of 25-80 mg/L with coldwater streams generally using the 25 mg/L standard and warmwater streams generally having an 80 mg/L standard (Adele Basham, Nevada Division of Environmental Protection, personal communication). Utah in their water quality management plan for the lower Bear River (Ecosystem Research Institute 1995) adopted two TSS targets - 35 mg/L or 90 mg/L - based on a 75th percentile concentration from historic TSS sampling. The Washington Department of Ecology in its TMDL for the Yakima River (Joy and Patterson 1997) set a TSS target of 56 mg/L for irrigation return drains and tributaries. For the Umatilla River (OR) sediment TMDL the target was set at <= 80 mg/L or the TSS value locally calibrated to a turbidity of 30 NTU (ODEQ 2001). In the Deep Creek (MT) TMDL, the target for TSS was related to discharge, where the slope of the regression of TSS on discharge was expected to be 0.26 or better (Endicott and McMahon 1996). Both the Gualala River and Trinity River TMDLs (CA) specified only decreasing trends in suspended sediments (U.S. EPA 2001a, U.S. EPA 2001b). Alberta water quality guidelines recommend suspended solids not exceed 10 mg/L above background for both acute and chronic conditions (Alberta Environment 1999).

Table 5. Suggested levels of TSS (mg/L) for categorizing fish habitat conditions.

Habitat Effects			
Least effects, High protection, Best conditions	**Some effects, Moderate protection, Moderate conditions**	**Definite effects, Low protection, Poor conditions**	**Citation**
< 25	25-80	>80	EIFAC 1964
< 25	26-80	>80	Alabaster 1972, NAS and NAE 1973, and Alabaster and Lloyd 1980
< 25	26-100	>100	Newport and Moyer 1974
<30	30-85	>83	Wilber 1969, 1983
<10			Hill 1974
0	1-100	>100	DFO 1983
<10	10 - 100	>100	Mills et al. 1985
>= 25 for <= 10 days and >= 80 for <=5 days in a year	>=25 for 11 - 30 days and >=80 for <=10 days in a year	>= 25 for > 31 days or >= 80 for >=11 days in a year	Matrix 1998

In British Columbia, the ambient water quality guidelines state that expectations for suspended sediments should be related to background conditions. When background levels are at or below 25 mg/L, induced suspended sediment concentrations should not exceed background levels by more than 25 mg/L during any 24-hour period (hourly sampling preferred) or by more than 5 mg/L for inputs that last between 24 hours and 30 days (daily sampling preferred). With turbid background conditions (25 - 250 mg/L), induced suspended sediment concentrations should not exceed background levels by more than 25 mg/L at any time. When background exceeds 250 mg/L, suspended sediments should not be increased by more than 10% of the measured background level at any one time.

2.3.3 Recommendation

We propose no specific targets for total suspended solids. The effects of sediment are dependent on concentration and duration of exposure. We recognize that there can be effects on biota at concentrations of total suspended solids above 25 mg/L, and many papers recommend a long-term exposure of not greater than 80 mg/l to maintain a good fish community (EIFAC 1964, NAS and NAE 1973). Any recommendations regarding concentration or duration would be difficult to generalize for the entire state because of differences in seasonal flows, episodic flows, geology, and hydrography. Site-, season-, and flow-specific targets should be developed using data collected from appropriate reference streams or upstream sites. To allow for spikes in TSS that may occur with spring runoff or episodic storm events, targets should represent averages per unit time (e.g., Total Suspended Solids not to exceed an average of 50 mg/L over a 28-day period). The TMDL writer would be well advised to consider these effects when establishing TSS targets.

3. Streambed Measures

The proportion of fine sediments among stream substrate components can affect salmonids in several ways. Spawning trout may have more difficulty building redds if sufficient quantity of appropriate sized gravel has been displaced, cemented, or buried by fine sediment deposits. When gravels are cleaned of fine sediments and eggs deposited, later intrusion of fine sediments into the redd can reduce egg and alevin survival. If gravels become clogged with fine sediments permeability is reduced and the resulting decrease in flow provides less oxygen to and removes less waste from incubating eggs. Fine sediments that clog interstitial spaces of a redd can physically block emergence of alevins. In addition, substrates that have interstitial spaces filled with fine sediments are poorer habitat for newly emerged salmonid fry and for invertebrate prey.

Surface fines and embeddedness are similar ways of measuring the suitability of stream substrates for invertebrate and salmonid habitation. Embeddedness measures the degree to which cobbles and large gravels are buried because of fine sediment deposition. Surface fines describe the percentage of streambed area with exposed fine sediments. Streambeds can be partially embedded without having fines exposed. There also can be exposed fines in some part of the streambed without embeddedness in others. The measures are related, but are not directly comparable. With either measure it is important to assess areas used by fish for spawning, e.g. riffles and pool tail outs.

The Wolman pebble count method yields not only percent surface fines, but also allows calculation of the median substrate size (d50), which has been used as a sediment target. The number of counts that represent fine sediment influence the median of the distribution, but other variables that are not related to fine sediment supply also determine the d50, such as underlying geology. A target regarding d50 may best be left as “improving trends”, though several TMDLs in California specify a threshold for the mean (>=69 mm) and minimum (>=37 mm) for multiple samples (see Appendix C). The geometric mean particle size of Yellowstone cutthroat trout spawning areas in Pine Creek, Idaho averaged 16.6 mm (Thurow and King 1994).

While surface fines and embeddedness are more apparent to the human observer, and thus easy to measure, it is subsurface or depth fines which really alter suitability of spawning habitats. The amount of subsurface fine sediments as measured at the head of riffles in likely spawning areas can be an indication of redd site suitability, conditions for egg survival and alevin emergence in the constructed redd, and habitat quality for emerged fry and prey. However, redd construction can actually change the ambient streambed by removing fine sediments and re-shaping the topography to induce water infiltration (Kondolf 2000). Subsurface sediments are measured by driving a metal cylinder into the streambed, carefully removing the sediment, and working the sample through a series of sieves to determine the particle size distribution. Exacting measurement requires in situ freezing of the core to assure complete removal.

Trying to relate surface fines or embeddedness to subsurface fines is tenuous at best. Platts et al. (1989) on the South Fork Salmon River found a significant but weak relationship between surface and subsurface fines. Nelson et al. (1997) found that relationships between Wolman pebble count estimates and estimates from core samples (i.e., depth fines) were poor.

The Riffle Stability Index (RSI) indicates the relative percentage of the streambed that is mobile during channel forming flows. Bed mobility affects habitat stability for invertebrates, scouring of redd sites, and formation or filling of pools. It is more related to pool quality and abundance than it is to fine sediments. In a survey of B-channel streams of the St. Joe River drainage in northern Idaho, reaches with lower RSI values had greater residual pool volume (Cross and Everest 1992). Pool habitat provides critical refuge for juvenile and adult salmonids.

3.1 Embeddedness

3.1.1 Biological background

Embedded substrates lack the interstitial spaces that allow intergravel flow and provide habitat and cover for benthic invertebrates and juvenile fish. The value of measuring embeddedness varies according to area. Embeddedness targets are applicable primarily to riffles in cobble-bedded streams, though interstitial spaces in pool and marginal substrates can also provide valuable habitat for juvenile salmonids. In a study of habitat restoration in a highly sedimented Idaho stream, Hillman et al. (1987) found that interstitial spaces among cobbles may be essential winter habitat for juvenile chinook salmon. When large cobble was added to an otherwise embedded stream, juvenile populations increased. When that same cobble became embedded, the population decreased.

Information relating embeddedness levels to effects on aquatic fauna is limited. Embeddedness in the range of 67% caused changes in the macroinvertebrate fauna (Bjornn et al. 1977). Nelson et al. (1997) found an average embeddedness of 35% in natural streams in granitic watersheds (i.e., South Fork Salmon River, Idaho). Based on their review of existing data, Chapman and McLeod (1987) were unwilling to generalize on the effects of embeddedness level of surface fines and salmonid rearing densities. They did conclude that abundance of insects declines at an embeddedness level of about 2/3 to 3/4. They go on to say, however, that embeddedness levels this high would probably violate spatial needs of overwintering fish for sediment-free interstices.

The Payette and Boise Forest Plan (cited by Nelson et al. 1997) specifies that embeddedness conditions should be demonstrably improving. It also sets thresholds for streams in the South Fork Salmon River watershed that are contingent on 1988 sediment conditions. For locations with 1988 embeddedness measured at greater than 32%, five year average embeddedness is not to exceed 32%, with no single year exceeding 37%. For locations with 1988 embeddedness measured at greater than 27%and less than 32%, five-year average embeddedness is not to exceed 27%, with no single year exceeding 29%. Nelson et al. (1997) found these thresholds to be too restrictive in light of natural embeddedness conditions, which were 35% embedded on average in the South Fork Salmon River. They suggested embeddedness targets and free matrix percentage appropriate for their findings (Table 6).

Table 6. Cobble embeddedness and free matrix criteria proposed by Nelson et al. (1997) for streams in granitic Idaho watersheds. Trend data must be based on a minimum of 3 years of data. Criteria 1 – 3 are always applicable. Only one of criteria 4 – 7 are applied, depending on starting conditions and the parameter being measured.

1	Demonstrated improvement in cobble embeddedness or establishment of a significant downward trend using either measured or predicted cobble embeddedness (but not both);		
2	Measured or predicted embeddedness levels consistently at or near 50% should be considered unacceptable;		
3	Demonstrated improvement in percent free particles from 30-hoop free matrix measurements or establishment of a significant upward trend;		
	Starting conditions	3 - 5 year average	No more than 2 of any 5 years
4	< 30% embedded	<30%	>35%
5	30 – 40% embedded	<40%	>45%
6	>20% free matrix particles	>20%	<15%
7	10 - 20% free matrix particles	>15%	<10%

Levels of embeddedness linked with high, moderate, or low habitat conditions for endangered species were determined for Clearwater and Nez Perce National Forests and Cottonwood (Idaho) area BLM (USDA-FS et al. 1998). High levels of habitat conditions were associated with embeddedness < 20%. At > 30%, habitat conditions were considered low. Intermediate embeddedness was considered a moderate habitat condition.

3.1.2 Collection Methods

A high degree of variability can result from embeddedness measures that are collected with different methods, calculations, or observers. Sylte (2002) and Kramer (1989) suggest that embeddedness values within a single method are sensitive to substrate size. Sylte also found that the embeddedness method used by Nelson et al. (2002a) and described below was more consistent and closer to visual estimates than other methods of calculating embeddedness. Both Nelson et al. (2002a) and Sylte (2002) found correlations between embeddedness values and free matrix particle counts. Nelson et al. went on to explain that the free matrix counts were more reliable, more representative of the entire stream reach, and could be used to predict embeddedness.

Cobble embeddedness: Embeddedness was measured within a 60 cm hoop randomly located in an area of potential spawning gravel with a water velocity between 24 and 67 cm/s and depth between 15 and 45 cm. Within the hoop, 100 particles were measured (extra hoops were used if 100 particles were not available in the first hoop). Two measurements per particle were recorded: the total height of the particle and the depth of the particle below the plane of embeddedness. Percent embeddedness for each particle is calculated as the embedded depth over the total particle height. Percent embeddedness for the sample is the average percent embeddedness.

Free matrix: The free matrix (those particles entirely unembedded) were counted within 30 randomly distributed 60 cm hoops. Embedded particles were then counted and tabulated separately. Only particles between 45 and 300 mm were counted, and only hoops in less than 60 cm of water were counted. The number of free particles divided by total particles is the percent free matrix.

3.1.3 Other states

Several approved TMDLs in California have a target for riffle embeddedness that is <= 25% or a decreasing trend toward 25% (see Appendix C). While the 25% figure is universal in the TMDLs that consider embeddedness, there is little supporting evidence for this threshold. The fact that an improving trend is also acceptable shows that the threshold was loosely interpreted.

New Mexico has established embeddedness thresholds for aquatic life use support. Streambeds that are less than 33% embedded represent fully supporting sediment conditions and are not compared to reference conditions. For streams with greater than 33% embeddedness, support is defined in comparison to reference conditions. Embeddedness values less than 27% greater than reference values are supporting and embeddedness values more than 40% greater than reference conditions are non-supporting (NMED 2002).

3.1.4 Recommendation

We cannot recommend a specific target for embeddedness of streambed cobble by fine (< 6.35 mm) material. IDEQ (1991) has previously recommended targets in the South Fork Salmon River TMDL: that is, for those streams with cobble embeddedness less than 32%, maintain the existing embeddedness level; for those streams that exceed the 32% threshold, reduce cobble embeddedness to a 5-year mean not to exceed 32% with no individual year to exceed 37%. Tim Burton (Boise National Forest, personal communication) also questioned trying to establish any universal embeddedness criteria, although he did feel that targets could be established for interstitial space using the Interstitial Space Index (ISI) method (Burton and Harvey 1990). Burton suggested that reference streams be used for establishing embeddedness, as measured by the procedure suggested by Burton and Harvey (1990), criteria within strata. For southern Idaho, streams would best be stratified according to geology (e.g., batholithic vs. metamorphic), size, and stream gradient.

3.2 Surface Sediment

3.2.1 Biological background

Salmonids prefer mid-sized substrates with interstitial cover to either fine sediment or boulders and bedrock. Ephemeroptera, Plecoptera, and Trichoptera (important fish-food organisms) also respond positively to gravel and cobble substrates (Waters 1995). However, the percent coverage of fine sediments by area and the effects on salmonids and invertebrates have not been extensively investigated. Several examples can be found that use a median or geometric mean particle size as an indicator of suitable habitat conditions (see Appendix C). The percent fines are integral to the particle size distribution, but Nelson et al. (1997) found no relationship between percent fines and median particle size. Some authors have argued against percent fines suggesting instead that geometric mean (Platts et al. 1979) or fredle index (Lotspeich and Everest 1981, Beschta 1982) be used. Richards and Bacon (1994) in their longitudinal study of Bear Valley Creek, Idaho, found stream size influenced macroinvertebrate colonization of the streambed surface more than fine sediment accumulation. Surface fines may be most useful in trend analysis.

Hill et al. (2000) found that percent fines (< 2 mm) negatively correlated with periphyton biomass in mid-Atlantic streams. In a study of 562 streams in four northwestern states, Raylea et al. (2000) found that changes in invertebrate communities (especially % Ephemeroptera, Plecoptera, Trichoptera [EPT]) occur as fine sediments (<= 2 mm) increase above 20% coverage by area. In an analysis of data from 279 stream sites in Idaho, Mebane (2001) found that higher levels of surface sediment less than 6.0 mm negatively affected EPT taxa and salmonid and sculpin fish species. Significant ($p < 0.05$) inverse relationships between number of EPT taxa and percentage of fine sediment measured across both bankfull and instream channel widths were found. More age classes of salmonids and sculpins were significantly ($p < 0.05$) associated with less instream fine sediments. Multiple age classes of both salmonids and sculpins were uncommon where average instream surface fines were greater than 30%, and nearly absent above 40%. Zweig et al. (2001) in their work on four Missouri streams determined that taxa richness significantly linearly decreased with increasing deposited sediment in 3 of 4 streams (over a range of 0 to 100% deposited sediments). Density, Ephemeroptera, Plecoptera, Trichoptera (EPT) richness, and EPT density were significantly negatively correlated with deposited sediment across all four streams. Taxa richness and EPT/Chironomidae richness were significantly negatively correlated in three streams.

A relationship exists between channel morphology and the expected sediment composition in a well adjusted or dynamically equilibrated channel. Overton et al. (1995) summarized sediment monitoring in the Salmon River basin, Idaho, and found that natural conditions for surface sediment averaged 25% in A-channels (SD = 23), 23% in B-channels (SD = 21), and 34% in C-channels SD = 25). Overall mean for all reaches equaled 26%with a standard deviation of 22. Mebane (2001) agreed with Overton et al. regarding natural surface sediment coverage. Percent surface fines (particles < 6 mm) were interpreted as indicating high, moderate, or low habitat conditions with respect to endangered species determinations in the Clearwater and Nez Perce National Forests and Cottonwood (Idaho) area BLM lands (USDA-FS et al. 1998). High levels of habitat conditions were associated with surface fines <= 10% in A- and B-channels and <= 20% in C- and E-channels. At >= 21% in A- and B-channels or >= 31% in C- and E-channels, habitat conditions were considered low. Intermediate sediment coverages were considered moderate habitat conditions. Surface fine sediment levels have been recommended by the Forest Service and Bureau of Land Management in their draft Environmental Impact Statement for the Upper Columbia River Basin (Interior Columbia Basin Ecosystem Management Project 1997). Their recommendations are stratified by channel type and watershed geology (Table 7).

Table 7. Surface fine sediment (< 6.0 mm) levels developed by the Forest Service and Bureau of Land Management for the Upper Columbia River Basin. In metamorphic C channels, fine sediment levels were to be established by local field units.

	Geologic Type		
Channel Type	**Plutonic**	**Volcanic**	**Metamorphic**
A	26	25	14
B	23	27	16
C	37	17	no data

In chinook salmon and steelhead trout spawning areas of the South Fork Salmon River (Idaho), surface and subsurface fine sediment (< 4.75 mm) accumulations were monitored for a 20-year period (Platts et al. 1989). The period began with a logging moratorium imposed because of detrimental logging activity, followed by streambed recovery, and resumption of limited logging activity. In the worst condition (1966), surface sediments covered as much as 46% of the stream area. By 1985, surface sediments averaged 19.7% of the spawning area and further recovery seemed possible.

3.2.2 Other states

Many states have general narrative standards that do not allow any activity which would result in the degradation of beneficial uses. The draft South Steens TMDL in Oregon references objectives in a water quality management plan developed by the Bureau of Land Management, one of which calls for a “downward trend” in “percent of silt and sand on substrate” with an eventual goal of 20% or less (ODEQ 1998). The Upper Grande Ronde River (Northeast Oregon) Sub-basin TMDL specified a target of 20% or less of the streambed area covered in fine sediments (ODEQ 2000 citing the PACFISH target). The Deep Creek TMDL in Montana, although not setting a surface fines target, does suggest surface fines monitoring through Wolman pebble counts (Endicott and McMahon 1996).

New Mexico has established surface sediment thresholds for aquatic life use support. Streambeds that have less than 20% fines (< 2 mm, by pebble count) are fully supporting. For streams with greater than 20% fines, support is defined in comparison to reference conditions. Percent fines values less than 27% greater than reference values are supporting and percent fines values more than 40% greater than reference conditions are non-supporting (NMED 2002).

3.2.3 Recommendation

Despite the congruence of the work of Overton et al. (1995) and Mebane (2001), we cannot recommend a specific target for surface sediment (i.e., surface fines). Chapman and McLeod (1987) found no functional predictors that would serve in evaluating quantitative effects of surface sediment on the natural incubation, rearing, or wintering phases of salmonids in the northern Rocky Mountains. Tim Burton (Boise National Forest, personal communication) agreed that establishing a target for surface sediment would be difficult. He did maintain that surface sediment information (e.g., Wolman pebble count) can be used to monitor trends. Burton pointed out that the Wolman pebble count, in addition to producing the percent surface fines, also allows for an estimate of median particle size. Potyondy and Hardy (1994) found pebble counts useful in assessing the effect of forest fires on fine sediment in streams of the Boise River drainage. Furthermore, the Payette and Boise National Forests have had success using the 30 hoop free matrix procedure (Nelson et al. 1997) for surface sediment in the granitic watersheds of the South Fork Salmon River, Idaho.

3.3 Subsurface Sediment

3.3.1 Biological background

Information on the biological effects of subsurface sediment varies according to the size of sediment and geographic area of concern. Some of the variability is reduced by standardizing the habitat and stream types (e.g., Rosgen [1994] level II) sampled. Subsurface sediment targets are most applicable in riffles and spawning areas in streams with gravel/cobble/boulder streambeds.

Excessive subsurface fines have detrimental effects on salmonid and invertebrate habitat suitability and redd conditions. The target for subsurface sediments is supported by studies of salmonid embryo survival rates in redds with varying fine sediment composition. The laboratory and *in situ* redd studies must be carefully applied such that expected redd conditions can be deduced from ambient streambed conditions. A comparison of ambient streambed subsurface fines to substrate composition in adjacent redds was made by Kondolf (2000), who found that redds typically had one-third less fine sediment than the adjacent streambed throughout the incubation period. Applying results of laboratory studies of redd sediment composition for predicting egg survival and fry emergence in natural conditions should take the gravel cleaning actions of spawning into account or be used only to detect trends or ranks of condition (not numerically absolute conditions).

Other studies on sediment and salmonid survival abound. Hall (1986) found survival (eyed egg to emergence) of coho, chinook, and chum salmon to be only 7-10% in gravel mixtures made up of 10% fines < 0.85 mm as compared to 50-75% survival in gravel mixtures with no fines < 0.85 mm. Reiser and White (1988) observed little survival of steelhead and chinook salmon eggs beyond 10-20% fines < 0.84 mm. In a laboratory study, fry survival declined significantly when fines < 0.25 mm in diameter approached 5% of the substrate in the egg pocket of artificial trout redds (Bjornn et al. 1998). In the Kootenai National Forest (MT), numbers of bull trout redds were compared to percent subsurface fines (Wegner 1998, 2003a). The numbers of redds were apparently negatively related to percent subsurface fines in spawning areas, though the comparisons were not statistically rigorous and another report showed ambiguous response to slight changes (Wegner 2003b). Based on Burton et al. (1990), a 27% target for subsurface sediment (< 6.5mm) would be applicable to central and southern Idaho.

In a study of Yellowstone cutthroat trout, Thurow and King (1994) described redd siting and substrate characteristics, and tested the effect of habitat conditions on the completed redds in Pine Creek, Idaho. They found that the spawned sites contained particles up to 100 mm, though

most were less than 32 mm, 20% were less than 6.35 mm, and 5% were less than 0.85 mm. Results from Nelson et al. (2002b) showed that in important spawning areas of the Payette and Boise National Forests, smaller fines (< 0.85 mm) consistently represented less than 10% of the core samples. With the exception of one site that had been severely degraded by historic mining activities, the percentage of smaller fines averaged approximately 5% over a 25-year monitoring period. However, in these regions of restricted logging, the percentages of larger fines (< 6.3 mm) from the same sample locations were routinely found to be near 30%. While these are not pristine watersheds, they have been managed for sediment reduction since the 1960s (with a 20-year logging moratorium followed by limited logging).
Upon testing a fisheries sediment response model in the Clearwater River drainage, Nelson and Platts (1988) recommended that three tiers of subsurface sediment conditions be delineated. At < 20% subsurface fines (< 6.3 mm), the conditions are considered good for embryo incubation and survival. From 20 to 27%, conditions are marginal and influences of other environmental factors cause variable survivability. Above 27% subsurface fines, survivability was considered improbable.

Federal land management agencies (Forest Service and BLM) have developed guidelines specific to their local conditions. Evaluation of the effects of subsurface sediment on habitat conditions on Clearwater and Nez Perce National Forests and Cottonwood (Idaho) area BLM lands showed high levels of habitat conditions associated with < 20% fines (<= 6 mm) at depth, while at > 25% fines, habitat conditions were considered low (USDA-FS et al. 1998).

On the Salmon-Challis National Forest, the Forest Plan for the Challis Zone sets a threshold of 30% fines < 6.3 mm such that activities which would result in the exceedance of the threshold are not allowed (Challis National Forest 1987). The Forest Plan for the Salmon Zone has standards of 20% fines by depth for streams supporting anadromous fish and 28.7% fines by depth for streams supporting only resident salmonid populations (Salmon National Forest 1987). Recent thinking on the Salmon and Challis National Forest bases subsurface sediment standards on watershed geology (Betsy Rieffenberger, Salmon and Challis National Forest, personal communication). In quartzite drainages, the Forest classifies streams in good condition as having subsurface sediment < 20%, streams in fair condition have 20-25% fines, and streams in poor condition will have over 25% fines. In granitic, volcanic, and sedimentary drainages, streams in good, fair, and poor condition will have < 25%, 25-30%, and > 30% fines, respectively.

Studies documenting effects of fine sediment on macroinvertebrates are limited. A field study of benthic invertebrate colonization of trays with varying percentages of fine sediments showed significant (though weak) responses to increases in sediment from 0 to 30% (Angradi 1999).

3.3.2 Collection Methods

Core sampling methods described by Nelson et al. (2002b) for the Salmon River watershed could be applied throughout the state. These or similar methods would produce data that are comparable to the recommended targets. Generally, 40 samples were collected using a 30.4 cm diameter core, worked into the gravel to a depth of 25 cm in randomly selected locations within potential spawning areas of specified reaches. Randomization was by way of a rectangular grid superimposed on the reach. Approximately 8–10 L of streambed material were excavated from the core sampler. Sediment samples were then strained through sieves of decreasing mesh size and drained to remove excess water. The volume of sediment retained by each sieve was determined on-site using water displacement measures. Sieve sizes should include, at a minimum, 0.85 mm and 6.3 mm.

3.3.3 Other states

Several states and one province have established targets for subsurface sediments. In British Columbia, targets for aquatic life use are that fine sediment in streambed substrates should not exceed 10% having a diameter of less than 2.00 mm, 19% having a diameter of less than 3.00 mm, and 25% having a diameter of less than 6.35 mm at potential salmonid spawning sites. Montana recognized a subsurface sediment target in the Deep Creek TMDL (Endicott and McMahon 1996). They set a subsurface sediment target of 30% fines < 6.35 mm, to be monitored by triplicate samples in at least three riffles.

Alaska's applicable water quality criterion for sediment for propagation of aquatic wildlife states that: the percent accumulation of fine sediment in the range of 0.1 mm to 4.0 mm in the gravel bed of waters used by anadromous or resident fish for spawning may not be increased more than 5 percent by weight above natural conditions. In no case may the 0.1 mm to 4.0 mm fine sediment range in those gravel beds exceed a maximum of 30 percent by weight.

Several approved TMDLs in California set targets for subsurface sediments that are based on multiple studies. The approved TMDLs (e.g., U.S. EPA 2000, U.S. EPA 2002) set targets that were within the ranges of fine sediments found to be suitable for spawning by Chapman (1988) and Kondolf (2000), who summarized conditions in redds and spawning reaches. Most of the targets were for <= 14% intrusive fines (< 0.85mm) and <=30% trapping fines (< 6.4 mm) in sediments of potential spawning areas (see Appendix C). These thresholds take into account the cleaning effect that spawning has on fine sediments, i.e., the measured sediments are from unspawned gravels, though the embryo and fry survival curves were developed from redd gravel composition. They are also selected such that 50% survival will be expected. Though this does not sound overly protective, natural survival rates are comparable (NCASI 1984, Maret et al. 2003).

3.3.4 Recommendation

We propose two criteria for subsurface sediment (i.e., depth fines) in riffles. Our first recommendation follows the South Fork Salmon River TMDL (IDEQ 1991). For those streams with subsurface sediment (< 6.35 mm) less than 27%, maintain the existing sediment volume level. For streams that exceed the 27% threshold, reduce subsurface sediment to a 5-year mean not to exceed 27% with no individual year to exceed 29%. Our second recommendation is that concentrations of subsurface fines < 0.85 mm not exceed 10%. These targets are appropriate only for those portions of a stream channel, such as riffles and pool tail outs, where spawning typically occurs.

3.4 Riffle Stability

3.4.1 Biological background

The Riffle Stability Index (RSI) has been used as an indicator of beneficial use, especially as related to cold water biota. The RSI is measured as the percentage of the substrate particles (from a Wolman pebble count) that are smaller than the largest particles that are moved in channel forming flows. Particles on point bars are measured to determine the largest mobile particles.

The substrate mobility expressed by RSI may be related to the density and species composition of stream insects (Kappesser 1993). Cobb, Galloway, and Flannagan (1992) reported a decrease in insect density up to 94% in an unstable riffle compared to no reduction in a stable riffle. In Colorado, von Guerard (1991) concluded that as the grain size of streambed material approaches that of bedload, benthic invertebrate populations might be adversely affected. Kappesser (1993) looked at RSIs from B-channel streams in northern Idaho. He reported an RSI range from 29 riffles in un-entered (e.g., relatively undisturbed) watersheds of 33 to 74 (mean 50.8) while RSIs from 286 riffles in entered watersheds ranged from 38 to 100 (mean 79.5). In a survey of B-channel streams of the St. Joe River drainage (Idaho), bull trout redds were consistently found in reaches with RSI values less than 65 and were missing from reaches with higher RSI values (Cross and Everest 1992).

Pools are critical habitat for salmonids (Spangler 1997, Saffel 1994, Stichert et al. 2001, Harwood et al. 2002, Kruzic et al. 2001, Jakober et al. 2000, Solazzi et al. 2000). As riffle stability degrades, pool habitat decreases, reducing daytime and winter refugia. Destabilized stream reaches may contain lengthened riffles and shallow pools (Lisle 1982). In the St. Joe River drainage (Idaho), reaches with lower RSI values had greater residual pool volume (Cross and Everest 1992).

Riffle stability may be a factor effecting redd scour if bankfull flows occur during the incubation period. The likelihood of mortality from scour increases for stocks of fish incubating during seasons when peak flows commonly occur (Seegrist and Gard 1972). To avoid scouring flows that would disturb deposited eggs, salmonids either bury their eggs below the annual scour depth or avoid egg burial during times of likely bed mobility. Such protective patterns were noted in west-slope pacific Northwest watersheds (Montgomery et al. 1999), and are likely to be prevalent throughout Idaho.

3.4.2 Other states

No state or province has a standard for riffle stability. However, the Heavenly Valley Creek (CA) TMDL specified a target for the related Pfankuch Stability Rating that showed improving trends towards a “good” rating and several approved TMDLs in California include a target for residual pool volume (V*) (see Appendix C). Residual pool volume (V*) is the percentage of pool volume that is filled with fine sediment, is a measure of the in-channel supply of mobile bedload sediment (Lisle and Hilton 1991), and may be comparable to the Riffle Stability Index.

A common target for V* is <= 0.21, based on north slope California streams (e.g., U.S. EPA 2001b, U.S. EPA 2002).

3.4.3 Recommendation

We recommend a Riffle Stability Index (RSI) not to exceed 70. Index numbers less than 70 indicate systems that are in dynamic equilibrium (Kappesser 1993). The RSI is most appropriately applied in belt series geology as found in northern Idaho (Kappesser 1993). The procedure also appears to be applicable to granitics, basalts, and mica schists, though applicability of the recommended target should be verified in those geologies.

4. Intergravel Dissolved Oxygen

4.1 Biological background

One effect of the accumulation of fine sediment in the aquatic environment is reduced permeability of the substrate resulting in less oxygen exchange to support fish embryos and macroinvertebrates. Salmonids excavate streambed substrate to deposit eggs then backfill the “egg pocket” to protect the eggs during the incubation period. The eggs are dependent on the flow of oxygen-rich water through the substrate to survive. The accumulation of fines in the redd restricts water flow and reduces oxygen to the eggs which results in decreasing survival (Shapovalov and Berrian 1939; Wickett 1954; Shelton and Pollock 1966). Intergravel dissolved oxygen is more of a concern in areas outside the Idaho batholith. Fines in the batholith are mostly in the sand to fine gravel range and permeability associated with these textures are not restrictive to the transport of dissolved oxygen (Burton et al. 1990).

Dissolved oxygen (DO) in intergravel flow is a more direct measure of streambed suitability for salmonid egg development than subsurface sediments. Intergravel flow may be more or less dependent on ambient streambed sediment conditions, depending on local hyporheic conditions. If water flows into the redd from the overlying water column then there is the chance of the flow being choked by the intrusion of fine sediments in the bedload. If, however, redds are located in areas of hyporheic discharge, then the surface sediment conditions and delivery during incubation may be less important because the oxygenated water source is from below the redd. Fall chinook salmon and bull trout select spawning sites based at least in part on influences of hyporheic flow (Spangler 1997, Geist 1998). Bull trout embryo survival was found to be significantly higher and less variable in areas with groundwater discharge and higher water temperatures over the incubation period (Baxter and McPhail 1999).

Several studies have related intergravel dissolved oxygen to egg/fry survival. Survival of embryos has been positively correlated with intergravel dissolved oxygen in the redds for steelhead (Coble 1961) and brown trout (Maret et al. 2003). Silver et al. (1963) found that embryos incubated at low and intermediate DO concentrations produced smaller and weaker alevins than embryos incubated at higher concentrations. Weak sac fry cannot be expected to survive rigorous natural conditions. In a review of embryo development studies, Chapman (1988) noted several examples of developmental impairment at lower DO concentrations, but did not recommend a single threshold. Bjornn and Reiser (1991) recommended that intergravel DO concentrations should be at or near saturation, and that temporary reductions should drop to no lower that 5.0 mg/L.

Observations of the effects of intergravel flow on macroinvertebrates are much less extensive than those for fish. Excessive sediment affects macroinvertebrates by accumulating on the body surfaces and reducing the effective area of the respiratory structures (Lemly 1982) or by covering pupae cases and reducing the flow of oxygenated water to the metamorphosing insect (Rutherford and Mackay 1986).

4.2 Other states

Several states, including Idaho, and British Columbia have standards for intergravel dissolved oxygen (Table 2). The minimum in Montana and Wyoming is 5 mg/L. In Oregon and British Columbia, the minimum is 6 mg/L. In British Columbia, the 30-day average guideline for intergravel dissolved oxygen in spawning areas is 8.0 mg/L. The Trinity River (CA) TMDL specified a target for a related measure, gravel permeability, which should show improving trends (see Appendix C).

4.3 Recommendation

We affirm the intergravel dissolved oxygen standard (Water Quality Standards and Wastewater Treatment Requirements 58.01.02.250.02.f.i.1) for Idaho's streams to protect salmonid spawning of not less than 6.0 mg/L for a 7-day mean and not less than 5.0 mg/L for a 1-day minimum (Idaho Department of Environmental Quality n.d.a.).

5. Conclusions and Recommendations

Setting targets for surrogate measures of sediment load is a process that attempts to account for yields, delivery, transport, and deposition in both natural and potentially disturbed conditions. A surrogate is often selected for relative efficiency of measurement and because the effects on biological endpoints are better understood than general effects of higher sediment loads. The targets recommended in this document are guidelines that may be directly applicable for a specific TMDL, or may serve as points of departure for development of modified targets based on local reference conditions.

If viable fish and macroinvertebrate assemblages are the primary beneficial uses of a waterway then maintenance of that viability becomes the goal of Idaho's water quality standard and it follows that measures of the assemblages should be the ultimate determinants of TMDL success. The fish and macroinvertebrate assemblages are the living resources that should be protected through TMDL planning and measurements of their condition should be integral to TMDL evaluation. If they do not show signs of impairment, then it may be assumed that environmental conditions are suitable and excessive sediments are not a problem. If, however, they do show impairment, then the sediment targets will help determine a probable cause of impairment and gauge progress towards elimination of sediment stressors.

In Idaho, macroinvertebrate and fish community integrity is measured using the Stream Macroinvertebrate Index (SMI, Jessup and Gerritsen 2000) and the Stream Fish Index (SFI, Mebane 2002), respectively. Reference conditions have been described for macroinvertebrates and fish after recognizing variability in natural stream types in Idaho. Departure from reference conditions (lower index score) indicates that the community is exposed to a stressor. Neither the SMI nor the SFI are specifically calibrated to sediments as a stressor, rather they are sensitive to a range of stressors in Idaho, including sediments. Procedures for integrating Idaho's bioassessment data with other data are detailed in "Waterbody Assessment Guidance II" (Grafe et al. 2002).
Eight instream parameters have been evaluated as appropriate measures of sediment pollution (Table 8), we have recommended target values for five. These parameters were selected for three reasons: 1) because data collection is relatively simple and repeatable, 2) because methods and baseline data have been established in Idaho for the parameters, and 3) because effects to periphyton, aquatic invertebrates, and sensitive fish species are understandable, documented, and generally quantifiable. Three of the parameters are measured in the water column, four are measurements of streambed substrates, and one is a measure of hyporheic oxygen supply.

Table 8. Recommended instream sediment parameters and associated target levels.

Instream Sediment Parameter	Recommended Target Levels
Turbidity	Not greater than 50 NTU instantaneous or 25 NTU for more than 10 consecutive days above baseline background, per existing Idaho water quality standard. Chronic levels not to exceed 10 NTU at summer base flow
Light Penetration	Not to reduce the depth of the compensation point for photosynthetic activity by more than 10% from the seasonally established norm for aquatic life
Total Suspended Solids and Suspended Sediment	No specific recommendation, establish site specific reference
Embeddedness	No specific recommendation, establish site specific reference
Surface Sediment	No specific recommendation, establish site specific reference
Subsurface Sediment in Riffles	For those streams with subsurface sediment less than 27% - do not exceed the existing fine sediment volume level. For streams that exceed the 27% threshold - reduce subsurface sediment to a 5-year mean not to exceed 27% with no individual year to exceed 29%. Percentage of subsurface sediment < 0.85 mm should not exceed 10%
Riffle Stability	Not to exceed a Riffle Stability Index of 70
Intergravel Dissolved Oxygen	Not less than 5.0 mg/L for a 1-day minimum or not less than 6.0 mg/L for a 7-day average mean, per existing Idaho water quality standard

5.1 Other options

In addition to the parameters addressed in detail above, other parameters may be appropriate for a specific TMDL. These include measurements of channel and watershed characteristics. The effects of channel and watershed conditions on aquatic life are less direct than instream measurements, and are therefore less reliable as predictors of impacts to individuals, populations, or habitats. However, a TMDL developer may determine that channel or watershed measurements provide better characterization of critical processes or compliment the recommended instream measures.

Channel characteristics appropriate as TMDL targets include the following with variations: width/depth ratio, sediment rating curves, pool frequency and quality, bank stability, and changes in peak flow (see Appendix A). Watershed characteristics that have been used in approved TMDLs in western states include the following and several variations: land area disturbed (especially in unstable areas) and road crossings, length, hydrologic connectivity, or condition (see Appendix C). Targets are difficult to establish for channel and watershed characteristics and are commonly narrative or specify improving trends.

The relationships between sediment sources and biological endpoints or critical habitat are documented, but with little general applicability for establishing numeric targets. It is not surprising that juvenile chinook salmon had higher survival rates in natural watersheds compared to those in watersheds with young, managed timberlands (Paulsen and Fisher 2001), but the results can not specify a degree of naturalness that is required to maintain acceptable survival rates. Likewise, correlation between bull trout redd numbers and the density of logging roads over time and across basins (Baxter et al. 1999) shows that the general link between source and endpoint exists without quantifying the linkage.

Numeric models have been developed to link sediment sources to habitat conditions and salmonid populations. Models are usually described with caveats regarding assumptions and limitations imposed by calibration data, so that results must be interpreted with a substantial degree of uncertainty. However, such models may be useful for investigating trends with simulations of load allocation, watershed management, or stream restoration alternatives. Sediment-habitat response curves were developed for the Nez Perce National Forest that related the percentage of sediment delivery above natural levels to embeddedness and subsurface fines (Stowell et al. 1983). These models were intended for use with a second model of sediment supply (Cline et al. 1981). The models were tested and improved by Nelson and Platts (1988) to address some of the inherent uncertainties. Espinosa (1992) outlined a model of habitat suitability for salmonid species in Idaho in which several of the habitat variables were related to sediment parameters. This model may be useful in identifying habitat conditions that may be limiting to the population, or at least in prioritizing habitat elements that are less than optimal.

The targets recommended in this paper were derived from literature values for studies primarily in the northwest U.S. While we sought out the best available sources of current information on sediment effects on stream biota, a comprehensive effort at assembling a database of sediment conditions in streams that are supporting their aquatic life uses would allow targets to be refined using local reference conditions. The State of Colorado assesses sediment impacts by establishing a scale of conditions calibrated to reference conditions, thus test conditions can be evaluated as a percentage of reference (CDPHE 2002). Attainment of certain percentages of the reference conditions (both sediment and biological conditions) is associated with acceptable or unacceptable sediment conditions. This model may be appropriate in Idaho when sufficient data are obtained.

Reference conditions for a specific stream should be defined using unimpaired streams that are in the same ecoregion, of approximately equal size (e.g., same stream order), and have similar geomorphology, geology, slope, topography, soils, etc. Because of uncertainty in categorizing existing stream geomorphology, appropriate geomorphology for the landscape, and stage of channel evolution, predictive modeling of expected sediment conditions should consider multiple factors in addition to (or instead of) stream type. Expected channel and sediment characteristics might be predicted for different morphological settings using continuous variables because systems are continuous, not fixed or categorical. Such models could set expectations for physical conditions. They could also be used to set acceptable ranges of conditions under different land uses.

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APPENDIX A

USE OF CHANNEL CHARACTERISTICS AS SEDIMENT TARGETS

Appendix A. Use of Channel Characteristics as Sediment Targets

Biological effects of channel characteristics are inherently more difficult to quantify than the effect of streambed and water column measures discussed earlier. Little published work is available to guide the regulator in establishing channel characteristic targets. Thus, targets based on channel characteristics will not be recommended, but must be site specific and established relative to reference conditions. For example, the percentage of stable banks could be determined from a similar watershed that is meeting its beneficial uses. The measure of achievement could be the percentage bank instability reduced from pre-TMDL conditions.

Width/Depth Ratio and Channel Cross-Section

The shape and dimension of a stream channel in a given location are sensitive to the balance between sediment load and stream flow or energy (Leopold et al. 1964). When sediment loads become excessive a channel will aggrade, becoming shallower with a loss of pools and an increased width to depth ratio (e.g., Clifton 1989). This ratio is also sensitive to the direct effects of bank trampling or breakdown leading to increased channel erosion and loss of near bank fish habitat (Bauer and Burton 1993). Others have found a direct relation of width/depth ratio to salmonid biomass (Kozel and Hubert 1989).

Expected width to depth ratios are dependent upon the geomorphic setting of a stream or channel type (Rosgen 1996). Recent research in the Salmon River subbasin of Idaho provides further data on expected width/depth ratios based upon channel type and major rock types - granitic, sedimentary, or volcanic (Overton et. al. 1995). Examples of bankfull width depth ratios that indicate high habitat quality in the Nez Perce and Clearwater National Forests and Cottonwood BLM lands are as follows, by channel type: A - <10, B - <20, C - <40, E - <7, F - <35, and G - <9 (USDA-FS et al. 1998).

To avoid the effect of differences in stream flow on measurement, width and depth must be based upon a fixed stage. The bankfull width and depth of a stream are most characteristic of channel cross-section. Such measurements are quite quickly and easily obtained. Calculation of a stream's average width/depth ratio should be based upon several (3-6) permanent transects representing a given reach. The Van Duzen River and Yager Creek (CA) TMDL for sediments (U.S. EPA 1999) specified a target for mean bed elevation (decreasing trends), which could be monitored over time using fixed transects.

A related, but more detailed and sensitive, measure of changes in channel cross-section is provided by the Gini-coefficient (Olson-Rutz and Marlow 1992). Calculation of this coefficient requires repeated measurements of channel depth at fixed distances across a permanent transect. Again, several transect should be established in order to provide an average condition characteristic of a particular reach of stream. A positive change in the Gini-coefficient indicates a narrowing and deepening of a stream channel.

Use of changes in channel cross-section is not appropriate in bedrock channels: channel cross-section is most sensitive to human influence in alluvial channels with banks consisting of fine grained material. As with other channel characteristics, width/depth is best used only as a relative measure of change or trend in channel condition. The Gini coefficient is strictly an indicator of change.

Although general guidelines for width/depth can be suggested based upon published literature, no absolute values can be offered. For example, one might look for a fifty percent reduction in width/depth ratio over several years for a Rosgen C-type channel with a current ratio of 40. It is essential that such relative targets be combined with a direct measure of beneficial use support, such as provided by the Idaho Division of Environmental Quality BURP results and Waterbody Assessment (IDEQ 1996a, b). Use of reference conditions is strongly recommended.

Channel shape can also be measured longitudinally and targets can be set for the thalweg profile. If aggradation has caused a loss of pools, the target for the thalweg profile might be to find increasing trends in channel complexity and pool depth, or increasing variation from the mean channel thalweg profile. This approach has been applied in several TMDLs in California (e.g., U.S. EPA 2000, U.S. EPA 2001b, U.S. EPA 2002).

Sediment Rating Curves

A stream's discharge of sediment is highly variable due both to variation in stream flow and because suspended sediment concentrations and bedload are strongly correlated with flow, although they typically exhibit hysteresis (i.e., the relation is different between increasing and decreasing flow) (Leopold 1994; Mount 1995; Leopold and Emmett 1997). As a result, sediment discharge ranges wildly from time to time due primarily to timing of weather events and the supply of hillslope and streambed sediment (Ketcheson 1986). This renders individual measurements all but useless, makes longer term load estimation suspect, and effects of human influence hard to detect through direct measurement of either concentration or load.

The relation of suspended sediment concentration and bedload to stream discharge, the sediment rating curve, is much more characteristic of erosional processes and long-term sediment discharge rate than any one concentration or load. This is because the sediment rating curve provides a characterization of sediment discharge over a range of flows thus overcoming day to day, or even year to year, differences in flow.

A sediment rating curve can be established with as few as ten to fifteen measurements if spread out across the full range of flows in an annual hydrograph (Ketcheson 1986). Using a sediment rating curve, reasonably accurate estimates of periodic sediment discharge can be made based upon more or less continuous records of discharge and relatively few sediment measurements (Campbell and Bauder 1940; Lewis 1996). Thus annual or partial-year loads can be estimated based upon an annual hydrograph or other record of flows. With greater flow variability, flow measurements should be recorded more frequently (Dolan et. al. 1981).

It is also possible to use a sediment rating curve to relate a given flow to an estimated concentration of total suspended solids (TSS), thus a record of flows could be used to determine the likely frequency of exceedance of a suspended solids target. Reductions in erosion and/or sediment delivery to a stream will be reflected in a decrease in the slope and/or intercept of the sediment rating curve (Rosgen 1996). This can be used to monitor post-implementation effectiveness of control measures.

Sediment rating curves also have direct application in the setting of TMDL targets and determination of needed load reductions. For example, using an average or typical hydrograph, a desired reduction in the frequency of exceedance of a TSS target and/or bedload can be related to a reduction in the slope of the sediment rating curve and a corresponding reduction in average annual or typical sediment load. While any particular series of post-implementation sediment discharge measurements might show an increase or decrease in sediment load, due primarily or even solely to differences in flow, a reduction in the slope of the sediment rating curve is evidence of improved conditions independent of wet or dry years.

Use of sediment rating curves as an indicator of changes in sediment discharge is usually only applicable where there exists a continuous flow gaging station and a companion record of suspended sediment and/or bedload measurements adequate to produce a reliable rating curve. However, for a given site with a limited flow record (i.e., 1 or 2 years of continuous record) which is near sites with long-term continuous records, the hydrograph can be extended using techniques summarized by Hirsch (1982) and Alley and Burns (1983). For rating curves to be truly useful, there must be a commitment to continue monitoring flow and sediment after TMDL development and implementation.

An alternative sediment rating curve method, proposed by Rosgen (1996), uses existing stream discharge-sediment load data in a more general way. Leopold et al. (1964) suggest rating curves for different stream systems are very similar and can be converted to dimensionless curves by expressing flow (Q) and TSS as ratios of their bankfull values:

$$(Qi/QBF) \text{ and } (TSSi/TSSBF).$$

Where Qi and TSSi are values for a range of flows, and QBF and TSSBF are the discharge and sediment concentration at bankfull flow. These dimensionless curves are stratified by channel type, watershed characteristics, and land use for comparison to other watersheds of interest. In effect, these curves are landform specific sediment-discharge relationships and provide expected values for the relationships.

At least one pair of measurements for a watershed needs to be at bankfull to construct the dimensionless ratio. Thus, for a watershed with no data, the TSS, bedload, and stream discharge are measured at bankfull flow. These measurements are used to calculate a ratio that should fall near the dimensionless sediment rating curve for watersheds with similar physical characteristics. A TSS or bedload target could then be set by taking into account the departure of this ratio from the dimensionless sediment rating curve.

Kunhle and Simon (2000) criticize the dimensionless ratio technique because it obscures differences in bankfull transport rates. Instead, they advocate standardization by carefully identifying comparable reference conditions, with particular attention to stage of channel evolution as well as channel form. When reference conditions are selected such that sediment transport processes are recognized, direct comparisons can be made between test and reference sediment delivery statistics (slope of sediment-transport rating, total sediment load at bankfull, and sediment magnitude-duration relations).

Pool Parameters

Numerous studies have demonstrated a link between management activities, sediment production, and reduction in pool frequency, depth, and volume (Overton et al. 1993, Meehan 1991, Sedell and Everest 1990, MacDonald et al. 1991). De-stabilized stream reaches (higher Riffle Stability Index values) may contain lengthened riffles and shallow pools (Lisle 1982, Cross and Everest 1992). As a result, pool measures like pool frequency and residual pool volume (V*) are practical and effective sediment targets. Much like pool frequency, the ideal pool volume is related to stream characteristics, so that the status of the stream in question should be defined in comparison to a reference stream. The two measures may be related; as V* is reduced, the pool frequency increases. Together, V* and pool frequency can be used as combined sediment targets with the conditions in a reference stream providing a reasonable target of desired conditions.

Pool Frequency:

Pool frequency as a sediment target is a measure of fish habitat availability in a given stream reach where the number of existing pools in a reach is related to the desired number of pools. The ideal number of pools for a stream reach is a function of geology, valley-channel morphology, stream flow, and sometimes large woody debris. Leopold et al. (1964) and Rosgen (1996) show that there are relationships between channel characteristics and pool frequency. The best way to determine the proper or desired pool frequency in a given stream reach is to use reference conditions (Overton et al. 1995).

Habitat conditions in the Clearwater and Nez Perce National Forests and the Cottonwood BLM lands were considered “high” when pool frequency and quality targets were met (Matrix 1998). For frequency, the targets were specified in a table relating number of pools per mile to channel width (e.g., channels 15 – 20 feet wide should have more than 56 pools per mile). Also considered were elements for sustaining pools such as a supply of large woody debris, which has been established as beneficial for salmonid habitat and sensitive to logging activities (Haur et al. 1999). Pool quality was rated using a locally developed methodology.

Predominance of pool habitat is a measure of the percentage of pool habitat in a given reach. As such, the number of pools is not as critical as the linear extent of the few or many pools. In several TMDLs approved in California, a target was specified for primary pool habitat to cover more than 40% of the reach (e.g., U.S. EPA 2000, U.S. EPA 2001b, U.S. EPA 2002). Primary pools were described as being at least 3 feet deep in third order or larger streams.

Residual pool volume (V*) and depth:

Residual pool volume (V*) is a measure of the fraction of pool volume filled with fine sediment (Lisle and Hilton 1991). Residual pool depth is a measure of pool depth which is not dependent upon discharge at the time of measurement (Lisle 1989). These measures are effective sediment targets because they primarily reflect chronic sediment sources (Lisle and Hilton 1991). Common targets for V* for north slope California streams are <= 0.15 (e.g., U.S. EPA 2000, U.S. EPA 2001a) or <= 0.21 (e.g., U.S. EPA 2001b, U.S. EPA 2002).

Bank Stability

Bank instability is often a chronic source of sediment in disturbed stream systems (Reid and Dunne 1996). Bank stability measures are a cost effective sediment target which are complemented by a wealth of historic data. Federal land management and state agencies, including DEQ, commonly collect this information using the method developed by Pfankuch (1975) as part of stream inventories and habitat assessments.

The desired condition of streambanks is typically near 100 percent stable. Overton et al. (1995) showed undisturbed streams typically have between 90 to 100 percent bank stability for source, transport, and response reaches. In the Nez Perce and Clearwater National Forests and Cottonwood BLM lands, streambank stability indicating high quality habitats is expected to be >90% in C channels, > 95% in A & B channels, and 100% in E channels (USDA-FS et al. 1998). In the Umatilla River Basin (OR), less than 25% eroding banks were expected to fulfill the streambank component of the sediment load allocation. The target was established through regression analysis of TSS and eroded banks, setting the eroded bank target as the value corresponding to the TSS target of 80 mg/L (ODEQ 2001).

Changes in Peak Flow

Management activities (i.e., activities which remove vegetation and increase soil compaction) are known to increase the magnitude and frequency of peak flow events (Jones and Grant 1996; Harr et al. 1975; MacDonald et al. 1991). Increased peak flows disrupt the balance between channel form and sediment flux. A stream out of equilibrium with sediment input is typically limiting to beneficial uses. If changes in peak flow magnitude and/or frequency can be statistically demonstrated, then a possible sediment target might be a measurable decrease in peak flow events. A possible statistical method is ANOVA using two periods of time (pre and post-TMDL) (Jones and Grant 1996; Riggs 1968) or a BACI design (before-after control-impact). The target might be a statistically significant decrease in the magnitude and frequency of peak flow events following implementation of the TMDL.

APPENDIX B

TOTAL SUSPENDED SOLIDS SAMPLING AND ANALYSIS

Appendix B. Total Suspended Solids Sampling and Analysis

Total Suspended Solids Sampling Protocols

Site selection:

Typically, total suspended solids (TSS) water samples are collected at or near a fixed gaging station or bridge to ease difficulties associated with high flow measurements. However, if TSS data are to be related to watershed and channel geomorphic characteristics, sample sites should be located in an area representative of the catchment (Edwards and Glysson 1998). In either case, sample sites are to be located where the channel is quasi-stable.

Sample collection:

TSS samples are collected using one of several depth-integrated samplers in resistant glass or plastic bottles. Edwards and Glysson (1998) discuss several different types of samplers commonly used. In general, the type of sampler depends on the characteristics, primarily size, of the stream. These samplers, such as the DH-48, have an intake port which restricts the size of particles sampled to 2.0 mm or less. Generally this causes little if any bias as particles greater than this size are not typically in suspension. However, the difference in particle size between TSS and the typical biological definition of fines as being less than 6.35 mm must be borne in mind when interpreting TSS measurements.

> When collecting TSS samples, stream stage or instantaneous stream discharge is also measured. Because TSS concentrations are ultimately used to calculate sediment flux or load, TSS samples should be collected frequently during high flow periods and infrequently during low flow periods. Flood events should be intensively sampled during the rising and falling limb of the hydrograph, if possible. Several authors offer strategies to optimize sampling of the hydrograph for load estimation purposes (Lewis 1996; Thomas and Lewis 1995; Preston et al. 1989; Dolan et al. 1981).

Depth-integrated TSS samples best represent the total amount of suspended sediment passing a point at a given time. However, a relationship can be developed between total TSS concentration and values obtained sampling a single point in the stream cross-section (Guy and Norman 1970). U. S. Environmental Protection Agency (1982) provides additional TSS sampling guidance.

Total Suspended Solids Sample Analysis

There are two common suspended sediment analytical methods. APHA et al. (1995) described total suspended solids analysis protocols, the method recommended by U. S. Environmental Protection Agency (1983b). The U. S. Geological Survey (USGS) analyzes samples for total suspended sediment (Guy 1969). The primary difference in these two methods is that the USGS protocol requires the entire field sample be filtered for analysis, while the U. S. Environmental Protection Agency (EPA) procedure allows sub-sampling of as little as 100 ml in the laboratory. By comparing the two analytical methods, the USGS has shown significant differences in the results (Greg Clark, personal communication). In general, the difference between the two methods is greater in sand dominated systems, whereas, in fine grain silt-clay systems the difference is less. An unpublished USGS document reports as much as a 2:1 difference of total suspended sediment to total suspended solids.

Total Suspended Solids Data Analysis

The TSS target needs to be related to natural sediment yield, watershed and channel characteristics, and existing land uses. Natural background TSS is determined using either conservative assumptions (e.g., natural background TSS is zero), the sediment budget method, or reference streams with similar geomorphic characteristics and limited land use. The TSS target value also needs to be related to stream discharge and/or season. The sediment rating curve is an effective method to achieve the latter.

Three different approaches have been used in recent TMDLs. The Deep Creek TMDL (Endicott and McMahon 1996) approved in Montana, used the sediment rating curve to set TSS reductions. The Yakima River TMDL (Joy and Patterson 1997) in Washington, uses the 90th percentile TSS concentration during a selected season. The Paradise Creek TMDL in Idaho (IDEQ 1998b) relates TSS back to the State of Idaho's turbidity standard, such that TSS cannot exceed 100 mg/L instantaneously or 50 mg/L for ten consecutive days above natural background. For Paradise Creek, natural background TSS was estimated using the sediment budget method.

APPENDIX C

LIST OF REVIEWED SEDIMENT TMDLs

Table C-1. List of reviewed sediment TMDLs.

Title	Submitting agency	Location	Date
Albion River TMDL for Sediments	U.S. EPA	CA	2001
Big River TMDL for Sediments	U.S. EPA	CA	2001
Careless Creek Sediment TMDL	MT DEQ	MT	2001
Cedar Creek TMDL	IL EPA	IL	2002
Deep Creek, Montana, Development of a TMDL to reduce non-point source sediment pollution to	MT DEQ	MT	1996
East Fork Kaskaskia River TMDL and Implementation Plan	IL EPA	IL	2002
Garcia River Sediment TMDL	U.S. EPA	CA	1898
Gualala River TMDL for Sediment	U.S. EPA	CA	2000 - 01
Heavenly Valley Creek TMDL		CA	2002
Lower Arkansas River Basin TMDL		AK	2002
Mattole River TMDL for Sediments and Temperature	U.S. EPA	CA	2003
Navarro River TMDL for Temperature and Sediments	U.S. EPA	CA	2000
North Fork Eel River TMDL	U.S. EPA	CA	2002
Noyo River TMDL for Sediments	U.S. EPA	CA	1999
Nutrioso Creek TMDL		AZ	2000
Redwood Creek TMDL for Sediments	U.S. EPA	CA	1998
San Miguel River TMDL for Sediment	CO Water Quality Control Division	CO	2000
South Fork Eel River TMDL for Sediment and Temperature	U.S. EPA	CA	1999
Styles Brook TMDL for Sediment (Draft)	VT DEC	VT	2001
Tammany Creek Sediment TMDL	ID DEQ	ID	2001
Ten Mile River TMDL for Sediments	U.S. EPA	CA	2000
Trinity River TMDL for Sediments	U.S. EPA	CA	2001
Umatilla River Basin TMDL and Water Quality Management Plan	OR DEQ	OR	2001
Upper Grande Ronde River sub-Basin TMDL	OR DEQ	OR	2000
Van Duzen River and Yager Creek TMDL for Sediments	U.S. EPA	CA	1999

Table C-2. Examples of indicators and targets for sediment TMDLs.

Indicator	Target	References in TMDL text	Title
Instream Indicators			
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa	Bybee 2000, Plafkin et al. 1989	Albion River TMDL for Sediments
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa	Bybee 2000, Plafkin et al. 1989	Big River TMDL for Sediments
Benthic Macroinvertebrates	improving trends		Gualala River TMDL for Sediment
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa	Bybee 2000, Plafkin et al. 1989	Mattole River TMDL for Sediments and Temperature
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa		Navarro River TMDL for Temperature and Sediments
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa		North Fork Eel River TMDL
Benthic Macroinvertebrates	Thresholds for 7 index metrics		Styles Brook TMDL for Sediment (Draft)
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa	Bybee 2000, letter to EPA	Ten Mile River TMDL for Sediments
Benthic Macroinvertebrates	improving trends, EPT, Richness & % Dominant Taxa		Trinity River TMDL for Sediments
Benthic Macroinvertebrates	Improving trends in indices for EPT, taxa richness, and % dominant taxa	Plafkin et al. 1989; DFG-WPCL 1996	Van Duzen River and Yager Creek TMDL for Sediments
Benthic Macroinvertebrates	improving trends in benthic invertebrate community metrics over time, compared to reference site		Heavenly Valley Creek TMDL
Benthic Macroinvertebrates	>=40% EPT in assemblage		Lower Arkansas River Basin TMDL

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Indicators (cont'd)			
d50	>=69mm (mean), >37mm (min), in 3rd order streams with slopes 1-4%		Garcia River Sediment TMDL
d50	>=69mm (mean), >37mm (min)	Knopp 1993	Redwood Creek TMDL for Sediments
d50	improving trend		Trinity River TMDL for Sediments
d50	Increasing trend toward >69mm	Klein 1998, Knopp 1993	Van Duzen River and Yager Creek TMDL for Sediments
Fine sediment volume of active bed matrix	decreasing trend in volume stored in subsurface of gravel bars	Lisle and Hilton 1999	Gualala River TMDL for Sediment
Fine sediment volume of active bed matrix	decreasing trend in volume stored in subsurface of gravel bars	Lisle and Hilton 1999	Navarro River TMDL for Temperature and Sediments
Frequently mobilized channelbed surface	see text - channel specific - perhaps a regulated river	US FWS 1999	Trinity River TMDL for Sediments
Large Woody Debris	increasing distribution, volume and number of key pieces or distribution of LWD-formed habitats	Flosi et al. 1998	Albion River TMDL for Sediments
Large Woody Debris	increasing distribution, volume and number of key pieces or distribution of LWD-formed habitats	Flosi et al. 1998	Big River TMDL for Sediments
Large Woody Debris	increasing distribution, volume and number of key pieces or distribution of LWD-formed habitats	Flosi et al. 1998	Mattole River TMDL for Sediments and Temperature
Large Woody Debris	increasing trend	Bilby and Ward 1989, Lisle 1986	Navarro River TMDL for Temperature and Sediments

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Indicators (cont'd)			
Large Woody Debris	increasing distribution, volume and number of key pieces	Bilby and Ward 1989, Beechie and Sibley 1997, USDA 1994	Noyo River TMDL for Sediments
Large Woody Debris	improving trends toward increased large woody debris		Redwood Creek TMDL for Sediments
Large Woody Debris	increasing distribution, volume and number of key pieces		Trinity River TMDL for Sediments
Large Woody Debris	increasing distribution, volume and number of key pieces	Bilby et al. 1989, Beechie et al. 1997, USDA 1994	Van Duzen River and Yager Creek TMDL for Sediments
Permeability of spawning gravel	improving trend, permeability standpipe driven 35cm into substrate (Matthews 2001a)		Trinity River TMDL for Sediments
Pfankuch Channel Stability Rating	increasing trend over time from "fair-poor" to "good"		Heavenly Valley Creek TMDL
Riffle Embeddedness	<=25% or improving (decreasing) trend toward 25%	Flosi et al. 1998, Mangelsdorf & Clyde 2000	Albion River TMDL for Sediments
Riffle Embeddedness	<=25% or improving (decreasing) trend toward 25%	Flosi et al. 1998, Mangelsdorf & Clyde 2000	Big River TMDL for Sediments
Riffle Embeddedness	<=25% or improving (decreasing) trend toward 25%		Gualala River TMDL for Sediment
Riffle Embeddedness	<=25% or improving (decreasing) trend toward 25%	Flosi et al. 1998, NCRWQCB 2001	Mattole River TMDL for Sediments and Temperature
Riffle Embeddedness	<=25% or improving (decreasing) trend toward 25%		North Fork Eel River TMDL
Riffle Embeddedness	Increasing percentage of riffle habitat units that are <25% embeddeded	Flosi and Reynolds 1994, DFG 1995	Noyo River TMDL for Sediments
Riffle Embeddedness	<25%		Styles Brook TMDL for Sediment (Draft)

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Indicators (cont'd)			
Riffle Embeddedness	<=25%		Ten Mile River TMDL for Sediments
Riffle Embeddedness	<=25% or improving (decreasing) trend toward 25%	Flosi et al. 1998	Trinity River TMDL for Sediments
Riffle Embeddedness	<25%	Flosi et al. 1998	Van Duzen River and Yager Creek TMDL for Sediments
Sediment Substrate Composition	<=14% <0.85mm and <=30% <6.4mm	Burns 1970, CDF 1994, McHenry et al. 1994, Mangelsdorf & Lundborg 1998, Valentine 1997	Albion River TMDL for Sediments
Sediment Substrate Composition	<=14% <0.85mm and <=30% <6.4mm	Burns 1970, CDF 1994, McHenry et al. 1994, Mangelsdorf & Lundborg 1998, Valentine 1997	Big River TMDL for Sediments
Sediment Substrate Composition	<=30% <6.35mm		Deep Creek, Montana, Development of a TMDL to reduce non-point source sediment pollution to
Sediment Substrate Composition	<=14% <0.85mm and <=30% <6.5mm		Garcia River Sediment TMDL
Sediment Substrate Composition	<=14% <0.85mm and <=30% <6.4mm	Burns 1970, Peterson et al. 1992, Kondolf 2000	Gualala River TMDL for Sediment
Sediment Substrate Composition	<=14% <0.85mm and <=30% <6.4mm	Burns 1970, CDF 1994, McHenry et al. 1994, Mangelsdorf & Lundborg 1998, Valentine 1997, NCRWQCB 2000	Mattole River TMDL for Sediments and Temperature

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Indicators (cont'd)			
Sediment Substrate Composition	<=14% <0.85mm and <=30% <6.4mm	Peterson 1992, Burns 1970, Kondolf 2000	Navarro River TMDL for Temperature and Sediments
Sediment Substrate Composition	<=10% <0.85mm, <=30% <6.4mm, and <=15% <2mm	Matthews 2001, Kondolf 2000, Chapman 1988	North Fork Eel River TMDL
Sediment Substrate Composition	<=14% (mean, as wet volume)	Burns 1970, CDF 1994	Noyo River TMDL for Sediments
Sediment Substrate Composition	<=14% <0.85mm, <=30% <6.5mm and <10-20% <2mm	Chapman 1988, Tappel & Bjorn 1983, Madej 1998, Peterson 1992, Burns 1970, Tappel & Bjorn 1983, Chapman & McLeod 1987, Young et al. 1991	Redwood Creek TMDL for Sediments
Sediment Substrate Composition	< 14% <0.85 mm	Peterson 1992, Burns 1970	South Fork Eel River TMDL for Sediment and Temperature
Sediment Substrate Composition	<8% fines (size not specified)		Styles Brook TMDL for Sediment (Draft)
Sediment Substrate Composition	<20% <8mm		Styles Brook TMDL for Sediment (Draft)
Sediment Substrate Composition	<=14% (mean, as wet volume) <0.85mm in pool tailouts or potential spawning areas	Burns 1970, CDF 1994, Mangelsdorf & Lundborg 1998	Ten Mile River TMDL for Sediments
Sediment Substrate Composition	<=10% <0.85mm, <=30% <6.4mm, and <=15% <2mm	Matthews 2001, Kondolf 2000, Chapman 1988	Trinity River TMDL for Sediments
Sediment Substrate Composition	<=20% streambed area fines (correlated to streambank vegetation)		Upper Grande Ronde River sub-Basin TMDL

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Indicators (cont'd)			
Sediment Substrate Composition	<=14% (mean, as wet volume)	CDF 1994, McHenry et al. 1994	Van Duzen River and Yager Creek TMDL for Sediments
Silt	<=34% of stream area dominated by silt		Cedar Creek TMDL
Silt	<=34% of stream area dominated by silt		East Fork Kaskaskia River TMDL and Implementation Plan
Instream Water Quality Indicators			
Suspended Sediment Concentration Curve Rating	decreasing temporal trend (flow v. TSS)		Gualala River TMDL for Sediment
Suspended Sediments	<=155 mg/l sediment concentration (suspended and bedload combined) during stable flow of 150 cfs		Careless Creek Sediment TMDL
Suspended Sediments	<=116 mg/l in all but one sample collected over 3 years		Cedar Creek TMDL
Suspended Sediments	<=116 mg/l in all but one sample collected over 3 years		East Fork Kaskaskia River TMDL and Implementation Plan
Suspended Sediments	Decreasing trend in days of turbidity exceedance, develop turbidity rating curve and relate to biological effects	Newcombe and Jensen 1996	Trinity River TMDL for Sediments
Suspended Solids	Narrative: excess suspended solids not to interfere with wildlife or its habitat		Lower Arkansas River Basin TMDL

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Water Quality Indicators (cont'd)			
Temperature	<=16.8, 7 day running mean		Ten Mile River TMDL for Sediments
TSS	0.26 slope of TSS v. Q plot		Deep Creek, Montana, Development of a TMDL to reduce non-point source sediment pollution to
TSS	<=80 mg/l or value locally correlated to 30 ntu turbidity		Umatilla River Basin TMDL and Water Quality Management Plan
TSS/Turbidity	183 lbs/day, spring flows; 19.8 lbs/day average base flow conditions		Nutrioso Creek TMDL
Turbidity	<= 20% above naturally occuring backgrounds	Basin Plan (NCRWQCB 1996)	Albion River TMDL for Sediments
Turbidity	<= 20% above naturally occuring backgrounds	Basin Plan (NCRWQCB 1996)	Big River TMDL for Sediments
Turbidity	<= 20% above naturally occuring backgrounds, decreasing days above threshold	Newcombe and Jensen 1996, Sigler et al. 1984	Gualala River TMDL for Sediment
Turbidity	<= 20% above naturally occuring backgrounds	Basin Plan (NCRWQCB 1996)	Mattole River TMDL for Sediments and Temperature
Turbidity	<= 20% above naturally occuring backgrounds		North Fork Eel River TMDL
Turbidity	<= 20% above background	Basin Plan 1994, Reid 1999	Noyo River TMDL for Sediments
Turbidity	<= 20% above naturally occuring backgrounds		South Fork Eel River TMDL for Sediment and Temperature

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Instream Water Quality Indicators (cont'd)			
Turbidity	<=50 ntu instantaneous and <=25 ntu for 10 days		Tammany Creek Sediment TMDL
Turbidity	<= 20% above naturally occuring backgrounds	Basin Plan (NCRWQCB 1996)	Trinity River TMDL for Sediments
Turbidity	<=30 ntu over 48 hours		Umatilla River Basin TMDL and Water Quality Management Plan
Turbidity	<= 20% above background	Basin Plan 1994	Van Duzen River and Yager Creek TMDL for Sediments
Channel Indicators			
Cross Sections (bed elevations)	Decreasing trend in mean bed elevations towards pre-1964 levels	Kelsey 1997, Klein 1998	Van Duzen River and Yager Creek TMDL for Sediments
Periodic channel migration	channel specific	US FWS 1999	Trinity River TMDL for Sediments
Periodic channelbed scour and fill	channel specific	US FWS 1999	Trinity River TMDL for Sediments
Pool depth	mean depth of pools at low flow exceeds 2 m	Flosi & Reynolds 1994	Redwood Creek TMDL for Sediments
Pool depth 3rd & 4th Order Tribs	mean depth of pools at low flow exceeds 1-1.5 m		Redwood Creek TMDL for Sediments
Pool Distribution	Increasing trends towards reference values		Ten Mile River TMDL for Sediments
Pool Residual Depth	>2' in low order, >3' in 3rd & higher order, at low flow	Flosi et al. 1999	Gualala River TMDL for Sediment
Pool/Riffle Distribution & depth of pools	increasing trend toward >40% length of pools > 2-3'	Flosi et al. 1998	Albion River TMDL for Sediments

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Channel Indicators (cont'd)			
Pool/Riffle Distribution & depth of pools	increasing trend toward >40% length of pools > 2-3'	Flosi et al. 1998	Big River TMDL for Sediments
Pool/Riffle Distribution & depth of pools	Pools > 2' deep (>3' in 3rd order) over 40% of length		Garcia River Sediment TMDL
Pool/Riffle Distribution & depth of pools	increasing trend toward >40% length of pools > 2-3'	Flosi et al. 1998	Mattole River TMDL for Sediments and Temperature
Pool/Riffle Distribution & depth of pools	increasing trend toward >40% length of pools > 2-3'	Flosi et al. 1998	Navarro River TMDL for Temperature and Sediments
Pool/Riffle Distribution & depth of pools	increasing trend toward >40% length of pools > 2-3'		North Fork Eel River TMDL
Pool/Riffle Distribution & depth of pools	Pools > 2' deep (>3' in 3rd order) over 40% of length	Flosi and Reynolds 1994	Noyo River TMDL for Sediments
Pool/Riffle Distribution & depth of pools	increasing trend toward >40% length of pools > 2-3'		Trinity River TMDL for Sediments
Pool/Riffle Distribution & depth of pools	Pools > 2' deep (>3' in 3rd order) over 40% of length	Flosi et al. 1998	Van Duzen River and Yager Creek TMDL for Sediments
Pools: Backwater	Increasing trend		Navarro River TMDL for Temperature and Sediments
Pools: Backwater	Increasing number per habitat length	Dietrich 1998	Noyo River TMDL for Sediments
Riffle Distribution	< 25-30% riffles (when gradient <2%)	Madej 1998	Redwood Creek TMDL for Sediments
Spatially complex channel morphology	channel specific	US FWS 1999	Trinity River TMDL for Sediments
Thalweg profile	increasing variation from the mean	Trush 1999, Madej 1999	Albion River TMDL for Sediments

Table C-2. (cont'd)..

Indicator	Target	References in TMDL text	Title
Channel Indicators (cont'd)			
Thalweg profile	increasing variation from the mean	Trush 1999, Madej 2000	Big River TMDL for Sediments
Thalweg profile	increasing variation from the mean		Gualala River TMDL for Sediment
Thalweg profile	increasing variation from the mean	Trush 1999, Madej 1999	Mattole River TMDL for Sediments and Temperature
Thalweg profile	increasing variation from the mean		Navarro River TMDL for Temperature and Sediments
Thalweg profile	increasing variation from the mean		North Fork Eel River TMDL
Thalweg profile	increasing trend in channel complexity and pool depth	Trush 1999, Madej 1999	Noyo River TMDL for Sediments
Thalweg profile	increasing variation in the thalweg elevation around the mean thalweg profile slope	Klein 1998	South Fork Eel River TMDL for Sediment and Temperature
Thalweg profile	increasing variation from the mean	Thrush 1999, Madej 1999	Ten Mile River TMDL for Sediments
Thalweg profile	increasing variation from the mean		Trinity River TMDL for Sediments
Thalweg profile	increasing trend in channel complexity and pool depth	Thrush 1999, Madej 1999	Van Duzen River and Yager Creek TMDL for Sediments
USFS Region 5 SCI "Stream Condition Inventory"	improving trends in channel morphology over time		Heavenly Valley Creek TMDL
V*, Residual pool volume	<0.21 or <0.10	Lisle & Hilton 1992, Knopp 1993, Lisle 1989, Lisle & Hilton 1999	Big River TMDL for Sediments
V*, Residual pool volume	<=0.21 (mean), <= 0.45 (max), in 3rd order streams with slopes 1-4%		Garcia River Sediment TMDL

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Channel Indicators (cont'd)			
V*, Residual pool volume	<=0.15	Lisle & Hilton 1992, 1999, Knopp 1993	Gualala River TMDL for Sediment
V*, Residual pool volume	<0.21 (fransiscan) or <0.10 (other)	Lisle & Hilton 1992, Knopp 1993, Lisle 1989, Lisle & Hilton 1998	Mattole River TMDL for Sediments and Temperature
V*, Residual pool volume	<=0.15	Lisle & Hilton 1999, Knopp 1993	Navarro River TMDL for Temperature and Sediments
V*, Residual pool volume	<0.21 (fransiscan) or <0.10 (other)	Lisle & Hilton 1992	North Fork Eel River TMDL
V*, Residual pool volume	0.27	Knopp 1993	Noyo River TMDL for Sediments
V*, Residual pool volume	<0.10	Lisle & Hilton 1992	South Fork Eel River TMDL for Sediment and Temperature
V*, Residual pool volume	<=0.21 (mean) in pools	Knopp 1993	Ten Mile River TMDL for Sediments
V*, Residual pool volume	<0.21 (fransiscan) or <0.10 (other)	Lisle & Hilton 1992	Trinity River TMDL for Sediments
V*, Residual pool volume	<0.21 or <0.10	Lisle & Hilton 1992, Knopp 1993, Lisle 1989, Lisle & Hilton 1998	Albion River TMDL for Sediments
Watershed Indicators			
Activities in unstable areas	avoid and/or eliminate	Dietrich et al. 1998, Weaver and Hagans 1994, PWA 1998	Albion River TMDL for Sediments
Activities in unstable areas	avoid and/or eliminate	Dietrich et al. 1998, Weaver and Hagans 1994, PWA 1998	Big River TMDL for Sediments

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Watershed Indicators (cont'd)			
Activities in unstable areas	avoid and/or eliminate	Dietrich et al. 1998, Weaver and Hagans 1994, PWA 1998	Mattole River TMDL for Sediments and Temperature
Activities in unstable areas	avoid and/or eliminate		Navarro River TMDL for Temperature and Sediments
Activities in unstable areas	avoid and/or eliminate		North Fork Eel River TMDL
Activities in unstable areas	avoid and/or eliminate	Dietrich et al. 1998, Weaver and Hagans 1994, Pitliick 1982, PWA 1998	Noyo River TMDL for Sediments
Activities in unstable areas	avoid and/or eliminate	Dietrich et al. 1998, Weaver and Hagans 1994, PWA 1998	Ten Mile River TMDL for Sediments
Activities in unstable areas	avoid and/or eliminate		Trinity River TMDL for Sediments
Activities in unstable areas	Reduce the number of roads and intensity of timber management located on inner gorge and potentially unstable headwall areas	PWA 1999	Van Duzen River and Yager Creek TMDL for Sediments
Annual road inspection and correction	Increasing % of road to 100%	EPA 1998	Albion River TMDL for Sediments
Annual road inspection and correction	Increasing % of road to 100%	EPA 1998	Big River TMDL for Sediments
Annual road inspection and correction	Increasing % of road to 100%		Gualala River TMDL for Sediment
Annual road inspection and correction	Increasing % of road to 100%	EPA 1998	Mattole River TMDL for Sediments and Temperature

Table C-2. (cont'd).

Indicator	Target	References in TMDL text	Title
Watershed Indicators (cont'd)			
Annual road inspection and correction	Prevent sediment delivery		Navarro River TMDL for Temperature and Sediments
Annual road inspection and correction	Increasing % of road		North Fork Eel River TMDL
Annual road inspection and correction	Increasing % of road to 100%	EPA 1998	Ten Mile River TMDL for Sediments
Annual road inspection and correction	Increasing % of road		Trinity River TMDL for Sediments
Balanced fine and course sediment budgets	channel specific	US FWS 1999	Trinity River TMDL for Sediments
Disturbed areas	decrease in area covered by roads, landings, trails, agricultural, etc.	Lewis 1998	Albion River TMDL for Sediments
Disturbed areas	decrease in area covered by roads, landings, trails, agricultural, etc.	Lewis 1999	Big River TMDL for Sediments
Disturbed areas	decrease in area covered by roads, landings, trails, agricultural, etc.	Lewis 1998	Mattole River TMDL for Sediments and Temperature
Disturbed areas	decrease in area covered by roads, landings, trails, agricultural, etc.	Lewis 1998	Noyo River TMDL for Sediments
Disturbed areas	decrease in area covered by roads, landings, trails, agricultural, etc.	Lewis 1999	Trinity River TMDL for Sediments
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994, Flanagan et al. 1998	Albion River TMDL for Sediments
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994, Flanagan et al. 1998	Big River TMDL for Sediments
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm		Gualala River TMDL for Sediment

Table C-2 (cont'd).

Indicator	Target	References in TMDL text	Title
Watershed Indicators (cont'd)			
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994, Flanagan et al. 1998	Mattole River TMDL for Sediments and Temperature
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	NMFS 2000, Flanagan et al. 1998	Navarro River TMDL for Temperature and Sediments
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994	North Fork Eel River TMDL
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994, Flanagan et al. 1998	Noyo River TMDL for Sediments
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994, Flanagan et al. 1998	Ten Mile River TMDL for Sediments
Diversion and stream crossing failure potential	<=1% of crossings divert or fail in 100 year storm	Weaver and Hagans 1994	Trinity River TMDL for Sediments
Diversion potential and stream crossing failure potential	Eliminate diversion potential (I.e., functional dips are in place at stream crossings); no unculverted fill or log crossings (designed for 50 yr. Flow)	Weaver and Hagans 1994 and 1999; Furniss et al. 1998	Van Duzen River and Yager Creek TMDL for Sediments
Fill failures	Prevent unstable fill failures that could deliver sediment to streams	Weaver and Hagans 1994 and 1999	Van Duzen River and Yager Creek TMDL for Sediments
Hydrologic connectivity of roads	decreasing length of connected roads to <=1%	Ziemer 1998, Flanagan et al. 1998, Furniss 1999	Albion River TMDL for Sediments
Hydrologic connectivity of roads	decreasing length of connected roads to <=1%	Ziemer 1998, Flanagan et al. 1998, Furniss 2000	Big River TMDL for Sediments
Hydrologic connectivity of roads	<=5% length of road draining to stream	Weaver and Hagans 1994	Gualala River TMDL for Sediment
Hydrologic connectivity of roads	decreasing length of connected roads to <=1%	Ziemer 1998, Flanagan et al. 1998, Furniss 1999	Mattole River TMDL for Sediments and Temperature

Table C-2 (cont'd).

Indicator	Target	References in TMDL text	Title
Watershed Indicators (cont'd)			
Hydrologic connectivity of roads	<=10% length of road draining to stream	RWB 2000a	Navarro River TMDL for Temperature and Sediments
Hydrologic connectivity of roads	decreasing length of roads	Weaver and Hagans 1995	North Fork Eel River TMDL
Hydrologic connectivity of roads	decreasing length of connected roads (and railroads)	Ziemer 1998, Furniss 1999	Noyo River TMDL for Sediments
Hydrologic connectivity of roads	decreasing length of connected roads to <=1%	Ziemer 1998, Furniss 1999	Ten Mile River TMDL for Sediments
Hydrologic connectivity of roads	decreasing length of connected roads to <=1%	Weaver and Hagans 1995	Trinity River TMDL for Sediments
Hydrologic connectivity of roads	Road surfaces and streams are disconnected from streams (<5% of stream crossings may be infeasible)	Weaver and Hagans 1994 and 1999	Van Duzen River and Yager Creek TMDL for Sediments
Road location, surfacing, sidecast	decreasing length next to stream, increasing % outsloped and hard surfaced roads	EPA 1998	Albion River TMDL for Sediments
Road location, surfacing, sidecast	decreasing length next to stream, increasing % outsloped and hard surfaced roads	EPA 1998	Big River TMDL for Sediments
Road location, surfacing, sidecast	decreasing length next to stream, increasing % outsloped and hard surfaced roads	EPA 1998	Mattole River TMDL for Sediments and Temperature
Road location, surfacing, sidecast	appropriate design construction and maintenance to reduce landslides		Navarro River TMDL for Temperature and Sediments
Road location, surfacing, sidecast	decreasing length next to stream, increasing % outsloped and hard surfaced roads		North Fork Eel River TMDL
Road location, surfacing, sidecast	decreasing length next to stream, increasing % outsloped and hard surfaced roads	EPA 1998	Ten Mile River TMDL for Sediments

Table C-2 (cont'd).

Indicator	Target	References in TMDL text	Title
Watershed Indicators (cont'd)			
Road location, surfacing, sidecast	decreasing length next to stream, increasing % outsloped and hard surfaced roads		Trinity River TMDL for Sediments
Sediment delivery	30% reduction of sediment from early spring runoff		San Miguel River TMDL for Sediment

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Evaluating habitat effects on population status: influence of habitat restoration on spring-run Chinook salmon

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SUMMARY

1. A key element of conservation planning is the extremely challenging task of estimating the likely effect of restoration actions on population status. To compare the relative benefits of typical habitat restoration actions on Pacific salmon (*Oncorhynchus* spp.), we modelled the response of an endangered Columbia River Chinook salmon (*O. tshawytscha*) population to changes in habitat characteristics either targeted for restoration or with the potential to be degraded.
2. We applied a spatially explicit, multiple life stage, Beverton-Holt model to evaluate how a set of habitat variables with an empirical influence on spring-run Chinook salmon survivorship influenced fish population abundance, productivity, spatial structure and diversity. Using habitat condition scenarios – historical conditions and future conditions with restoration, no restoration, and degradation – we asked the following questions: (i) how is population status affected by alternative scenarios of habitat change, (ii) which individual habitat characteristics have the potential to substantially influence population status and (iii) which life stages have the largest impact on population status?
3. The difference in population abundance and productivities resulting from changes in modelled habitat variables from the 'historical' to 'current' scenarios suggests that there is substantial potential for improving population status. Planned restoration actions directed toward modelled variables, however, produced only modest improvements.
4. The model predicted that population status could be improved by additional restoration efforts directed toward further reductions in the percentage of fine sediments in the streambed, a factor that has a large influence on egg survival. Actions reducing fines were predicted to be especially effective outside the national forest that covers most of the basin. Scenarios that increased capacity by opening access to habitat in good condition also had a positive but smaller effect on spawner numbers.
5. Degradation in habitat quality, particularly in percent fine sediments, within stream reaches located in the national forest had great potential to further reduce this population's viability. This finding supports current forest planning efforts to minimise road density and clear-cut harvests and to return forest stand structure in dry regions to the historical condition that promoted frequent low-intensity fires rather than catastrophic stand-replacing fires, as these landscape factors have been shown to influence percent fine sediment in streams.

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6. Together, these results suggest that planning focusing on protecting currently good habitat, reducing fine sediments to promote egg survival and increasing spawner capacity will be beneficial to endangered spring-run Chinook population status.

Keywords: Columbia River, life cycle, modelling, *Oncorhynchus tshawytscha*, Shiraz

Introduction

Predicting the response of populations to changing habitat is a challenging but necessary step toward optimally allocating limited resources in restoration efforts (Brooks *et al*., 2006). However, such predictions are made difficult by a lack of monitoring data to describe habitat condition and variability as well as by a limited understanding of how key habitat characteristics are influencing a species' population status (Bernhardt *et al*., 2005; Katz *et al*., 2007). These challenges are exacerbated when species use more than one ecosystem as they progress through their life-history stages (Rich, 1939; Abell, 2002).

Pacific salmon (*Oncorhynchus* spp.) are an exemplary case in point. A dramatic decline in wild salmon populations in the U.S. Pacific Northwest followed pervasive human impacts during the 19th and 20th centuries (Nehlsen, Williams & Lichatowich, 1991; National Research Council, 1996; McClure *et al*., 2003). Obvious among these impacts are habitat degradation and loss. Freshwater habitat for salmon spawning and rearing has been altered by floodplain and upland development, past forest management policies and dam construction for irrigation, flood-control, navigation and hydropower. Habitat restoration is therefore a major component of recovery plans for salmonid populations listed as threatened or endangered under the U.S. Endangered Species Act (e.g. Williams *et al*., 1999; Shared Strategy for Puget Sound, 2005; Upper Columbia Salmon Recovery Board, 2007) with hundreds of millions of dollars thus far spent in the U.S.A. to restore habitat for Pacific salmon (Pacific Coastal Salmon Recovery Fund, 2007). The economic and cultural importance of this resource, as well as the high cost of recovery, increase the need for tools to direct recovery efforts where they will be most effective.

Our objective was to model and evaluate the effects on spring-run Chinook salmon (*O. tshawytscha* Walbaum) of stream habitat change resulting from either further degradation or a suite of proposed restoration actions targeting Chinook spawning and rearing habitat in the Wenatchee River and its tributaries in the interior Columbia River basin. Wenatchee spring-run Chinook salmon are one of three extant independent populations (ICTRT, 2003) that make up the upper Columbia spring-run Chinook salmon Evolutionarily Significant Unit (ESU) which is listed as endangered under the ESA (National Marine Fisheries Service, 1999a,b). The quality and quantity of spring-run Chinook salmon habitat in the Wenatchee River basin have been degraded by the influences of roads, agricultural and residential development, reduced connectivity of off-channel floodplain habitat in the lower reaches due to berm construction and channelisation, decreased density and recruitment of large wood and water withdrawal during summer low flow periods (Andonaegui, 2001). Several local conservation plans have recently been developed to address these threats (Northwest Power and Conservation Council, 2005; Upper Columbia Salmon Recovery Board, 2007; Upper Columbia Regional Technical Team, 2008). These plans propose habitat restoration in the more heavily impacted lower catchment and conservation of habitat in the upper catchment which remains relatively intact.

To investigate the response of wild spring-run Chinook to habitat change resulting from restoration or degradation, we adapted a spatially explicit, life stage specific, population dynamics model, Shiraz (Scheuerell *et al*., 2006; Battin *et al*., 2007), to address the following questions for the Wenatchee basin population:

- How does population status change in response to alternative scenarios of habitat change?
- Which individual habitat characteristics have the potential to substantially influence population status, through either improvement or degradation?
- Do life stage specific habitat influences determine which life stage has the largest effect on population status?

Application of this population dynamics model involved developing new relationships between habitat characteristics and population vital rates (survivorship or carrying capacity) specific to this region. The model included direct effects of harvest, survival through the series of seven dams on the Columbia River, competition with hatchery fish, removal of wild fish for hatchery broodstock and climate effects on ocean survivorship in order to assess the extent to which freshwater habitat is a key factor limiting the abundance, productivity and distribution of spring-run Chinook salmon in the Wenatchee River basin. We used this model to compare the relative influences of important habitat characteristics on population status and to describe where in the basin those habitat characteristics may be altered by restoration actions and other landscape changes.

Methods

Study area and species life history

The Wenatchee River catchment drains approximately 3400 km^2 in a southeasterly direction east of the crest of the Cascade Range in central Washington State (Fig. 1). While approximately 80% of the area of the catchment is in federal ownership (95% of which is managed by the USDA Forest Service), mostly in the upper catchment, a disproportionate amount (*c.* 33%) of the riparian zones of stream reaches currently accessible to anadromous salmonids is in private ownership (Northwest Power and Conservation Council, 2005). Jorgensen *et al.* (2009) provide a more detailed description of the basin.

Wenatchee River spring-run Chinook salmon are 'stream-type' Chinook (Healey, 1991): after juveniles emerge from gravels in spring, they rear in freshwater for approximately a year before outmigrating ('Ocean-type' fish migrate shortly after hatching). A varying percentage (15–60%) move downstream through the first summer or autumn and over-winter in the mainstem Wenatchee (Don Chapman Consultants Inc., 1989; Washington Department of Fish and Wildlife, WDFW, unpubl. data), before out-migrating to the ocean in the second spring along with those that over-wintered in the tributaries. To reach the ocean, juveniles must swim 754 km down the Columbia River and pass through seven public and private dams of the Columbia River hydropower system: Rock Island, Wanapum, Priest Rapids, McNary, John Day, The Dalles and Bonneville. Adults begin their return to the Wenatchee after 1–4 years at sea, most after 2 years, re-entering the Columbia from late March to early April (Washington State Department of Fisheries, 1993). After making their way upstream past the dams, adults remain in deeper reaches of the Wenatchee system from early May to late June before moving to the upper Wenatchee mainstem and upstream tributaries to spawn from August to mid-September, with the peak in mid- to late August (Mullan *et al.*, 1992; Chapman *et al.*, 1995). Between 1960 and 1993, the average return of wild spring-run Chinook salmon to the Wenatchee basin was 2356 spawners; however between 1994 and 2003, the average return was only 423 wild fish (Fig. 2; West Coast Salmon Biological Review Team, 2003; ICTRT, 2007a).

We focused our study on the Wenatchee River basin because this subbasin of the Columbia River provided

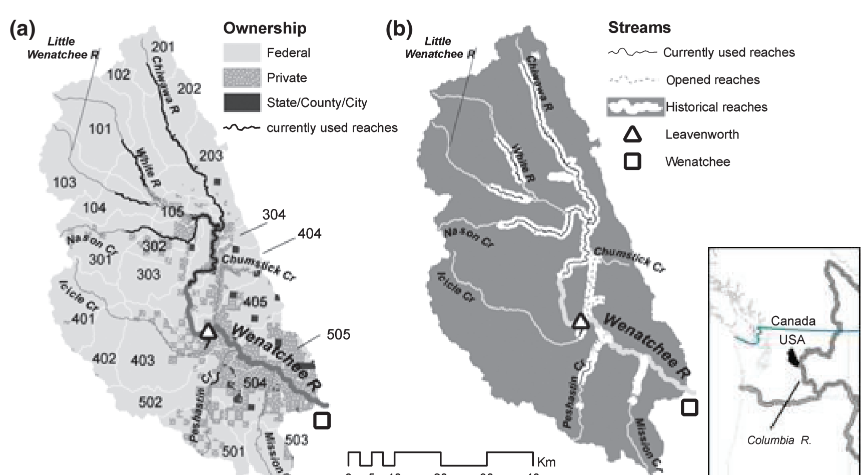

Fig. 1 Maps of the Wenatchee River basin showing (a) HUC6 model areas, current ownership and use by spring-run Chinook and (b) estimated extent of stream network occupied by Chinook historically, currently (same under no restoration and degradation scenarios), and under restoration.

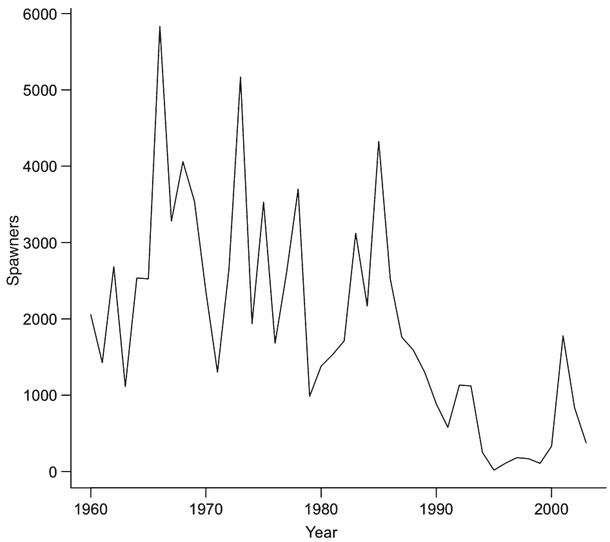

Fig. 2 The number of spring-run Chinook salmon spawners observed in the Wenatchee basin, 1960–2003.

a number of opportunities. It is included in the Intensively Monitored Watershed Project, a multi-agency effort in Washington State to determine the influence of habitat factors on salmon populations. Therefore, substantially more habitat and fish population data are available for the Wenatchee River basin than for others in the region. The diversity of impacts on spring-run Chinook salmon in the basin allowed us to produce a model that may be characteristic of populations in other subbasins of the Interior Columbia River basin; the active recovery community provided a forum for developing scenarios of restoration actions. These findings will inform future projects and monitoring efforts in the basin.

Population-habitat modelling

Population structure For modelling purposes, we separated Wenatchee basin spring-run Chinook salmon into four distinct and interacting groups, one wild and three hatchery, due to observed life stage dependent variations in spatial distributions and differences in fish response to habitat condition detailed below. The three hatchery groups were (i) the Leavenworth National Fish Hatchery (LNFH) group, produced to support a recreational and tribal fishery of spring-run Chinook salmon in Icicle Creek and to supplement harvest in the Columbia River; (ii) a Chiwawa hatchery group produced in an 'integrated recovery program' at the Rock Island Fish Hatchery Complex and intended to increase the production of wild spring-run Chinook salmon in the Chiwawa River; and (iii) a White River Hatchery group, produced in a captive broodstock program established to support the recovery of spring-run Chinook salmon in the White River (Grant PUD, WDFW & Yakama Nation, 2007).

Separating hatchery groups allowed us to (i) account for the multiple locations of broodstock collection and fry release, (ii) set hatchery-specific fractions of the wild return to be collected for broodstock each year, and (iii) have the influence of habitat condition on survivorship be group-specific. Group-specific survivorship may result when hatchery fish differ phenotypically and genetically from local wild fish. Such differentiation may occur when the original broodstock were taken from another basin, as is the case with the LNFH group (Columbia River Basin Hatchery Review Team, 2006; Murdoch *et al.*, 2006), and when selection pressures differ between hatchery and natural habitats (Busack & Currens, 1995; Knudsen *et al.*, 2006; McClure *et al.*, 2008a). Each of the hatchery groups also had a hatchery facility-specific survivorship between the life stage collected for broodstock and the stage released.

We included the hatchery groups in the model because of the potential for substantial influence on the wild population; however, our interest is in the status of the wild population in response to changes in habitat condition. Therefore all model output (e.g. productivity, mean number of smolts or spawners) is expressed in terms of wild fish.

Life history We modelled the wild fish through the following life-history stages: egg, fry, overwinter, smolt, ocean adult, upstream adult and spawner (Fig. 3). Spawners that mature without going to sea, predominantly male and termed 'mini-jacks', were not included because mini-jacks are not commonly observed among Wenatchee wild spring-run Chinook spawners (Murdoch *et al.*, 2006). Hatchery groups progressed through the same life stages after release as smolts until captured as spawning adults for broodstock. At hatchery broodstock collection, we removed an additional 3000 spawners from the LNFH group to account for those donated to tribes and other groups (Cooper, 2006). Hatchery fish that were not removed for broodstock or donation were modelled to

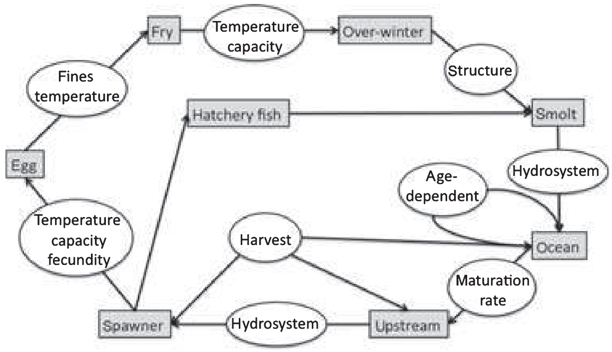

Fig. 3 Model life cycle with stages (shaded rectangles) and factors influencing stage transitions (ovals).

spawn naturally (WDFW, 2005; Columbia River Basin Hatchery Review Team, 2006) and the resulting progeny were added to the wild fish.

Harvest Harvest inflicts both direct mortality and has the potential to influence fish response to freshwater habitat changes (Scheuerell *et al.*, 2006), particularly when survival between life stages is density-dependent. The catch of interior Columbia River spring-run Chinook salmon is heavily regulated due to its importance to tribal fisheries, and the potential impacts of harvest on the recovery of these depleted populations. The harvest rates for the wild group were taken from the Spring Management Period Chinook Harvest Rate Schedule (Parties to U.S. v. Oregon, 2005). Run-size categories given on the schedule were scaled to the Wenatchee wild group based on the estimated proportion of wild fish from the Wenatchee basin among the total observed at Bonneville Dam, 1979–2001. The proportion of wild Wenatchee fish at Bonneville was back-calculated from the number and proportions of wild and hatchery spawners observed in the Wenatchee and the number of spring-run Chinook salmon counted at Bonneville Dam. A fishery for the wild group was modelled to take place only in the mainstem Columbia, reflecting current management policy (Parties to U.S. v. Oregon, 2005).

Sport and ceremonial tribal fisheries of hatchery fish (but aimed at LNFH fish) occur on Icicle Creek and in the mainstem below the hatchery facility. The harvest rates in these fisheries for the LNFH group were based on fishery-specific catches for 1999–2005 (Cooper, 2006). Ocean catch, including by-catch, took *c.* 0.2% of the return of the LNFH group and was combined with the fishery occurring in the Columbia River mainstem for simplicity. The other hatchery groups, for which we had no group-specific harvest data, were modelled at the same harvest rate as the LNFH group below Icicle Creek, because individuals in these groups have their adipose fins clipped to indicate hatchery origin and so are indistinguishable by fishers at the point of harvest. None were modelled to be harvested above Icicle Creek where there is no spring-run Chinook salmon fishery (WDFW, 2008).

Habitat-associated survival We modified a spatially explicit population dynamics model, Shiraz (Scheuerell *et al.*, 2006; Battin *et al.*, 2007), to investigate habitat influences on the status of Wenatchee basin spring-run Chinook salmon. In the model, fish were classified according to population group, life history stage, natal location and current location. Each class progressed through the life history stages and we modelled successive generations over 100 years. This sequence was repeated 500 times for each scenario of habitat conditions described below. A multi-stage, Beverton-Holt spawner-recruit function (Moussalli & Hilborn, 1986) was applied to each class at each life stage transition to determine the number of fish surviving to the next life stage:

$$N_{\text{stage}+1} = \frac{N_{\text{stage}}}{\frac{1}{p_{\text{stage}}} + \frac{1}{c_{\text{stage}}} N_{\text{stage}}} \tag{1}$$

where N_{stage} and $N_{\text{stage}+1}$ are the number in the current and next life stages, respectively, p_{stage} is the productivity or survivorship through residence in the current location and $c_{\text{stage}+1}$ is the capacity of the next location to which the group moves (more about movement below). Survivorship depended on fish location as a consequence of the relationship described below between habitat parameters (e.g. fine sediment, water temperature, habitat structure) and fish survivorship. The capacity parameter was used to cause a density-dependent response of population size at the fry and spawner life stages. To determine the density-dependent response at each location, the numbers of all wild and hatchery groups of the same life stage at that location were included in the calculation.

We incorporated all habitat variables with empirical links to spring-run Chinook salmon survivorship and for which data were available in the Wenatchee basin.

Some habitat–survival relationships were identified from the literature while others were developed from data collected in the basin, as detailed below. Where functional relationships linking habitat parameters to survivorship through a life stage were not available, survivorship through that stage was given a fixed value from the literature or based on data available from the basin as described below.

Spawner stage: Survivorship of spring-run Chinook spawners is influenced by water temperature (see reviews by McCullough, 1999; and Richter & Kolmes, 2005). We used a water temperature-dependent survivorship function developed by Scheuerell *et al.* (2006) from observations by Cramer (2001) of wild spring-run Chinook:

$$p_{1,\mathrm{Tw}} = \begin{cases} 1 & \text{if } T_{\mathrm{pre}} < 16 \\ 1 - 0.15(T_{\mathrm{pre}} - 16) & \text{if } 16 \leq T_{\mathrm{pre}} < 22.6 \\ 0.01 & \text{if } T_{\mathrm{pre}} \geq 22.6 \end{cases} \tag{2}$$

where T_{pre} is the mean of daily maximum temperature (°C) August–September. We developed a separate function for hatchery spring-run Chinook survival based on Cramer's (2001) observations of reduced survivorship of hatchery fish in the same conditions:

$$p_{1,\mathrm{Th}} = \begin{cases} 1 & \text{if } T_{\mathrm{pre}} < 16 \\ 5.43 - 0.28 * T_{\mathrm{pre}} & \text{if } 16 \leq T_{\mathrm{pre}} < 19 \\ 0.01 & \text{if } T_{\mathrm{pre}} \geq 19 \end{cases} \tag{3}$$

Fecundities of age-three, -four, -five and -six females from LNFH were derived from the mean fecundity of grouped ages and mean age distribution 1994–2005 reported by Cooper (2006) (Table 1). The fecundities for age-four wild and Chiwawa hatchery females were taken from Murdoch *et al.* (2006). For age-three and -five spawners of the wild and Chiwawa hatchery groups, we selected the values used in another modelling effort (Cooney *et al.*, 2002) that incorporated age-specific fecundities for upper Columbia River spring-run Chinook which were derived from data in Chapman *et al.* (1995). The White River hatchery spawner fecundities were assumed to be the same as those of adults from the Chiwawa hatchery. The fecundity of age-six females of each group was assumed to be the same as that of age-five fish from the respective groups, except for the LNFH group for which data were available for age-six females (Cooper, 2006).

Table 1 Fecundity per spawner

Spawner age	Wild	LNFH	Chiwawa and White hatcheries
3	1000	500	1000
4	2417	2100	2338
5	2700	2500	2700
6	2700	2500	2700

We estimated spawner capacity using the intrinsic potential analysis of the Interior Columbia Technical Recovery Team (ICTRT, 2007b) which predicts historical fish numbers based on stream gradient, width and valley confinement – applied to available spawning area. We also considered actual spawner and redd counts conducted by the Chelan County Public Utility District and the WDFW from 1958 to 2003 (C. Baldwin, WDFW, W.A. Wenatchee, pers. comm.). When the maximum number of spawners observed in an area was greater than the number estimated based on the intrinsic potential analysis, we used the observed values.

Egg stage: Water temperature influences egg-to-fry survivorship in a nonlinear fashion with decreased survival above and below an optimal range (Fowler, 1972; Murray & McPhail, 1988). We used the same survivorship function employed in Scheuerell *et al.* (2006):

$$p_{2,T} = \begin{cases} 0.273T_{\mathrm{inc}} - 0.342 & \text{if } 1.3 \leq T_{\mathrm{inc}} < 4.7 \\ 0.94 & \text{if } 4.7 \leq T_{\mathrm{inc}} < 14.3 \\ -0.245T_{\mathrm{inc}} + 4.44 & \text{if } 14.3 \leq T_{\mathrm{inc}} < 18.1 \\ 0.01 & \text{if } T_{\mathrm{inc}} \geq 18.1 \end{cases} \tag{4}$$

based on the findings of Velsen (1987) and Beacham & Murray (1989), where T_{inc} is the mean of 24 h daily means of water temperature (°C) during the incubation period (August–May).

The percentage of fine sediments in the streambed also has a strong negative effect on egg-to-fry survivorship (Tappel & Bjornn, 1983; Wood & Armitage, 1997). We used data from Tappel & Bjornn (1983) to develop a relationship for fines:

$$p_{2,f} = \begin{cases} 0.93 & \text{if } f < 11.6 \\ -5.21 + 1.54 & \text{if } 11.6 \leq f < 28.3 \\ 0.06 & \text{if } f \geq 28.3 \end{cases} \tag{5}$$

where f is % fines < 1.7 mm.

Fry stage: Survivorship through the fry stage to the overwintering stage is influenced by summer water temperatures (see reviews by McCullough, 1999; Richter & Kolmes, 2005). We used the survivorship function developed by McHugh, Budy & Schaller (2004) based on data from Brett (1952), McCormick, Hokanson & Jones (1972), and Coutant (1973):

$$p_{3,T} = \begin{cases} \exp\left\{-\left[\left(\frac{T_{\text{sum}}}{27.0271}\right)^{10.74}\right]\right\} & \text{if } T_{\text{sum}} > 17.8\,^{\circ}C \\ 1 & \text{if } T_{\text{sum}} \le 17.8\,^{\circ}C \end{cases} \quad (6)$$

where T_{sum} is mean daily temperature (ºC) August–September.

We estimated fry capacity using the intrinsic potential analysis of the ICTRT (2007b), which predicts historical fish numbers based on a relationship they developed between maximum fry densities observed in relatively pristine reaches of Salmon River drainage (Idaho) tributaries (Petrosky & Holubetz, 1988), and stream gradient, width and valley confinement.

Overwinter stage: Structures in pools have a strong influence on survivorship through the overwintering stage (Hillman, Chapman & Griffith, 1989a,b). To model the influence of structure we used a function developed by Cramer (2001) based on work by Raleigh, Miller & Nelson (1986):

$$p_{4,\text{str}} = \begin{cases} \left(20 + 80 * \frac{\%\,\text{structure}}{15}\right)/100 & \text{if } \%\,\text{structure} < 15 \\ 1 & \text{if } \%\,\text{structure} \ge 15 \end{cases} \quad (7)$$

where *%structure* is the percent of pool area covered by cobbles and boulders. We assumed that fish numbers were not limited by capacity during this stage, given the combination of downstream movement and capacity limits during the previous fry stage in summer when there was less habitat area due to lower discharge.

Smolt and ocean stages: We used literature values for survival through the Columbia River mainstem (Grant PUD, 2003; Skalski *et al.*, 2005). From Rock Island dam (rkm 729.7), downstream of the mouth of the Wenatchee River (rkm 753.8), to Bonneville dam (rkm 235.1), upstream of the Columbia River Estuary, survivorship was set at 0.441. We assumed that capacity was unlimited during the smolt stage.

Survival rate for the first ocean year included survival through the estuary as well, following McClure *et al.* (2008b) (Table 2). The wild fish group was assigned a rate of 0.0643 ± 0.05 (SD), reflecting mean survivorship through this stage as estimated by McClure *et al.* (2008b) for the entire period of record (1966–2001). The survival rates of hatchery groups were set at 50% (LNFH group) and 75% (all other hatchery groups) of that of the wild group (Cooney *et al.*, 2002). Survival rates for subsequent ages of ocean fish were taken from an upper Columbia River spring-run Chinook salmon model (Cooney *et al.*, 2002) which used values from the Pacific Salmon Commission (2001) for simulating harvest management scenarios. Capacity during all ocean ages was assumed to be unlimited.

Maturation and Columbia mainstem survivorship: Age-specific maturation rates, i.e. the probability that ocean fish will return upstream to spawn (Table 3), were derived from the age distribution of all spawners and age-specific sex ratios (Chapman *et al.*, 1995; Cooper, 2006; Murdoch *et al.*, 2006). For wild and Chiwawa hatchery fish, the sex ratio of age-five spawners was not available, so we used the same sex ratio as for age-four fish. The maturation rates for White River hatchery fish were assumed to be the same as those from the Chiwawa hatchery. The maturation rates were based on females because they produce the eggs for the next generation.

The survival rate for maturing adults returning upstream through the Columbia mainstem was set at 0.794 based on the analysis by McClure *et al.* (2008b) of recent PIT-tag data. Capacity was assumed to be unlimited for adults in the mainstem Columbia River.

Table 2 Survival rates for ocean stages

Ocean stage	Wild	LNFH	Chiwawa and White hatcheries
First year	0.064 (0.05)	0.032 (0.05)	0.048 (0.05)
Second year	0.80	0.80	0.80
Third year	0.90	0.90	0.90
Fourth year	0.90	0.90	0.90

Values in parentheses are SD.

Table 3 Rates at which ocean stages mature to upstream stages

Ocean stage	Wild	LNFH	Chiwawa and White hatcheries
First year	0	0.051	0.485
Second year	0.650	0.723	0.986
Third year	0.999	0.987	1
Fourth year	1	1	1

Juvenile movement and spawner distribution With sixth-field hydrologic unit codes (HUC6; Seaber, Kapinos & Knapp, 1987) as our unit of scale, we allowed fish to redistribute themselves at the beginning of the fry stage by either remaining in their natal location or moving one HUC6 upstream or downstream, within observed upstream limits (NMFS unpublished GIS layer). Within these limits, fry distributed themselves in an ideal-free manner by moving to the HUC6 with habitat variable values that resulted in the greatest survivorship as constrained by capacity for each area.

We developed another movement function to address observations that a variable percentage of fry move downstream in late summer to overwintering habitat in the Wenatchee mainstem (Don Chapman Consultants Inc, 1989). To identify predictors for the number of early emigrants observed from the Chiwawa River 1992–2003 (Andrew Murdoch, WDFW, Wenatchee, WA, pers. comm), we used multiple linear regression to investigate various predictors related to discharge and fish density. The model with the lowest AIC ($P < 0.001$, adjusted $R^2 = 0.872$, AIC = 189.2886) was

$$mvmt_{4,Q} = -17040 + 102.9Q_{8\text{low}} + 0.03221\ \text{egg} \quad (8)$$

where $\text{mvmt}_{4,Q}$ is the number of fish in a tributary moving downstream to overwinter in the mainstem Wenatchee, $Q_{8\text{low}}$ is minimum August discharge (cfs) at the tributary mouth and egg is the total number eggs deposited in the tributary. We excluded water temperature as a predictor because we had only 3 years of data from the Chiwawa River. Minimum August discharge at the mouth of each tributary was estimated based on a relationship between yearly minimum August discharge and drainage area at each of 14 USGS stations for which data were available in the Wenatchee basin (1907–2005, with the range of years of data varying with stations; USGS, 2006; Raymond R. Smith, USGS, Spokane, WA, pers. comm). This movement function was applied following summer survivorship of the fry stage, when fry transitioned to the overwintering stage.

We used the distribution of model output spawners among the four Level IV Ecoregions (Omernik, 1987) present in the Wenatchee basin to characterise the diversity of Wenatchee spring-run Chinook salmon. In this way we used spatial distribution across distinctly different habitats, ecoregions in this case, as a proxy for genetic diversity.

Scenarios of change in habitat variables We used the habitat–survivorship relationships described above to model spring-run Chinook salmon response to five scenarios of habitat quality and quantity: (i) current conditions, (ii) historical conditions, a depiction of what the basin might have been like before European settlement, (iii) no restoration, where current rates of change in natural and human activities were extended into the future, (iv) restored conditions resulting from implementation of restoration actions proposed in local conservation plans (Northwest Power and Conservation Council, 2005) (Upper Columbia Salmon Recovery Board, 2007) and (v) a prediction of future habitat degradation (described below). Jorgensen *et al.* (2009) describe the development of scenarios one to four.

For the restoration scenarios involving increases in habitat, the locations of removed culverts and reconnected side channels were determined by actions currently proposed for the basin (Northwest Power and Conservation Council, 2005). Where descriptions were only generally given (e.g. 'Peshastin River below Ingalls Creek'), we placed side-channels in unconfined valleys (valley width > four times bankfull width) and estimated area as the length of the main channel by an arbitrary 0.25 of the width of the main channel. For the historical scenario, we removed all culverts that blocked Chinook passage and we used the same side-channel additions as in the restoration scenario due to the absence of data describing historical side-channel distribution. Table 4 shows the resulting scenario-specific fry and spawner capacities.

We also developed a scenario of future degradation of habitat to predict the impact on the wild population of a reasonable decline in habitat quality. We estimated habitat degradation in each HUC6 by increasing or decreasing habitat values from the no restoration future scenario by one standard deviation, derived from the posterior distributions of the habitat estimates (Jorgensen *et al.*, 2009), depending on whether increasing or decreasing the value decreased fish survivorship. For example, the percent of fine sediment in spawning gravels was increased while percent cobble and boulders in pools was decreased. We did not have a distribution for the capacity estimates or a reliable means of estimating degradation of habitat quantity, so we used the current

Table 4 Fry and spawner capacities for each model scenario (separated by '/'). 'No restoration' and 'degradation' scenarios used the same values as the 'current' scenario

Area	Historical	Current	Restoration
101	13 837/92	13 837/92	13 837/92
102	229 144/1060	224 325/1038	224 325/1038
103	0/0	0/0	0/0
104	121 764/563	106 549/493	106 549/493
105	9059/41	6910/31	6910/31
201	20 976/97	17 778/95	17 778/95
202	239 042/1404	233 240/1404	233 240/1404
203	237 617/1100	209 937/971	209 937/971
301	66 746/283	51 715/245	57 159/245
302	219 471/929	197 201/912	219 471/929
303	5104/23	0/6	0/6
304	271 169/1255	270 778/1253	270 778/1253
401	0/0	0/0	0/0
402	0/0	0/0	0/0
403	48 118/539	35 242/539	35 242/539
404	49 712/192	0/0	49 712/192
405	86 185/395	0/5	26 377/118
501	281/25	0/25	0/25
502	67 597/354	23 675/354	28 103/354
503	0/0	0/0	0/0
504	41 198/190	0/0	0/0
505	0/1	0/1	0/1

capacity estimates with the degraded habitat characteristics in this scenario.

Sensitivity analysis We conducted sensitivity analyses to evaluate which specific habitat variables had the greatest influence on fish population dynamics, where those key habitat variables had the greatest potential to effect change in fish numbers, and which life stages were therefore the most sensitive to habitat changes likely to be influenced by restoration or degradation. For this sensitivity analysis, we changed one variable by ±1 SD from its estimated value in either the historical scenario (for improvement) or the no restoration future scenario (for degradation) across all HUC6 areas while each of the other variables was held at its estimated current value. We then repeated the analysis for each habitat variable in turn, changing only one variable at a time. Because the SD used was a measure of the variation in posterior estimates of habitat condition under different scenarios (Jorgensen *et al*., 2009), these values fell inside the range of current observed values and are therefore realistic values of improvement or degradation. To test the sensitivity of response to changes in capacity, we used estimates of historical capacity.

Results

Comparing predicted and observed population parameters

A comparison between estimates from field surveys and model results under the current habitat conditions showed a close correspondence in values for smolts, spawners and spawners-per-spawner, thus providing evidence for the validity of the model and its assumptions. The predicted mean number of wild spawners (1600, SD 800) was similar to that observed (1276, SD 1097) over the years 1980–2001 (ICTRT, 2007a). The mean number of smolts predicted by the model (338 800 SD 690 200) was greater than that estimated for brood-years for which smolt-trap data were available (1999–2002: 164 011, SD 122 094; Andrew Murdoch, WDFW, Wenatchee, WA, unpubl. data). However, there were few years with smolt observations and the model estimate fell within the range observed during that period.

Scenarios of habitat change

The restoration scenario had approximately the same abundance and productivity of wild spawners as the scenario with current habitat conditions, as did the scenario of no future restoration actions (Fig. 4). The scenario of future degradation had 51% fewer spawners and 40% lower productivity at its peak relative to the scenario with current conditions. The historical habitat condition scenario resulted in 54% more wild spawners than the estimated number of wild spawners in the scenario with current habitat conditions (excluding hatchery strays in counts under current conditions in all of these reported values). Productivity was greatest in the historical conditions scenario as well, with spawner-to-spawner survivorship greater than the replacement rate at abundances less than *c.* 3400 spawners.

The geographical distributions of spawners were similar among scenarios (Table 5). In all scenarios, more than 95% of spawners occurred in the same two Ecoregions: Chiwaukum Hills and Lowlands (49–54%) and Wenatchee/Chelan Highlands (42–48%). A small proportion of spawning was predicted to occur in the North Cascades Highland Forests in all scenarios. A fourth ecoregion, the Channeled Scablands, is located in the lower mainstem and the predicted historical spawning areas in this ecoregion are now

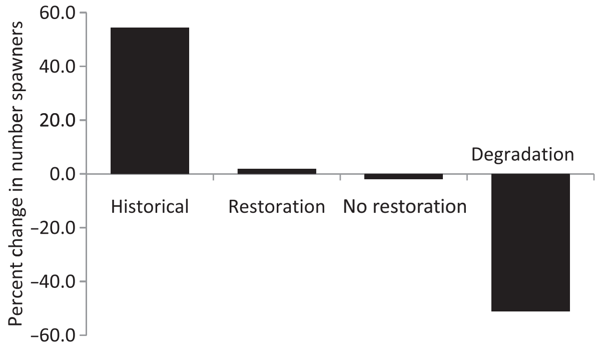

Fig. 4 Percent change in annual spawners, relative to the current scenario, for scenarios of habitat change.

encompassed by the city of Cashmere. No spawning was predicted in the other scenarios to occur in the now degraded reaches of this ecoregion.

Sensitivity analyses

Across the variables we tested, the greatest increase in mean smolt and spawner numbers occurred with a decrease in percent fine sediments in the Middle and Lower Chiwawa, Lower Nason, Lower White and Upper Wenatchee mainstem (Table 6). Increasing spawner capacity also increased fish numbers, although not as much as fines. Spawner capacity increases resulted in small increases in spawner numbers in the Lower Chiwawa, Upper Nason and Lower Little Wenatchee Rivers. The variables with the greatest potential to contribute to reductions in both mean smolt and spawner numbers were percent fine sediments and incubation temperature. The negative effect of increasing percent fine sediments was greatest in the Lower Little Wenatchee, Middle Chiwawa and Upper Nason and White Rivers. Decreasing incubation temperature had the greatest effect in the Middle and Lower Chiwawa and Upper Wenatchee mainstem.

Table 5 Distribution of spawners among Level IV Ecoregions, as estimated under three scenarios. 'No restoration' and 'degradation' scenarios had the same values as the 'current' scenario

Ecoregions	Historical	Current	Restoration
Channeled Scablands	0.01	0	0
Chiwaukum Hills and Lowlands	0.54	0.49	0.51
North Cascades Highland Forests	0.03	0.03	0.03
Wenatchee/Chelan Highlands	0.42	0.48	0.46

Table 6 Change relative to current scenario in the number of smolts and spawners resulting from sensitivity analysis: improvement and degradation of individual habitat variables with other variables held at estimated current values

	Improved (%)		Degraded (%)	
Habitat variable	Smolts	Spawners	Smolts	Spawners
Fine sediment	161*	75*	−29*	−12*
Incubation water temperature	1	0	−17*	−10*
Spawner capacity	2	5*	−1	−1
Fry capacity	3	1	0	−1
Spawner water temperature	0	0	−2	−3
Fry water temperature	0	−1	−1	−1
Cobble and boulder in pools	0	0	−1	−1

*Significantly different from result of current scenario with *t*-tests, $\alpha = 0.05$ and Bonferroni adjustment for multiple comparisons.

Improving all variables for particular life stages showed that, among freshwater stages, survival through the egg stage is the most sensitive to restoration, a response driven primarily by the influence of fine sediment on survival (Fig. 5). The greatest potential increases in spawner abundance due to maximum habitat improvement occur in those areas where survival through the egg stage is limiting in the current scenario. We did not include first year ocean survival in the sensitivity analysis because we were unable to identify empirical influences of freshwater habitat change on survival through this life stage (although see McGurk, 1996). However because the value in the model for mean survival through this stage is quite low (0.0643), first year ocean survival also has a substantial influence on spawner numbers.

Discussion

Our modelling suggests that, historically, populations had substantially higher productivity and abundance. While the restoration actions that we were able to model are by themselves not predicted to meet restoration goals, the results of the degradation scenario indicate that these actions are critical to prevent substantial worsening of this population's status. Our measure of diversity, distribution of

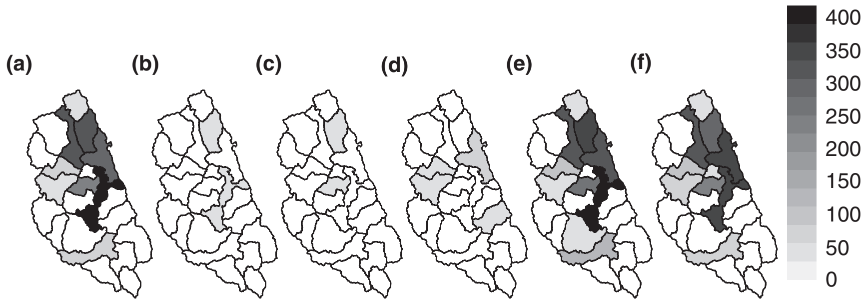

Fig. 5 Change, relative to current scenario, in mean number of annual spawners and their distribution within the basin resulting from optimising: (a) habitat characteristics influencing egg-to-fry survivorship, (b) habitat characteristics influencing fry-to-overwintering stage survival, (c) fry capacity, (d) spawner capacity, (e) both a and c, (f) both a and d.

spawners among ecoregions, was little affected by scenarios of future habitat condition. However, in contrast to abundance and productivity, current diversity was not markedly different from the historical habitat scenario. This is consistent with the lack of spatial structure impairment identified by the ICTRT (2005).

The potential for increases in population abundance and productivity, as indicated by the difference between the current and historical conditions scenario, suggests that restoration efforts may need to be redirected or the level of actions increased in order to improve natural production of Wenatchee River spring-run Chinook salmon. Results from our sensitivity analysis indicated where additional and redirected restoration efforts may achieve a more positive fish response, as well as where habitat degradation posed the greatest risk. Of the habitat variables we modelled, percent fine sediment in the streambed had the greatest potential to either increase or decrease the spawner numbers and productivity of spring-run Chinook salmon. In fact the influence of fines was responsible for most of the decrease in numbers from the historical to current to degraded scenarios. The areas with the greatest potential for a reduction in fine sediment from estimated current values are the upper Wenatchee mainstem and the lower reaches of the major spawning tributaries, spawning areas where higher values of percent fines were correlated with less forest cover, more anthropogenic impervious surface area and higher road density (Jorgensen *et al.*, 2009). The areas with the greatest potential to be degraded by an increase in fines, from for example future development, are the upper White and Nason Rivers, the middle section of the Chiwawa River and the lower section of the Little Wenatchee. These important areas for Chinook production currently have relatively low fine sediment values and lie almost entirely within the Wenatchee National Forest where high quality habitat is being protected. In fact, clear-cuts and roads, factors likely to contribute to increased fine sediment (Meehan, 1991; Jorgensen *et al.*, 2009), are to be further minimised according to the most recent draft Forest Plan (Hayman & Bond, 2006). By decommissioning roads, eliminating clear-cuts and returning forest structure to a state that promotes frequent low-intensity fires rather than catastrophic stand-replacing fires, the draft Forest Plan promises to maintain current conditions of fine sediments that are favourable to spring-run Chinook salmon production.

Spawner numbers were also sensitive to changes in mean water temperature during the incubation period. Road density was most closely associated with water temperature during the incubation period (Jorgensen *et al.*, 2009). It seems unlikely that there is a causal connection between road density and water temperature; although Bartz *et al.* (2006) found a similar relationship using different methods. Perhaps road density is related to some causal process not explicitly accounted for, but somehow incorporated into the road density variable (Jorgensen *et al.*, 2009). At any rate, the current draft of the Wenatchee Forest Plan would prevent increased road density in most of the Chiwawa basin, one of the two areas with potential for reduced egg-to-fry survival due to degradation of water temperature during this period. In the other area, the upper section of the Wenatchee mainstem, a greater percentage of the area is in private ownership. Increased development and any associated increase in road density may degrade water temperature during the incubation period. In addition, the future increase in air temperature predicted for the region due to climate change (Mote *et al.*, 2003) also may have a significant impact on water temperature and thus egg-to-fry survivorship in the future.

Our model predicted that actions increasing spawning capacity beyond the amount estimated for the restoration scenario may also be effective, although not as much as reducing fine sediment (Fig. 5). When we modelled an increase in spawner capacity only, by removing culverts that are barriers to upstream passage, the mean number of spawners increased. Increases in spawner abundance only occurred where the newly accessible habitat was able to support spring-run Chinook salmon. Some of the culverts scheduled for removal or improvement opened stream reaches with a relatively high gradient, targeting steelhead (*O. mykiss*, Walbaum), but not suitable for spring-run Chinook salmon (Everest & Chapman, 1972; Petrosky & Holubetz, 1988). In other cases, newly accessible habitat was encompassed by urban or rural development and of poor quality due to extensive impervious area, high road density and limited forest cover. Sensitivity analyses highlighted reaches where additional barrier removal would increase adult abundance. For example, ICTRT (2007b) estimated that currently inaccessible portions of Big Meadow Creek, a tributary of the Chiwawa River, have high intrinsic potential to support fish. Removal of barriers to that habitat would likely further increase spring-run Chinook salmon population size. On the other hand, Mission Creek, another stream that includes some reaches with high intrinsic potential ICTRT (2007b), is currently degraded and additional barrier removal there was not predicted to significantly increase spawner success.

Areas for future exploration

This first step in developing a habitat model for the Wenatchee basin indicates some important areas for further work. For example, available data did not allow us to include some restoration actions planned for the Wenatchee basin, such as the placement of large wood in channels and salmon carcass additions for nutrient enhancement. With sufficient data to incorporate such relationships into the model, larger suites of recovery actions could be evaluated to determine their effects on the predicted number of spawners.

The influence on Chinook salmon population dynamics of such other types of restoration actions can be incorporated easily into the model via the Moussalli & Hilborn (1986) multi-stage Beverton-Holt spawner-recruit function as data become available to link specific habitat changes to fish survivorship or capacity. For this reason, monitoring fish response to restoration actions and other habitat change is key to establishing and validating links between landscape change, habitat change and species response (McDonald *et al.*, 2007), thereby improving models. To be useful in this respect, monitoring must explicitly link fish survivorship between life stages to measurable habitat variables at those stages. Our model used habitat variable values based on data collected from the Wenatchee River basin; however the habitat–survivorship relationships were developed from observations of other spring-run Chinook salmon populations. Current monitoring efforts in the Wenatchee River basin, as part of the multi-agency Intensively Monitored Watershed Project, promise to result in habitat–survivorship relationships specific to this population. These can be readily incorporated into our model, thereby increasing confidence in its results. Models based on relationships so established will be invaluable in assessing the relative impacts and interactions of the multiple factors contributing to species recovery.

Another important area for additional work is exploring the impact of artificial propagation on this population. Hatchery fish can influence the viability of wild spring-run Chinook salmon primarily by competing for shared resources (Fresh, 1997) and by interbreeding with them (Gharrett & Smoker, 1993; Utter, 2001). The ambitious hatchery supplementation programs that have been initiated in the Wenatchee River have the potential to generate a substantial number of returns to natural spawning areas in the Wenatchee River, resulting in a significant number of hatchery fish competing with wild fish for spawning sites and opportunities to fertilise eggs. For example, stray returns from the Leavenworth hatchery program have contributed up to 35% of the naturally spawning Chinook salmon in extremely low natural return years. Any interbreeding between hatchery and wild fish may lead to reduced fitness of endangered wild fish (Taylor, 1991; Araki *et al.*, 2008). The Shiraz model framework is well suited to exploring how population responses to habitat restoration may be influenced by life stage specific survivorship decrements due to hatchery parentage when there is interbreeding between hatchery and wild fish.

This model may also be used to predict the influences of other factors on life stage specific survivorship and fecundity. These include climate change impacts on freshwater habitat characteristics such as water temperature and quantity (Battin *et al*., 2007; Crozier, Zabel & Hamlet, 2008), toxic chemicals (e.g. Spromberg & Meador, 2005) and variability in predation (e.g. Good *et al*., 2007). The flexibility to account for diverse impacts at each life stage in a spatially explicit manner makes this modelling framework ideal for informing the management of any species by directing the most appropriate actions toward the locations and life stages where they will be the most effective.

Our model of Wenatchee basin spring-run Chinook salmon population dynamics predicted that a subset of proposed restoration actions would not appreciably increase mean smolt or spawner numbers. However, increases were predicted with further improvements in modelled habitat variables, particularly the percentage of fine sediments in spawning gravels and to a lesser extent opening access to habitat in good condition. Furthermore, the model indicated strong potential for further deterioration of this population's status if habitat conditions worsen. Productive stream reaches with currently low fine sediment values, primarily in the Wenatchee National Forest, should therefore be a priority for preservation. The current draft of the Wenatchee Forest Plan, scheduled to be complete in 2009, addresses the key human-influenced landscape factors impacting percent fine sediments: roads and forest cover.

Using a spatially explicit model that integrates across life stages the known factors influencing fish population dynamics, we have shown that habitat restoration has the potential to increase spring-run Chinook salmon abundance and productivity and thereby contribute to their recovery. Equally importantly, our work strongly suggests that protecting and restoring freshwater habitat is important to prevent further declines. Such actions will also be necessary for increasing the resilience of endangered salmon populations to other threats, such as poor ocean conditions (McClure *et al*., 2003; Scheuerell & Williams, 2005).

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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.

KEY WORDS salmonid survival; respiration; hyporheic; habitat quality

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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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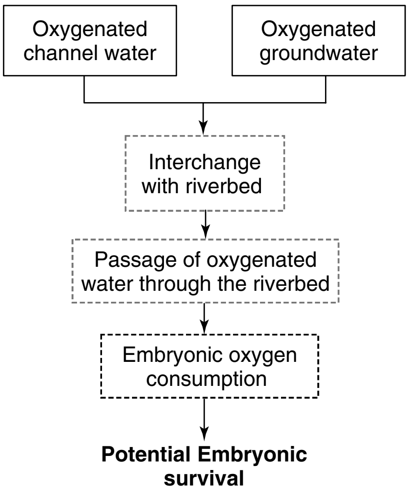

Figure 1. Summary of the dominant factors (solid boxes) and processes (dotted boxes) controlling the availability of oxygen to respiring salmonid embryos

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

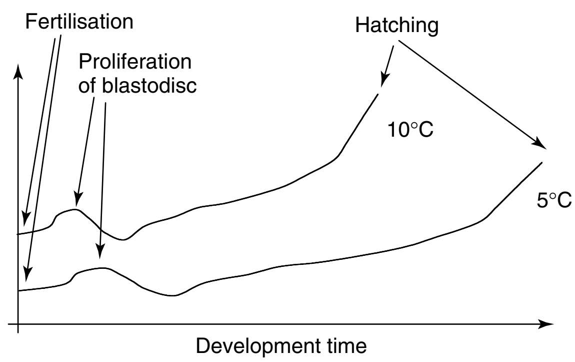

Figure 2. Summary of the influence of temperature and stage of development on rates of oxygen consumption

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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

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(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

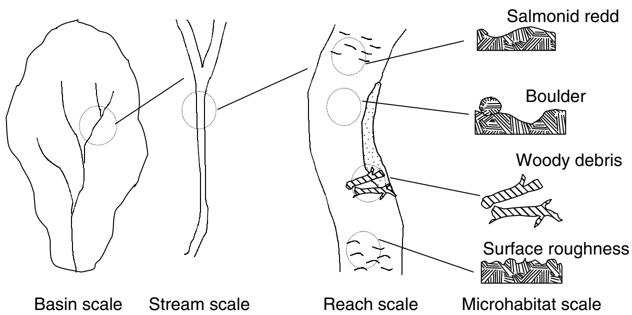

Figure 3. Spatial hierarchy adopted to describe exchange processes (modified from Frissell *et al.* (1986))

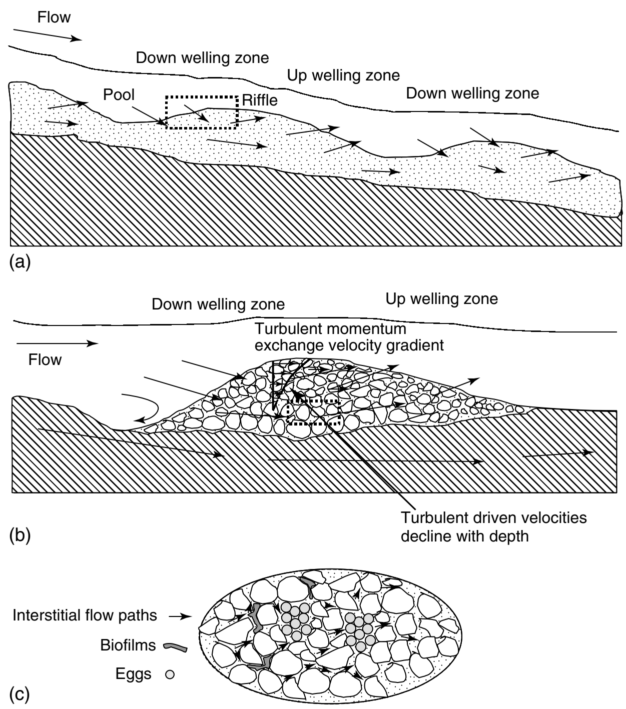

Figure 4. (a) Reach-scale surface subsurface exchange flows. (b) Micro-scale exchange flows (redd). (c) Interstitial flow paths within the egg pocket (see below)

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

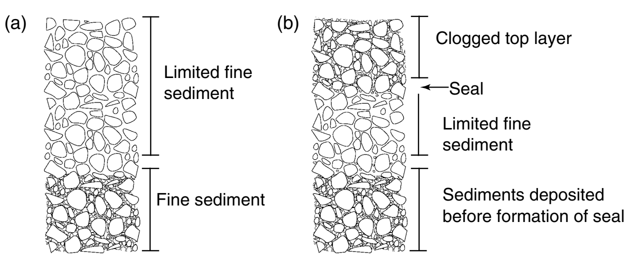

Figure 5. Trends in fine sediment accumulation: (a) 'bottom-up' sediment deposition; (b) formation of a seal near the bed surface (after Alonso *et al*. (1996))

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).

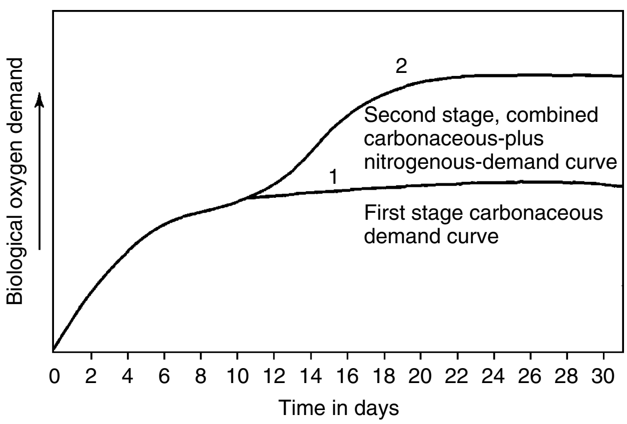

Figure 6. Typical oxygen demand response curve: (1) first stage BOD curve for oxidation of organic matter; (2) second stage NOD, influence of nitrification after Delzer and Mckenzie (2003)

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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).

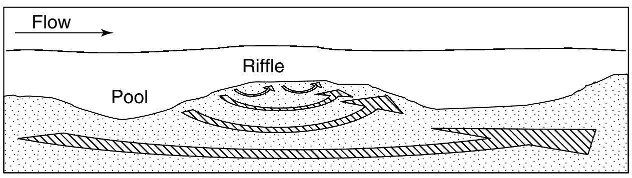

Figure 7. Summary of hyporheic flow paths. The thickness of the lines schematically represents the potential depletion in oxygen concentration of water within that flow path

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.

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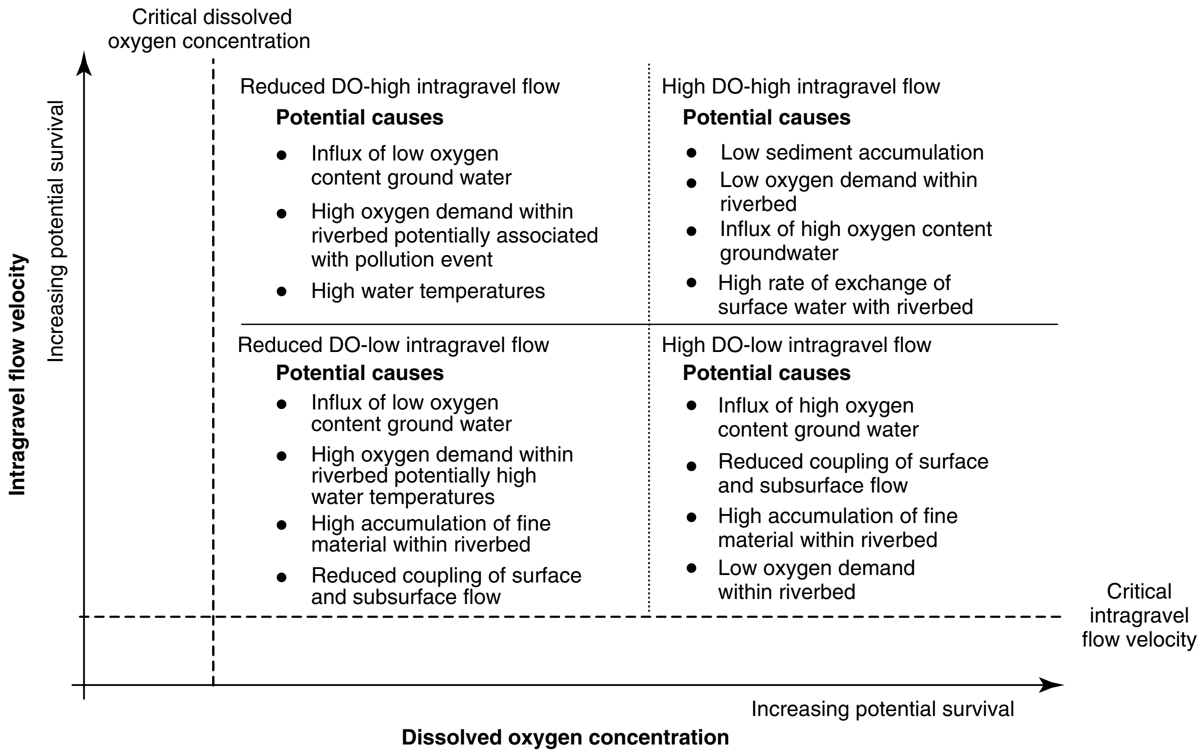

Figure 8. Overview of factors influencing the availability of oxygen to incubating salmonid embryos

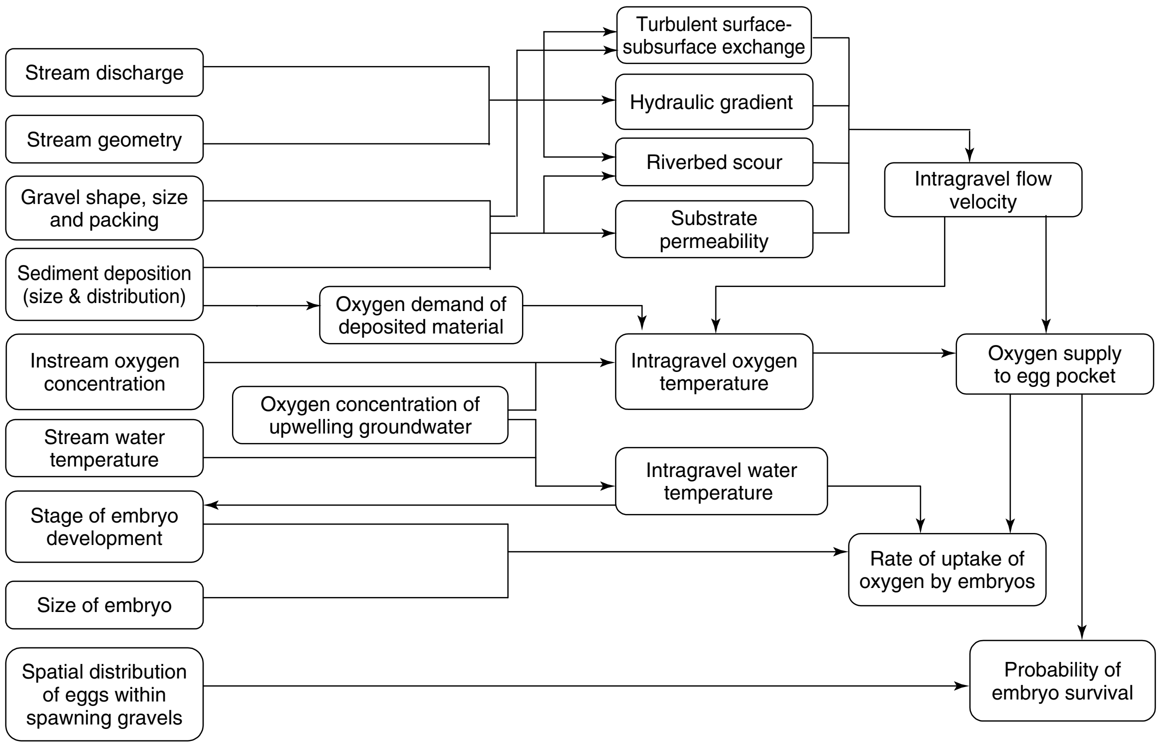

Figure 9. Conceptual model of the relationship between oxygen supply (flux) and embryonic survival. Also detailed are hypothetical scenarios potentially influencing oxygen fluxes

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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