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Hyporheic zone processes in a canalised agricultural stream: implications for salmonid embryo survival

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With 10 figures and 3 tables

Abstract: Agricultural practices have the potential to influence hyporheic exchange through increased fine sediment loads and through reduced hydraulic conductivity, bed roughness and morphological diversity. These impacts can reduce connectivity between stream and hyporheic waters to the detriment of salmonid embryos. Salmonids bury their eggs in streambed gravels, typically to depths of up to 300 mm and for incubation periods of up to 6 months. Embryo survival is dependant on a complex range of factors which critically includes the delivery of oxygen from surface waters. This paper investigates hyporheic zone exchange processes, oxygen concentration and embryo survival in a canalised agricultural stream at a range of nested spatiotemporal scales. Results are contrasted with those from the Girnock Burn, a relatively undisturbed catchment. Conservative tracer experiments were used to assess reach average hyporheic exchange using the USGS OTIS model. Artificial redds were used to assess reach scale variability in hyporheic processes. Incubation stacks were used to assess embryo mortality and hyporheic water quality with depth at the scale of individual redds. Optodes (optical dissolved oxygen sensors) were used at a sub-set of sites to assess fine scale temporal variability in hyporheic oxygen and temperature. Stream and hyporheic hydrochemistry were used to infer source water contributions and provenance. Data showed that reach average hyporheic exchange in the Newmills Burn was ca. five times less than in the Girnock Burn. Dissolved oxygen (DO) concentrations related strongly to spatiotemporal patterns of groundwater (GW) discharge. Embryo survival was significantly correlated with DO. It is suggested that low DO in the Newmills Burn relates to groundwater upwelling and limited hyporheic exchange caused by a combination of low morphological diversity, hydraulic conductivity and bed roughness. It is suggested that future studies of embryo survival should look beyond the single issue of fine sediment effects to include a broader understanding of hyporheic zone processes.

Key words: fine sediment loads, bed roughness, reduced hydraulic conductivity, oxygen concentration, groundwater, surface waters, optodes.

Introduction

In recent years there have been major advances in hyporheic sampling methods (Malcolm et al. 2004, Zimmerman & LaPointe 2005, Fritz & Arntzen 2007, Malcolm et al. 2009, Soulsby et al. 2009) and modelling approaches (Storey et al. 2003, Cardenas & Wilson 2006, 2007, Boano et al. 2009). These advances have improved understanding of controls on hyporheic exchange at spatial scales ranging from small catchments (Malcolm et al. 2005) to reaches (Malcolm et al. 2003, Conant et al. 2004, Schmidt et al. 2006), particular geomorphic units (Cardenas & Wilson 2007) and specific micro-scales (Vollmer et al. 2002). Similarly,

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temporal scales ranging from inter-annual (Soulsby et al. 2009) to individual hydrological events (Malcolm et al. 2006) have been examined. Surface water exchange with the hyporheic zone is known to scale with bed roughness (Packman et al. 2004), permeability (Packman & Salehin 2003), water velocity (Packman et al. 2004), bed morphology (Tonina & Buffington 2007) and local groundwater-surface water interactions (Malcolm et al. 2004, 2006, Cardenas & Wilson 2006, Boano et al. 2009). Many insights have been delivered through the study of hyporheic environments in relatively undisturbed systems where processes are not grossly affected by anthropogenic activity. However, applying new methods and improvements in process understanding to situations with higher levels of human impact allows greater understanding of the hydro-ecological functioning of these environments and also the potential for remediation (Hancock 2002, Kasahara & Hill 2006, Sarriquet et al. 2007, Meyer et al. 2008).

Agricultural practices have the potential to influence hyporheic exchange at a range of spatial and temporal scales through increased fine sediment loads (Soulsby et al. 2001a, Hancock 2002) and through reduced hydraulic conductivity (Kasahara & Hill 2006, Crenshaw et al. 2010), bed roughness and morphological diversity (Gooseff et al. 2007). These impacts have the potential to reduce connectivity between stream and hyporheic waters to the detriment of stream ecology. The health of salmonid fish populations is considered to be adversely affected by many of these agricultural impacts because of the fishes' reliance on sub-streambed habitat during the egg incubation stage. In spite of this, many agricultural catchments still support abundant local populations of salmonids (Soulsby et al. 2001a). As a consequence, a greater understanding of hyporheic processes and their influence on embryo survival and juvenile recruitment is required to inform evidence based fisheries management in stream environments that are affected by agriculture.

During spawning, salmonid fish bury their eggs in the hyporheic zone in composite nest structures known as redds, typically to depths of between 0.05 and 0.5 m (DeVries 1997). Survival in the protracted period between spawning time and the emergence of free swimming juvenile fish (up to six months) is dependent on a complex range of physical, biological and chemical processes that are discussed in detail elsewhere (Malcolm et al. 2008). Critically however, survival is dependant on the delivery of oxygen and removal of metabolites from the redd environment which in turn depends on hyporheic exchange. Immediately after spawning the open gravel structure and the morphology of the redd promotes surface water exchange. However, the persistence of these features is typically short lived as high discharge events alter redd morphology and cause fine sediment intrusion returning the redd towards the pre-spawning streambed condition (Peterson & Quinn 1996a, Soulsby et al. 2001a).

Most studies of salmonid embryo survival have focussed on the impact of fine sediment intrusion (Everest et al. 1987, Chapman 1988, Jensen et al. 2009). While sediment intrusion potentially reduces hyporheic exchange and therefore embryo survival, an increasing number of studies have highlighted the limitations of focussing on this single variable (Sowden & Power 1985, Peterson & Quinn 1996b). Instead, a complex suite of factors influences the hyporheic processes that affect embryo survival (Groves & Chandler 2005, Greig et al. 2007, Malcolm et al. 2008).

This paper investigates the temporal and spatial variability of hyporheic exchange processes in a canalised reach of the Newmills Burn, an agricultural tributary of the River Don, Scotland. The importance of hyporheic exchange processes for streambed oxygen availability and salmonid embryo survival are assessed at spatial scales ranging from reach scale to the micro-scale typically associated with egg pockets. The results are compared with those from a surface water dominated reach of the Girnock Burn, a relatively undisturbed catchment of the neighbouring River Dee which represents a best case scenario for hyporheic exchange and embryo survival.

Specifically this paper aims to: (1) characterise hyporheic exchange in the Newmills Burn at nested spatial and temporal scales relevant to understanding embryo survival (2) assess the influence of hyporheic exchange processes and water quality on embryo mortality (3) assess the potential influence of land management practices on hyporheic exchange and embryo survival through a comparison of the Newmills and Girnock Burn study sites.

Material and methods

Field sites

The study focussed on a set of five test locations in the Newmills Burn, an agricultural tributary of the River Don, North East Scotland . For comparative purposes, a more limited study of a single site on the relatively undisturbed Girnock Burn on the River Dee was conducted. Both sites lie within the Aberdeenshire district of North East Scotland (Fig. 1).

The environmental characteristics of the Newmills (Soulsby et al. 2001a, Petry et al. 2002, Malcolm et al. 2003) and

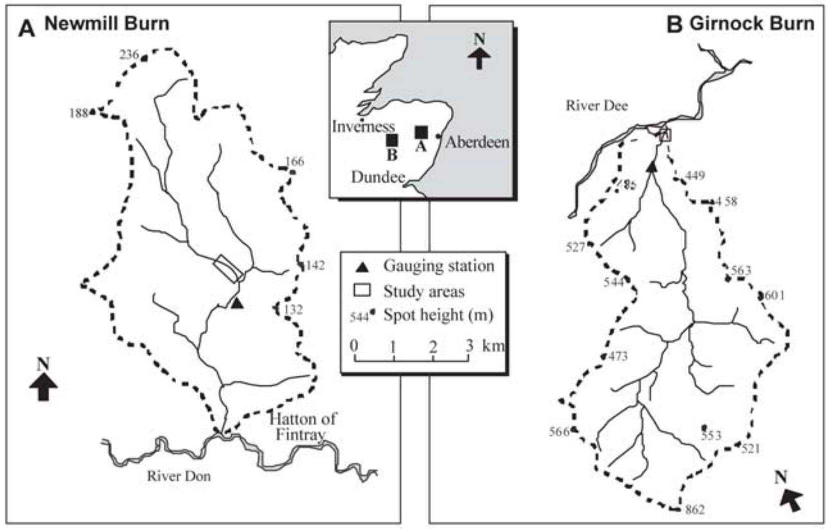

Fig. 1. Map showing the location of the study catchments and reaches.

Girnock Burn (Moir et al. 1998, Malcolm et al. 2005, Soulsby et al. 2007) catchments are described in detail elsewhere. Briefly however, the Newmills Burn is a low lying catchment covering an area of ca. 25 km^2, ranging in altitude from 50 to 236 m. The solid geology is composed of psammite and pelite, overlain by glacial till and meltwater deposits. Landuse is predominantly arable farming with some smaller areas used for livestock. The channel was straightened and deepened over 190 years ago. Consequently, the study reach has a simple bed with limited morphological variability and a relatively uniform channel cross section 1.5–2 m in width. The D_{50} (median size) of spawning gravels is ca. 11 mm, with 23 % of sediment composed of particles < 2 mm, although most of this material consists of course sand (Moir 1999, Soulsby et al. 2001a).

The Girnock Burn is an upland tributary of the River Dee. It covers a catchment area of ca. 30 km^2 ranging in altitude from 230 to 900 m. The geology is composed primarily of granite and schist overlain by glacial and fluvioglacial deposits. Landuse is dominated by heather moorland, with small areas of commercial and semi-natural forest in the lower catchment. Spawning gravels at the study site have a D_{50} of ca. 21 mm (Moir 1999) with less than 10 % fines < 2 mm. The channel width within the study reach spans up to 8 m and is highly dynamic, consisting of pools, riffles and bars. Previous work at the reach used in the present study show that it is surface water dominated with high embryo survival rates (Malcolm et al. 2005, Soulsby et al. 2009). Taken together, the morphological, sedimentary and hydrochemical characteristics of the site represent a best case scenario for hyporheic exchange and embryo survival providing a potentially informative contrast to the Newmills Burn study reach.

Methods

Because hyporheic exchange and water quality influence embryo survival at a range of spatial and temporal scales, and because no single methodology is capable of characterising exchange at the relevant range of scales, multiple sampling methods were deployed in a stratified approach. At the coarsest scale, reach averaged hyporheic exchange was characterised using a single base flow application of the USGS OTIS model. At progressively finer scales, variability in hyporheic exchange and water quality at the reach scale was assessed through hydrochemical sampling of multiple artificial redds (Newmills only). Within redd variability was assessed using stratified hyporheic samplers. At the finest spatial (< 25 mm) and temporal (15 minute) scales variability was assessed using Anderaa™ DO optodes.

Reach average hyporheic exchange (conservative tracer studies)

Conservative tracer studies were used to determine reach average hyporheic exchange. The procedures were standardised to summer baseflow conditions and carried out using a modified version of the approach described by Webster & Ehrman (1996). Data were input to the USGS (United States Geological Survey) OTIS (One-Dimensional Transport with Inflow and Storage) model. Details of the OTIS model, its assumptions and limitations are provided in detail elsewhere and are beyond the scope of this paper (Bencala & Walters 1983, Stream Solute Workshop 1990, Runkel 1995, Harvey et al. 1996, Runkel 1998, Harvey & Wagner 2000, Runkel 2000, Gooseff et al. 2003). However, in general terms the OTIS model assumes that solute transport occurs by a combination of advection, dispersion and storage. The ratio of storage area (As) to channel area (A) gives an estimate of the level of storage averaged over the reach, and assuming limited in-channel storage, estimates the degree of short residence hyporheic exchange. The model was manually fitted by the trial and error approach described by Bencala & Walters (1983) and The Stream Solute Workshop (1990). Initial parameter estimates were based on field observations, which were later optimised according to a range of feasible values reported in the literature. The experimental Damkohler number (DaI), a measure of the balance between down stream processes and storage processes was used to assess the reliability of parameter estimates and determine the reach length to be used at each site (Wagner & Harvey 1997, Harvey & Wagner 2000). Accordingly, due to differences in channel characteristics, tracer data from 50 m were used for modelling hyporheic storage in the Newmills Burn, while a 100 m length was used for the Girnock Burn. Parameter estimates from OTIS were used to es-

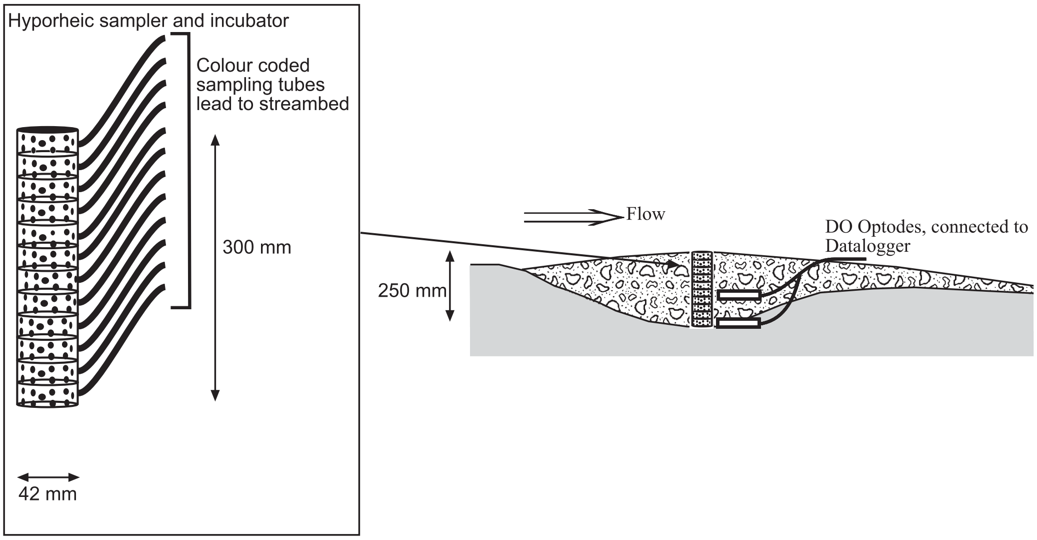

Fig. 2. Design and deployment of hyporheic incubators and DO optodes in artificial redd structures (after Youngson et al. 2005, Malcolm et al. 2008).

timate average hyporheic extent using approaches suggested by Harvey & Wagner (2000). Together these approaches provided a first approximation of reach averaged hyporheic storage and a means of comparing short residence hyporheic exchange between the two study streams.

Reach and redd scale variability in hyporheic exchange and water quality (artificial redds and incubators)

Hyporheic hydrochemistry and embryo survival (see below) were measured at five artificial redd locations within a 120 m section of in the Newmills Burn and at a single location on the Girnock Burn using methodologies described previously (Malcolm et al. 2008). Artificial redds were constructed at previous spawning locations identified using historical redd maps. Construction took place approximately one week prior to spawning time (November 2006). At spawning time, vertically stratified (12 containers, 25 mm in height) incubation chambers were inserted into the artificial redds (Fig. 2). Containers were lined with a 1 mm plastic mesh and contained a colour coded 4 mm i.d. Nalgene™ hyporheic water sampling tube which led to the stream surface. Monitoring in the Newmills Burn took place between 14/11/2006 and 20/02/2007 reflecting spawning time and estimated hatch time, respectively. The starting date for the Girnock Burn was the same but monitoring took place over an extended period until 27/03/07 to accommodate the lower temperatures and consequently slower embryo development.

Hyporheic water sampling took place at approximately fortnightly intervals between spawning and hatch. Dissolved oxygen (DO) concentration and temperature were measured in the field using a Pre-Sens™ Fibox3 oxygen meter connected to a 2 mm DO micro-sensor and a thermistor. Water samples were returned to the laboratory for analysis of major cations (Ca, Mg, Na, K, NH_4), anions (NO_3, Cl, SO_4, NO_2), total dissolved N, P and DOC. Hydrochemical variables were used to infer the temporal and spatial variability of source water contributions to the hyporheic zone and to infer the nature of hyporheic exchanges.

Fine scale variability in hyporheic exchange and water quality (DO optodes)

Continuous measurements (15 minute resolution) of DO and temperature were obtained in surface water and at depths of 150 and 300 mm at a sub-set of two artificial redds on the Newmills Burn (NM1 and NM2) and the single artificial redd on the Girnock Burn using Aanderaa™ DO optodes (Model number 4175) (Malcolm et al. 2006, 2008, Soulsby et al. 2009). Equipment was cross-calibrated prior to deployment. The DO output was used to supplement measurements made by the fortnightly spot sampling. Temperature measurements provided additional information on hyporheic exchange to supplement hydrochemical data.

Embryo survival

Twenty water hardened Atlantic salmon (*Salmo salar)* eggs were inserted into alternate compartments of the vertically stratified incubators at depths ranging from 50–300 mm. Eggs for the Newmills Burn were obtained from the River Don hatchery at Newe. Eggs for the Girnock Burn were obtained from the Marine Scotland (formerly Fisheries Research Services – FRS) experimental facility at Littlemill on the Girnock Burn. Eggs were produced from a single male × female pairing. Incubation chambers were also placed in surface water fed containment facilities to control for hyporheic water quality effects. Surface water temperature data from the sites were input into the embryo development model of Elliot & Hurley (1998) to estimate hatch dates. When embryos were estimated to be close to hatch the incubators were removed from the stream bed for counting of live and dead eggs. Although the Elliot and Hurley model was actually developed for sea trout, it was felt that it was adequate to provide indicative hatch dates given the similarity of temperature-growth responses between the species.

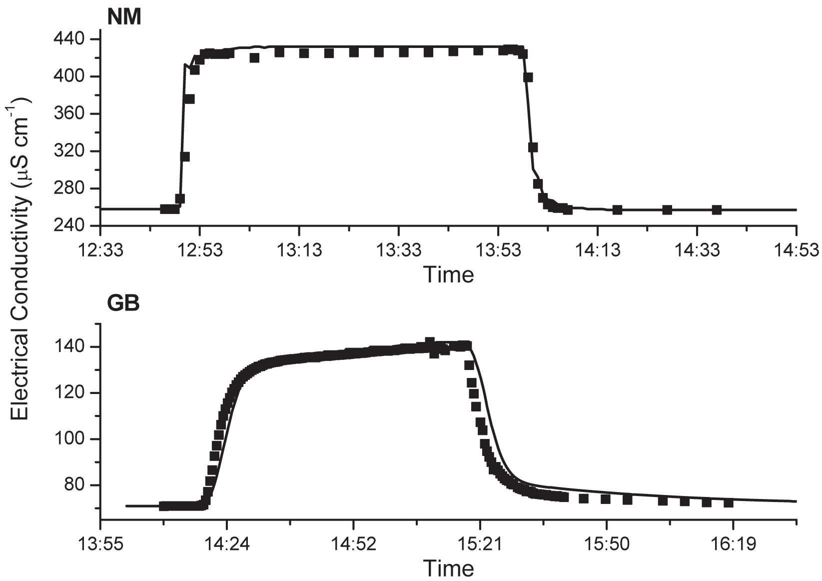

Fig. 3. Observed and modelled solute breakthrough curves for reach scale tracer experiments in the Newmills (NM) and Girnock (GB) Burn study sites. Modelled data was produced by manual fitting of the USGS OTIS model.

Statistical analysis

Hydrochemical data were used to infer source water provenance and hyporheic exchange processes. Stream and hyporheic hydrochemical data were included in a Principle Component Analysis (standardised data) to identify co-varying parameters and simplify interpretation of the complex suite of determinants. Components 1 and 2 were used in the analyses as these explained most of the variability. Bi-plots of Components 1 and 2 were used to assess inter-site variability in source water contributions and hyporheic zone processes; temporal plots of Component 1 scores were used to assess temporal variability. Newmills and Girnock samples were included in separate PCA analyses because inter-catchment differences in hydrochemistry were greater than within site differences.

A generalised linear model (GLM) was used to assess the relationship between mean DO concentrations and embryo survival rate. Because the data were overdispersed, (scale = 10.8) analyses were carried out using a quasibinomial GLM. The significance of the mean DO concentration was determined using an F test (Zuur et al. 2007). The explanatory power of different predictor variables (DO % sat. and DO mg l^{-1}) was assessed by examining residual deviance in the models and AIC scores. All analyses were carried out in the software package R, version 2.9.1. (R Development Core Team, 2009)

Table 1. Output from PCA analysis of Newmills Burn hydrochemical spot samples (NM1–5). Component loadings and proportion of variance explained by components 1 and 2 (PC1 and PC2).

	PC1	PC2
Proportion of variance explained	0.50	0.19
Na	–0.32	0.07
NH_4	–0.10	–0.45
K	–0.17	–0.55
Mg	0.33	–0.15
Ca	0.38	–0.06
Cl	–0.35	0.00
NO_2	–0.14	–0.17
NO_3	–0.38	0.19
SO_4	0.38	–0.02
Total P	–0.04	–0.59
Total N	–0.38	0.12
DOC	–0.16	–0.20

Results

Reach scale hyporheic exchange – conservative tracer experiments and modelling

Measured and modelled conservative tracer concentrations for the Newmills and Girnock Burn are shown in Fig. 3. A marked difference was observed in the shapes of the response curves indicating differences in hyporheic exchange. In the Newmills study site the solute response was essentially step-wise and constrained to the period of tracer addition, indicating low levels of short residence hyporheic exchange. By contrast, the attenuated response of the Girnock site at both the onset and cessation of tracer application indicated a greater degree of hyporheic storage.

In general, there was a reasonable fit between observed and modelled tracer responses (Fig. 3). Parameter estimates from the fitted OTIS models, calculated metrics of hyporheic exchange and calculations of average hyporheic extent are shown in Table 3. The A_s/A ratio (the ratio of channel area to storage area) provides a metric indicating the degree of reach average hyporheic storage (exchange). This was calculated as 1.41 for the Girnock site but only 0.18 for the Newmills site.

To investigate further the implications of the OTIS outputs for hyporheic spatial extent, the hyporheic zone dimensions (d_s) were assessed according to methods described by Harvey & Wagner (2000). Reach average estimates indicated an average spatial extent of approximately 0.57 cm for the Girnock site (range 0.46–11 cm) but only 0.035 cm for the Newmills site.

Spatial variability in hyporheic exchange (reach and redd scale)

Table 1 shows the component loadings for the first two components (PC1, PC2) for the Newmills site. PC1 accounted for 49 % of the variance in the data, PC2 accounted for 18 % of the variance (68 % total). No single hydrochemical parameter dominates the first two components. Instead, a number of parameters offer similar levels of loading, with PC1 being positively associated with Mg, Ca and SO_4 and negatively associated with Total N, NO_3, Cl and Na. Remaining parameters showed markedly weaker associations with PC1. PC2 showed stronger associations with fewer determinants, being negatively associated with NH_4, K and Total P.

Table 2 shows the component loadings for PC1 and PC2 for the Girnock analysis. Together these components explained 80 % of the variance in the data (PC1-59 %, PC2-21 %). In common with the Newmills analysis, PC1 was not dominated by any individual determinands but was positively associated with DOC and negatively associated with Na, K, Mg, Ca, Cl and sulphate. PC2 was negatively associated with NH_4, NO_2 and Total N.

The component scores for PC1 and PC2 were extracted and plotted as a biplot to investigate spatial variability in hydrochemistry between sites and depths in order to infer the nature of local hyporheic exchange. Fig. 4 shows biplots of PC1 and PC2 for Newmills locations 1–5 (NM1–NM5) and the Girnock Burn site (GB). NM1 showed clear hydrochemical separation between surface and hyporheic water at all depths, with no overlaps between stream and hyporheic chemistry. Only the 50 mm sample exhibits similar characteristics to surface water and this is only for a single sample. Separation occurred primarily in relation to PC1, with single samples from 250 and 300 mm exhibiting differentiation in relation to PC2. At NM2 shallow hyporheic samples tended to group with surface water samples, while deeper samples (200–300 mm) were characterised by progressively greater separation and higher PC1 scores. Only a single sample at 100 m showed any notable differentiation in relation to PC2. NM3 was characterised by intermediate characteristics to NM1 and NM2, with limited differentiation between stream and hyporheic samples on PC1, primarily at 250–300 mm. NM3 exhibited greater separation in relation to PC2 than sites NM1 and NM2, but there were no clear patterns with depth. Stream and hyporheic samples at NM4 exhibited simi-

Table 2. Output from PCA analysis of Girnock Burn (GB) hydrochemical spot samples. Component loadings and proportion of variance explained by components 1 and 2 (PC1 and PC2).

	PC1	PC2
Proportion of variance explained	0.59	0.21
Na	–0.36	0.08
NH_4	–0.15	–0.54
K	–0.34	–0.07
Mg	–0.35	0.05
Ca	–0.35	0.06
Cl	–0.36	0.05
NO_2	–0.07	–0.58
NO_3	–0.28	0.10
SO_4	–0.36	0.09
Total P	–0.13	0.03
Total N	–0.05	–0.57
DOC	0.34	–0.07

Table 3. Parameter estimates and derived metrics for OTIS modelling of stream tracer experiments in the Newmills and Girnock study sites.

Parameter estimates and metrics	Newmills Burn	Girnock Burn
Discharge (Q, m^3s^{-1})	0.019	0.095
Channel x-sectional area (A, m^2)	0.1	0.523
Storage zone x-sectional area (A_s, m^2)	0.018	0.740
Dispersion (D, m^2s^{-1})	0.001	0.04
Exchange co-efficient (μ, s^{-1})	0.001	0.0002
Damkohler number (DaI)	2.16	0.24
As/A	0.18	1.41
Average hyporheic dimensions (ds, m)	0.00035	0.0057 (0.0046–0.11)

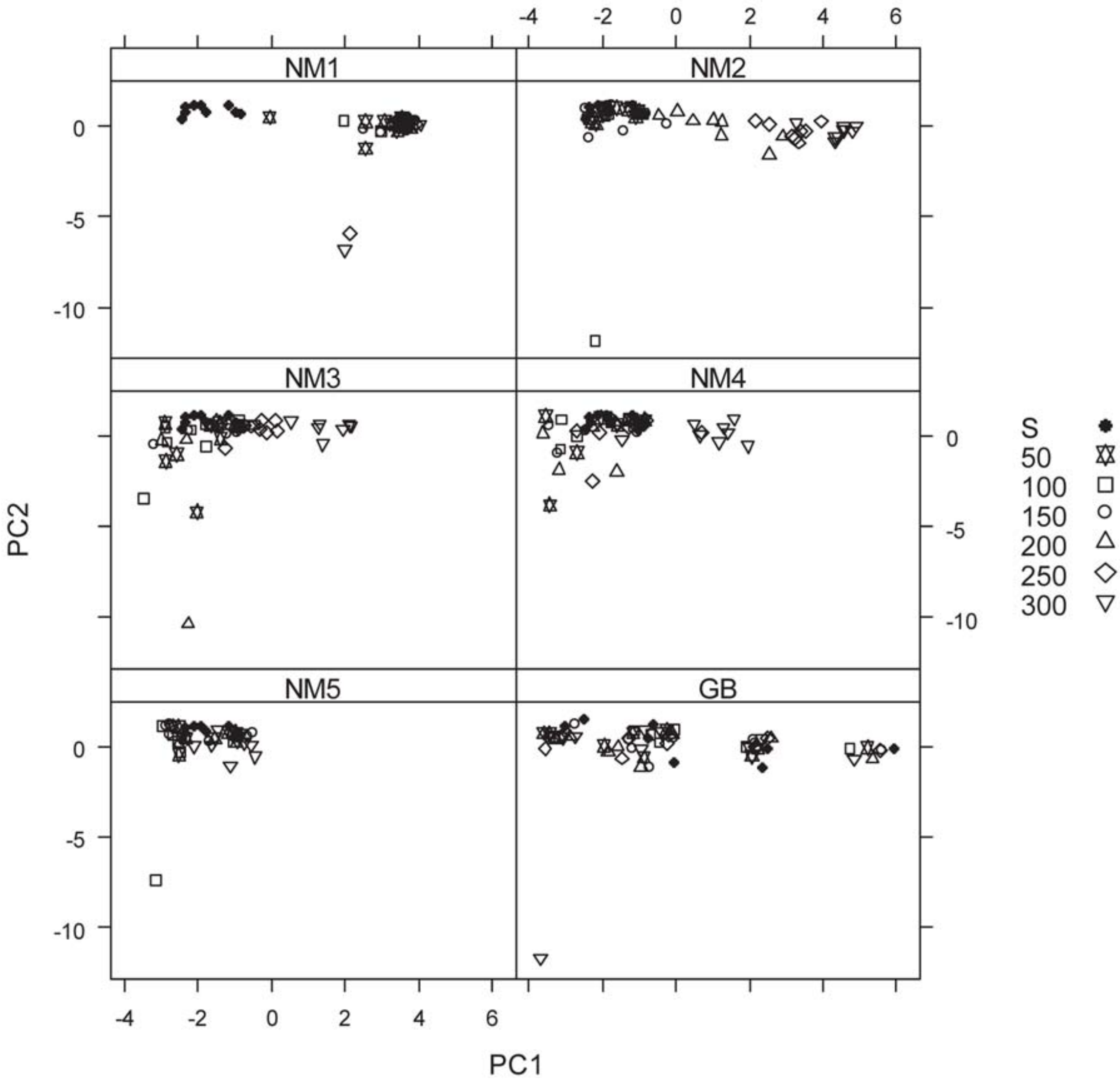

Fig. 4. Bi-plot showing component scores (PC1 and PC2) from PCA analysis of Newmills and Girnock Burn hydrochemical spot sample data. Individual redd locations NM1–5 and GB are plotted separately. Newmills and Girnock hydrochemical samples were analysed separately.

lar PC1 scores with the exception of 300 mm samples, which were generally characterised by higher scores. Again there was some separation on PC2, but this did not show clear spatial patterns. NM5 showed no clear differentiation between stream and hyporheic water quality on PC1. A single sample from 100 mm showed differentiation in relation to surface water samples on PC2. For the Girnock Burn site, component scores primarily separated samples according to sampling date and consequently hydrological conditions at the time of sampling. Surface water samples spread almost the entire range of PC1 and PC2 scores and there were no clear spatial differences in water quality.

Temporal variability in hyporheic exchange (reach and redd scale)

PC1 scores were plotted against sampling date and discharge for each of the 6 locations (NM1–NM5 plus GB) to reveal spatiotemporal variability in stream and hyporheic hydrochemistry (Fig. 5). At NM1, an initial sample in mid-November showed depth related gradients in PC1 scores. However, hyporheic gradients were reduced over the subsequent two sampling occasions and by the third sampling occasion all hyporheic samples exhibited similar PC1 scores which were distinct from surface water. Depth related gradients in PC1 scores were re-established on the final sampling

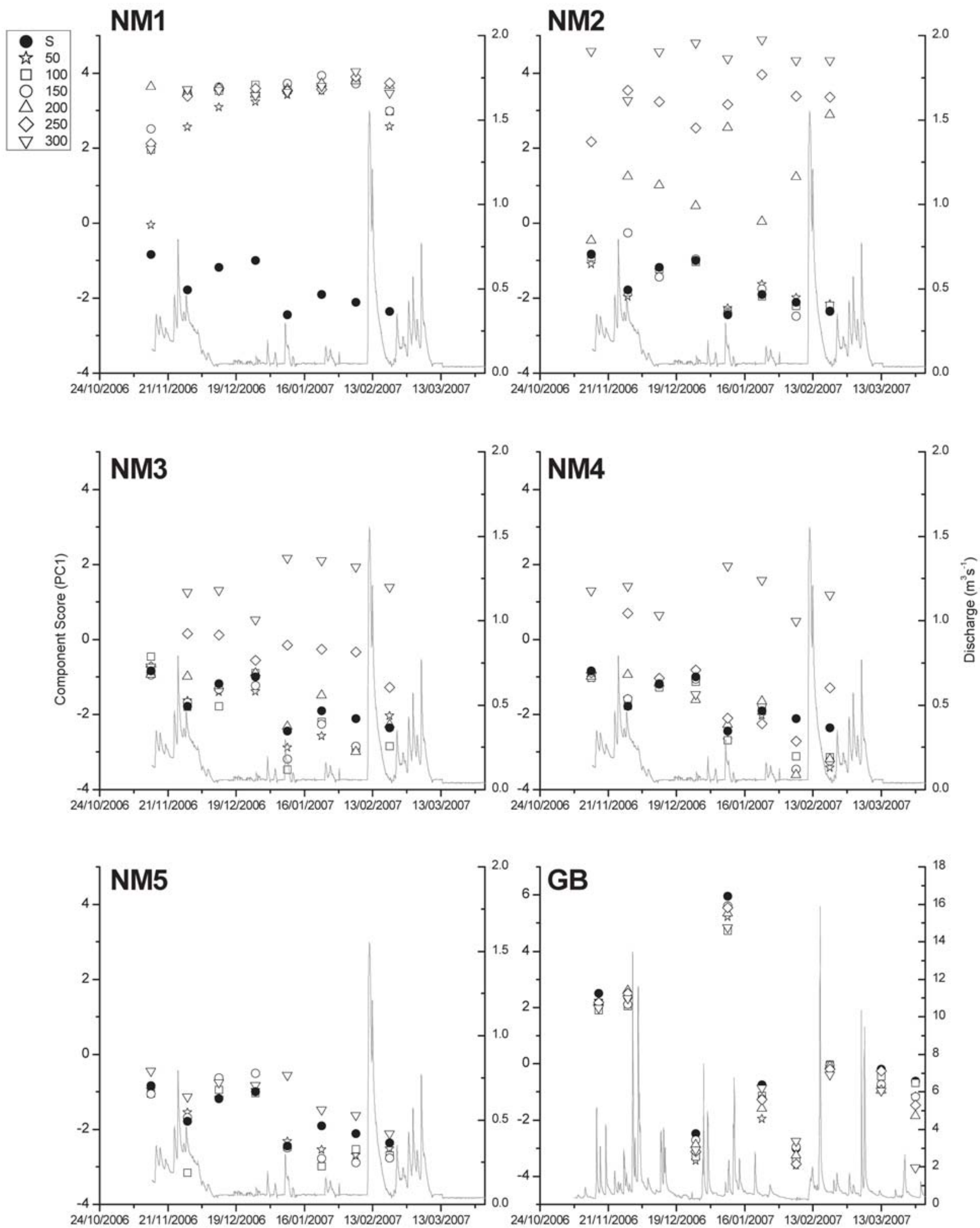

Fig. 5. Temporal variability of Component 1 scores at sites NM1–5 (A–E) and GB(F). NM1–5 scores are from a single PCA analysis. GB Scores are from a separate PCA analysis. Discharge is shown as a solid line.

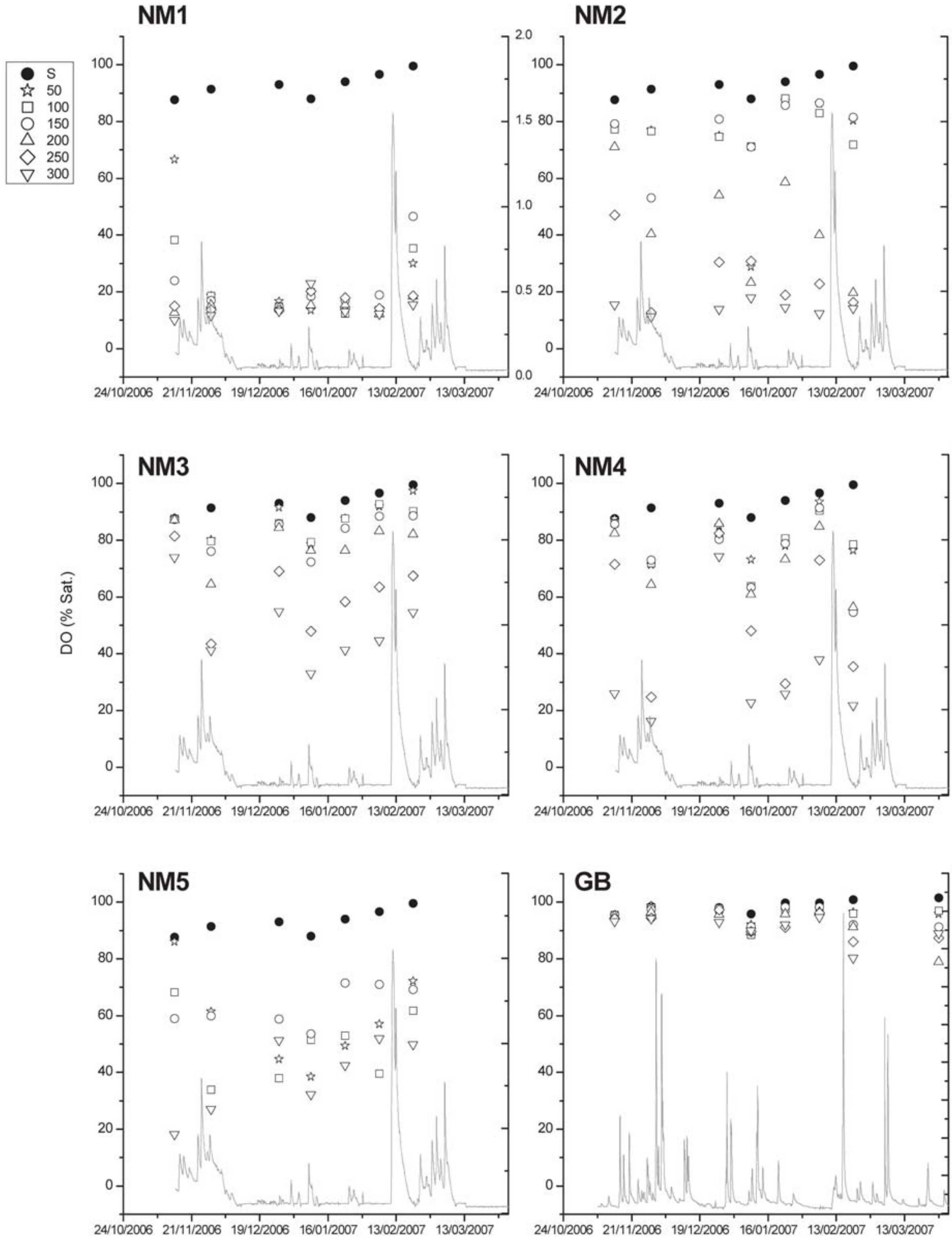

Fig. 6. Temporal variability of dissolved oxygen in spot samples taken from stratified incubators at artificial redd sites NM1–5 and GB. Discharge is shown as a solid line.

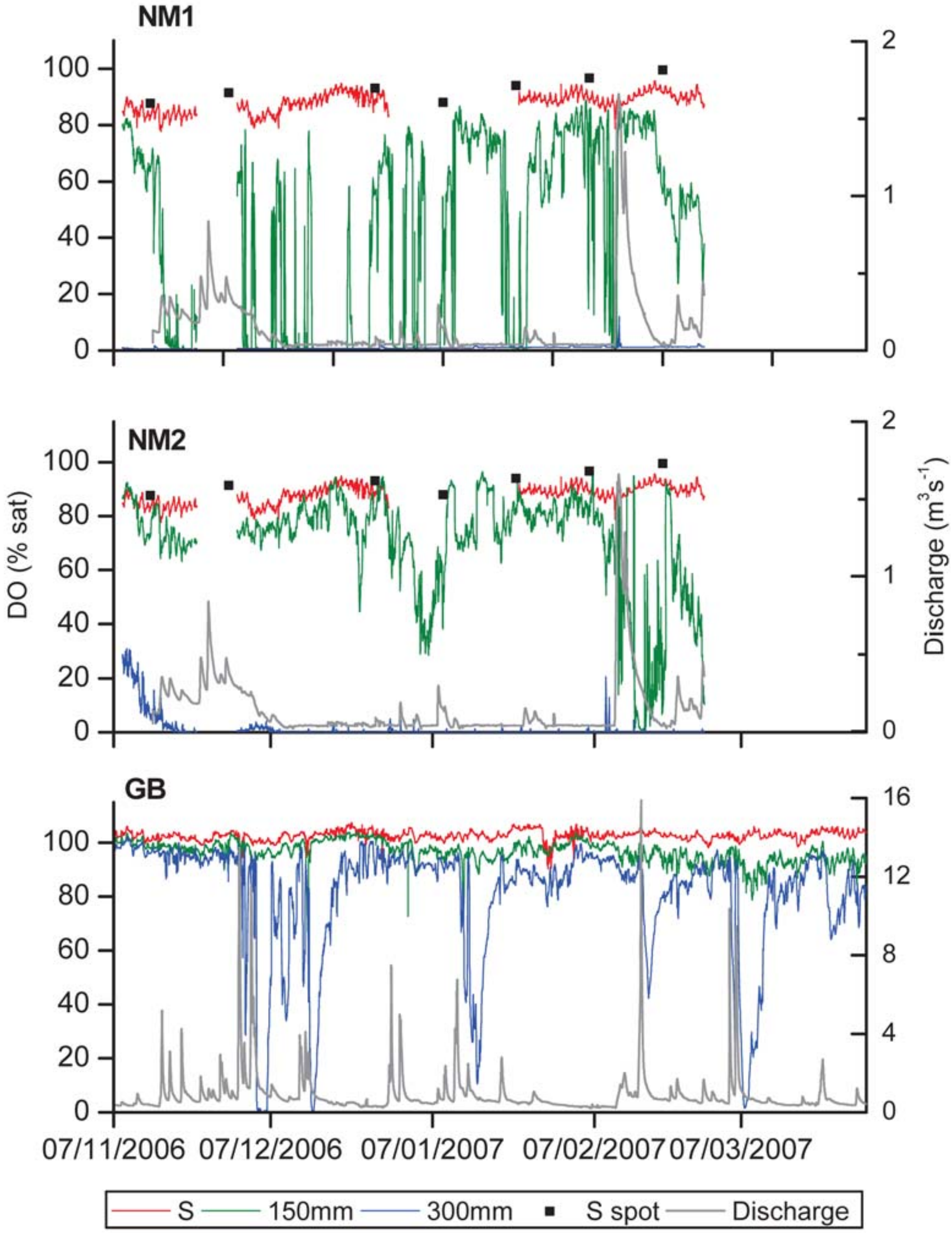

Fig. 7. Temporal variability of DO as revealed by continuously logging Aanderaa™ DO optodes located in surface water and in artificial redds at depths of 150 and 300 mm in NM1, NM2 and GB. Spot samples of surface water DO are also shown for NM sites.

occasion towards the end of February where sampling followed the highest discharge event of the winter period. NM2 was characterised by gradients in PC1 scores particularly between 150 and 300 mm, with stream and hyporheic water characterised by similar scores at depths < 150 mm. Samples taken from 250 and 300 mm were characterised by relatively stable and high PC1 scores; 200 mm samples were more dynamic varying between scores typical of surface water and scores more typical of deeper hyporheic water (09/01/07 and 21/02/07). NM3 was initially characterised by similar stream and hyporheic scores. However, after the first sample, stratification by depth was evident at 200 mm and below. NM4 was characterised by a similar chemical signature to surface water at depths ranging from 50–250 mm with a markedly different signature at 300 mm. Stream and hyporheic samples at NM5 were generally similar and followed

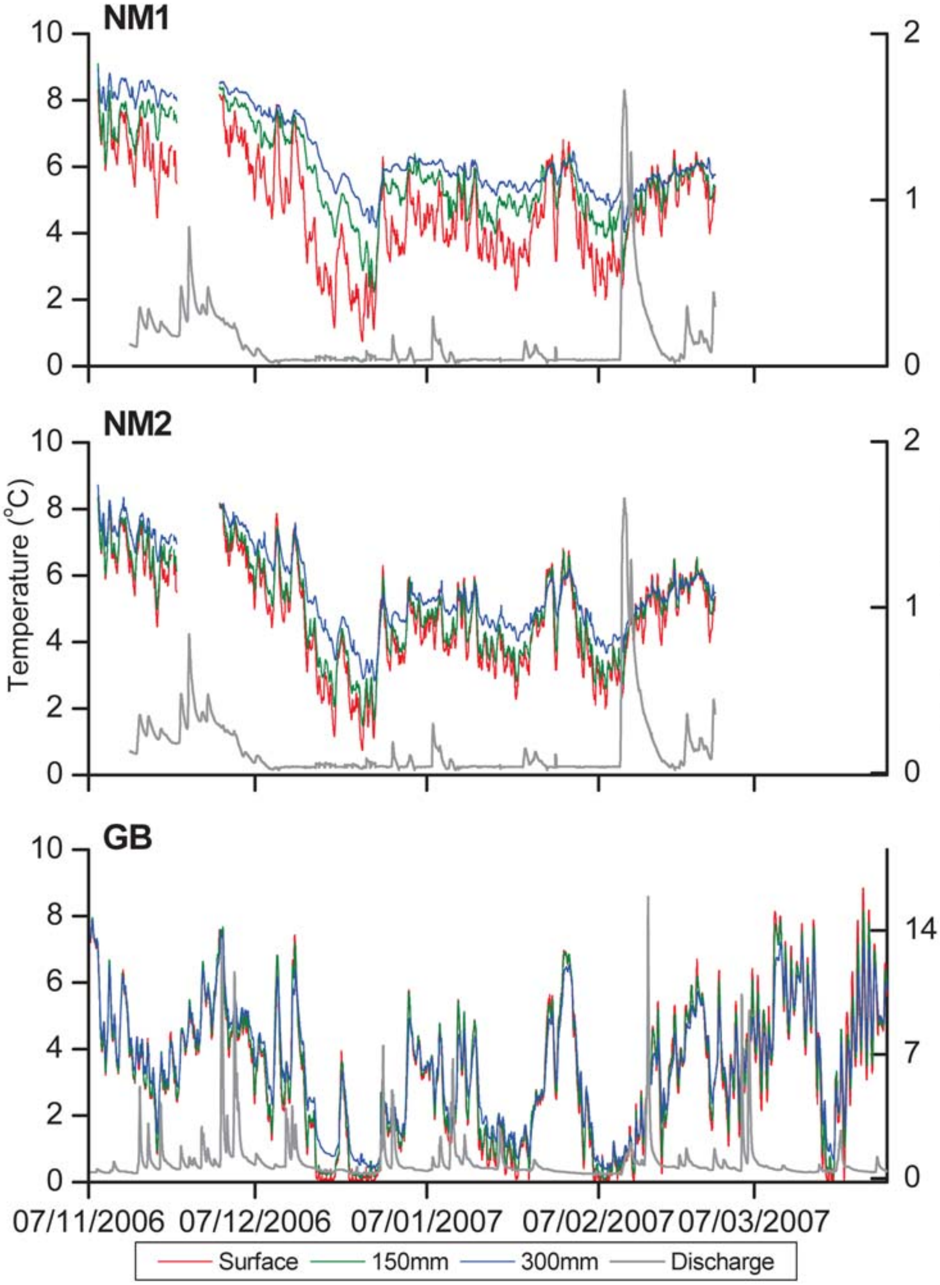

Fig. 8. Temporal variability of temperature obtained from logging Aanderaa™ DO optodes located in surface water and in artificial redds at depths of 150 and 300 mm in NM1, NM2 and GB.

similar patterns of variability. Hyporheic samples were often distributed either side of surface water samples in terms of PC1 scores. The only notable differentiation was observed on the 09/01/07 when the 250 mm hyporheic sampler was characterised by markedly higher PC1 scores than surface water and the other hyporheic samples which grouped tightly. At GB, PC1 scores were generally similar between stream and hyporheic water, with temporal variability greatly exceeding spatial variability. The only notable exception was on the final sampling occasion when depth related separation was evident, particularly at 300 mm where the PC1 score was considerably lower than other depths.

In general, hyporheic DO concentrations mirrored PC1 scores for the Newmills site although gradients with depth tended to be more apparent (Fig. 6). Surface water DO trended upwards over the monitoring period ranging from 86–100 % sat. At the Girnock site, surface water DO approached saturation throughout ranging from 96–102 %. At NM1 DO initially declined with depth, but following the first sampling occasion DO at all depths declined to < 25 % and was sometimes around 10 %, being greater only at shallow depths during the final sampling occasion. DO concentrations at NM2 showed clear reductions with depth. Gradients were more marked than those seen in the PC1 scores with even shallow samples showing some DO reduction compared to surface water. DO variability at NM3 and NM4 again closely mirrored PC1 scores with 250 and 300 mm samplers showing particularly low DO concentrations. NM5 was unusual in showing markedly different patterns of variability in PC1 scores and hyporheic DO. While PC1 scores had closely tracked those of surface water, DO declined markedly with depth, especially during the early part of the monitoring period. DO in deeper hyporheic samplers also increased over time reducing percentage differences between stream and hyporheic water. DO concentrations at GB closely tracked surface water, with the exception of the 20/02/07 and 27/03/07 when low DO concentrations were observed, primarily between 200 and 300 mm.

Fine scale variability in hyporheic exchange

Data acquisition from Aanderaa™ optodes was generally good (Fig. 7). Battery failure resulted in the loss of all Newmills data between 22/11/06 and 30/11/06 and technical problems caused the loss of Newmills surface water DO data between 29/12/06 and 23/01/07. Spot DO samples were used to provide an indication of surface water DO during the periods of technical failure. At GB, DO in surface water and at 150 m was generally close to saturation but several transient periods of low DO at 300 m corresponded with the recession limb of hydrological events. These were not identified by spot sampling. At NM1 DO at 300 mm was consistently near zero, except during the large event on 11/02/07 when values reached 12 % sat. DO at 150 m exhibited a high level of temporal variability which appeared to relate in part to small hydrological events although patterns of response were inconsistent. At NM2 DO at 300 mm declined from ca. 30 % to near zero during the first 2 weeks of monitoring. Thereafter values remained low, rarely exceeding 5 % Sat.. DO at 150 mm was generally higher than NM1 with concentrations above 60 % for prolonged periods. Lower DO periods occurred during early January and mid to late February and in the latter period DO dropped to around 5 %.

At GB, surface water and 150 mm temperature data closely tracked each other over the entire monitoring period. Only small temperature differences (< 0.7 °C) were observed at temperature extremes, particularly towards the end of the monitoring period (Fig. 8). Temperatures at 300 mm were similar to stream and 150 mm samples during November, but showed marked thermal moderation from December onwards, particularly during periods of icing when 300 mm samples remained up to 1.4 °C warmer than surface water.

Temperature differences at the Newmills site were considerably more marked than in the Girnock, with maximum temperature differences between surface and hyporheic water of up to 6 °C (NM1-300) (Fig. 8). At NM1, temperatures tended to increase and exhibit less temporal variability with depth. Differences were greatest during periods of low stream temperature. At NM2, depth related temperature gradients were weaker and 150 and 300 mm temperatures were more similar to one another than at NM1. Towards the end of the monitoring period both NM1 and NM2 showed a transition from hyporheic temperatures being higher than stream temperatures towards being lower.

Embryo survival

Survival in control groups of embryos in surface water from both the Newmills and Girnock Burns was 100 %. However, embryo survival in the hyporheic zone varied markedly within NM sites and also between NM and GB (Fig. 9). All NM sites exhibited some embryo mortality at the shallowest depth (50 mm) and total mortality at the greatest depth (300 mm). NM1 was characterised by 100 % mortality at all depths, NM2 exhibited decreasing survival between 50 and 150 mm below which all embryos died. NM3 was characterised by high survival (80–100 %) between 100 and 250 mm, with total mortality at 50 and 300 mm. NM4 had 90 % survival at 100 and 150 mm with total mortality at all other depths. NM5 exhibited unusual patterns of variability with survival at 50 (45 %) and 150 (100 %) mm and zero survival at all other depths. GB was characterised by 100 % survival at 50–250 mm and 80 % survival at 300 mm.

In previous studies, the relationship between DO and embryo survival in freshwater fish and other species has been reported in relation to mass concentration (mg l^{-1}), percent saturation (% sat.) or partial pressure (mm Hg) (this context is discussed below). In the present study, the predictive power of both mass

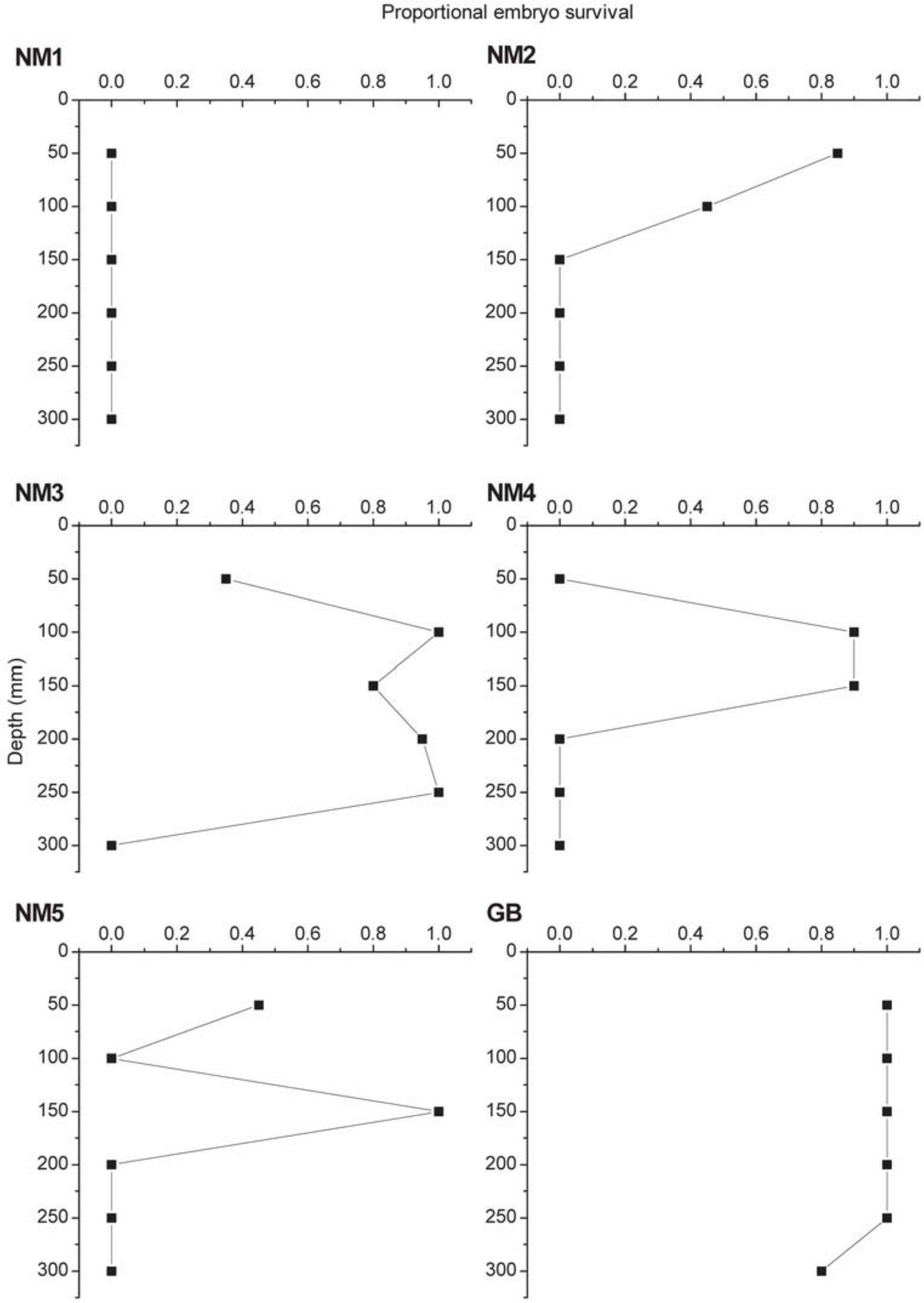

Fig. 9. Spatial variability in the proportion of embryos surviving to hatch time in depth stratified incubators, located in artificial redds at NM1–5 and GB.

concentration and percent saturation was tested and compared. Analysis was carried out on the DO values from spot sampling and the proportion of embryos surviving in each of the incubation containers. Data from NM4-50 were excluded from the analysis because the sampler was exposed by bed scour and the ova exposed to mechanical disturbance. Figs 10A and B show scatter plots of mean spot sample DO (mg l^{-1} and % Sat respectively) against survival rate. Fitted logistic regression models are shown as solid lines. Both DO mg l^{-1} ($F_{[1,31]} = 58.71$, $p < 0.001$) and % sat. ($F_{[1,31]} = 55.56$, $p < 0.001$) were found to be significant predictors of survival explaining 63 % and 62 % of the null deviance, respectively.

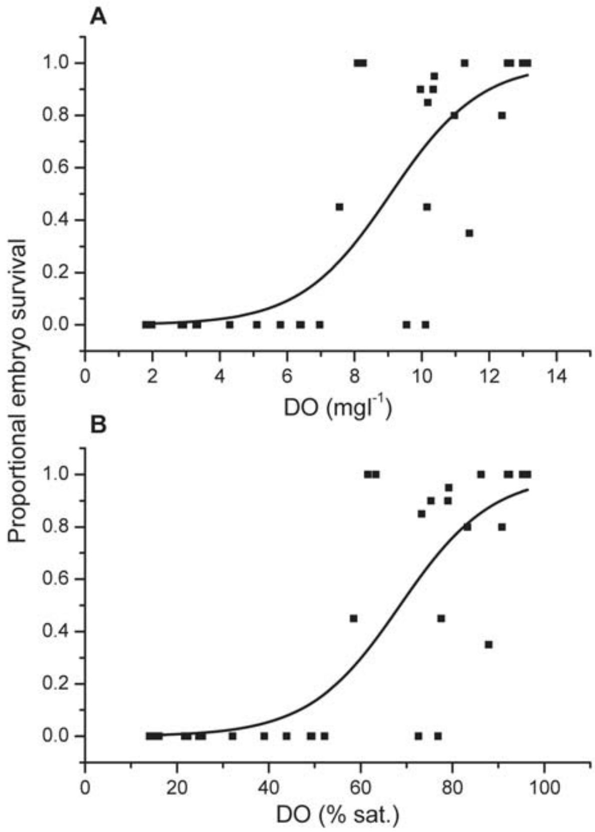

Fig. 10. Relationship between DO and the proportion of embryos surviving to hatch in depth stratified incubators, located in artificial redds at NM1–5 and GB. Symbols represent observed data. Solid lines indicate the fitted logistic regression model. A and B show fitted models for DO (mg l^{-1}) and DO (% sat.), respectively.

Discussion

Hyporheic water quality and embryo survival are influenced by hyporheic exchange at a range of temporal and spatial scales (Malcolm et al. 2008). The high costs of the methods deployed at fine spatial scales prevented their deployment at sufficient locations to characterise variability at larger scales. Instead, the present study aimed to achieve this synthesis by characterising exchange using an additional range of accessible methods at nested spatiotemporal scales.

Conservative tracer assessments and OTIS modelling suggested low levels of short residence hyporheic exchange in Newmills Burn, with low As/A ratios and a small estimated average hyporheic extent (ds). Estimates of As/A ratios for the Girnock Burn indicated that hyporheic exchange (scaled for stream size) was around five times greater than observed in the Newmills Burn. For both sites the Damkohler numbers were within limits (0.1–10) considered acceptable for reliable parameter estimates by Wagner & Harvey (1997). The gross differences in hyporheic exchange indicated by OTIS modelling probably reflects a number of differences between the sites. The Newmills Burn has been canalised and now exhibits little of the morphological diversity and channel complexity which often drives short residence hyporheic exchange (Gooseff et al. 2007). The Newmills Burn is also characterised by small bed material resulting in low hydraulic conductivity and further reduction in the potential for exchange (Storey et al. 2003, Schmidt et al. 2006, Leek et al. 2009, Kalbus et al. 2009). Finally, the combination of small bed material and fine sediment deposition results in low bed roughness lowering potential for turbulent exchange (Vollmer et al. 2002, Packman et al. 2003, 2004).

Hydrochemical tracers provided a useful method for assessing spatio-temporal variability in hyporheic exchange at the sub-reach scale. Although single hydrochemical tracers such as alkalinity and electrical conductivity have proved useful for source water differentiation in the study of upland streams (Soulsby et al. 2007), the use of a broad suite of hydrochemical tracers proved necessary to achieve the same purpose in the agricultural Newmills Burn. Surface water in the Newmills Burn was generally lower in Mg, Ca and sulphate and higher in Total N, NO_3, Cl and Na than hyporheic water as indicated by low PC1 scores. This probably reflects high levels of near-surface, short residence runoff from soils and under drainage containing low concentrations of weathering derived base cations (Ca, Mg), but high levels of soil derived nutrients (Petry et al. 2002, Soulsby et al. 2003) and NaCl from marine/road salt (Soulsby et al. 2001b). Of the Newmills sites, only NM5 showed similar hyporheic and surface water hydrochemistry. NM1 was characterised by marked deviations from surface water hydrochemistry at all depths indicating a strong groundwater influence, and supported by DO and temperature values. The remaining NM sites showed intermediate characteristics, indicating similarly intermediate variation in groundwater influence. The high degree of spatial variability within the Newmills Burn site is surprising given its morphological uniformity. However, the results are in general agreement with those reported at this and other sites previously (Käser et al. 2009, Leek et al. 2009) and probably reflect a combination of heterogeneous aquifer (Malcolm et al. 2003, Schmidt et al. 2006) and streambed (Conant et al. 2004, Kalbus et al. 2009) hydraulic conductivity.

At the Girnock site, temporal variability in hydrochemistry was greater than spatial variability with depth. This probably reflects variable source water contributions to stream flow over the winter sampling period and the overall dominance of surface water at the depths examined.

Within individual redd locations there was a general tendency for hyporheic hydrochemistry (including DO) to vary with depth. The strength of gradients most likely reflected the strength of local GW upwelling. Cardenas & Wilson (2006) and Boano et al. (2009) have shown that where strong GW upwelling occurs, surface water infiltration of the streambed is impaired. These observations align with those for the present study streams (Malcolm et al. 2006, 2008, Soulsby et al. 2009). In addition, substantial temporal variability was revealed by shifts in hydrochemical boundaries in the spot sample data and/ or by rapid changes in DO concentrations in the optode data. In common with previous studies (e.g. Malcolm et al. 2006, Käser et al. 2009), rapid reductions in streambed DO concentrations were associated with short transients immediately following the recession limb of hydrological events, probably as a result of increases in GW flux. Spot sampling was not sufficient to fully characterise the temporal variability of hyporheic exchange processes shown by the high frequency DO data collected from the optodes (Malcolm et al. 2006).

At Newmills the DO values derived from sampling generally mirrored hydrochemical PC1 scores, indicating that upwelling of chemically reduced GW was a dominant control on hyporheic DO. However, DO gradients were also present at NM5 where the hydrochemical data did not indicate a GW influence. This suggests that *in situ* sediment oxygen demand caused local reduction in hyporheic DO. In contrast, spot sampling data at the surface water dominated site on the Girnock Burn indicated only very limited DO reduction with depth and then only during the final month of sampling. This was associated with hydrochemical separation of other determinants associated with PC1, suggesting that the dominant effect was temporally variable groundwater input rather than *in-situ* oxygen consumption.

Embryo survival was characterised by complex spatial patterns. Mortality at the shallowest depth (50 mm) at NM4 probably reflected mechanical shock as a consequence of partial scour in the vicinity of the sampler (Youngson et al. 2005). Elsewhere, however, a significant positive relationship was observed between mean DO values and embryo survival.

Previous studies have used different measures of oxygen to assess critical DO thresholds including mass concentration (mg l^{-1}), percent saturation (% sat.) and partial pressure (PO_2; mm hg) (Davis 1975, Rombough 1988, Czerkies et al. 2002). However, it is gradients in PO_2 that drive O_2 diffusion rates between hyporheic water and the interior of the ovum where oxygen is consumed. Values for PO_2 are only marginally affected by changes in temperature because changes in oxygen content are countered by changes in molecular activity (Davis 1975). Percentage saturation is closely related to PO_2 as it describes the deviation from the equilibrium condition for a given temperature and pressure. DO as measured in mg l^{-1} can vary substantially with temperature due to the variable solubility of oxygen in water, without necessarily having a marked impact on oxygen diffusion and availability to respiring embryos. At higher temperatures, lower O_2 mass concentration may limit O_2 availability for organisms with correspondingly higher O_2 demand. However, at the relatively low temperatures appropriate to salmonid ova and given their relatively low O_2 demand, theory would suggest that PO_2 (or % sat.) should be the primary determinant of oxygen delivery and therefore embryo survival, especially where studies extend over a range of sites and temperatures. In this study we compared the explanatory power of DO % sat. and DO mg l^{-1} for embryo survival, finding that they performed similarly. However, this probably reflected the relatively low variation in hyporheic temperature observed in this particular study.

We observed no survival below 52 % sat. (7.0 mg l^{-1}), with 50 % survival (LC_{50}) predicted at 69 % sat. (9.1 mg l^{-1}). The critical DO levels reported for embryo survival in this study lie within the range for field based studies of salmonid embryo survival reported elsewhere. For example, at the lower end of the range, Sowden & Power (1985) reported a critical DO value of 4.3 mg l^{-1} for rainbow trout (*Oncorhynchus mykiss*), while at the upper end of the range Rubin & Glimsater (1996) reported a critical value of 9.9 mg l^{-1} for brown trout (*S. trutta*). However, critical DO levels reported in field studies are often substantially higher than those reported in the laboratory. For example, Hamor & Garside (1976) identified a critical DO level (LC_{50}) of 3.7 mg l^{-1} for Atlantic salmon subject to a 77 day low DO exposure, while Alderdice et al. (1958) identified an LC_{50} of 0.4–0.6 mg l^{-1} over a period of 7 days for chum salmon (*O. keta*) depending on the time post-fertilisation. Some of the variability in critical DO thresholds will reflect differences in the oxygen tolerance of individual salmonid species. However, it will also reflect a range of other issues associated with sampling and experimental design such as duration of exposure, stage of embryo development, temperature, spatial precision of sampling and sampling frequency (Malcolm et al. 2008). Whereas previous studies have often used large depth integrating sample volumes (Malcolm et al. 2009), the small volume samples used in the present study, were designed to resolve the problems associated with spatial precision by directly relating DO in the vicinity of the ova to survival. Similarly, although coverage was restricted by cost, continuous monitoring of DO by optodes demonstrated the real extent of temporal variation relative to the generally higher and more stable levels indicated by spot sampling. Wider use of continuous monitoring would probably resolve some of the seeming inconsistencies in reported values for critical DO levels for survival.

Despite the problems involved in deriving and interpreting critical DO thresholds, from a practical perspective, hyporheic sampling provides a useful method of assessing the general suitability of spawning habitat given appropriate sampling methods and frequency. In the absence of continuous logging, high average DO values may not indicate uniformly favourable hyporheic conditions due to the potential for unmeasured low DO episodes, However, consistently low DO values below critical thresholds are likely to identify unfavourable hyporheic habitat and the likelihood of associated embryo mortality.

Previous studies of embryo survival have tended to focus on the single issue of the effects of fine sediment infiltration (e.g. Jensen et al. 2009). While fine sediment is undoubtedly an important constraint on oxygen delivery to streambed sediments, other processes including GW-SW interactions, sediment oxygen demand, hyporheic flowpaths and residence times are undoubtedly in play, On these grounds, it will be necessary to use a more generalised approach to understanding constraints on salmonid embryo performance and to gauge the potential for functional and sustainable restoration of spawning habitat. There has been increasing interest in the remediation of the hyporheic zone as part of river restoration or habitat improvement strategies (Hancock 2002, Kasahara & Hill 2006, Sarriquet et al. 2007, Meyer et al. 2008). Proposed measures include gravel addition, gravel cleaning and increased morphological diversity (riffles, steps, pools, meanders). However, the functional benefits of such activities can be short lived where, for example, sediment delivery is not also reduced (Soulsby et al. 2001a, Hancock 2002, Kasahara & Hill 2006). In general, therefore, hyporheic restoration may prove practicable only in the context of management activities instituted on much broader, catchment-wide scales.

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References

Alderdice, D., Wickett, F. & Brett, J. R., 1958: Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. – J. Fish. Res. Board Can. **15:** 229–249.

Bencala, K. E. & Walters, R. A., 1983: Simulation of solute transport in a mountain pool-and-riffle stream: A transient storage model. – Water Resour. Res. **19:** 718–724.

Boano, F., Revelli, R. & Ridolfi, L., 2009: Quantifying the impact of groundwater discharge on the surface-subsurface exchange. – Hydrol. Process. **23:** 2108–2116.

Cardenas, M. B. & Wilson, J. L., 2006: The influence of ambient groundwater discharge on exchange zones induced by current-bedform interactions. – J. Hydrol. **331:** 103–109.

Cardenas, M. B. & Wilson, J. L., 2007: Hydrodynamics of coupled flow above and below a sediment–water interface with triangular bedforms. – Adv. Water Resour. **30:** 301–313.

Chapman, D. W., 1988: Critical review of variables used to define effects of fines in redds of large salmonids. – Trans. Amer. Fish. Soc. **117:** 1–21.

Conant, B., Cherry, J. A. & Gillham, R. W., 2004: A PCE groundwater plume discharging to a river: influence of the streambed and near-river zone on contaminant distributions. – J. Contam. Hydrol. **73:** 249–279.

Crenshaw, C. L., Grimm, N. B., Zeglin, L. H., Sheibley, R. W., Dahm, C. N. & Pershall, A. D., 2010: Dissolved inorganic nitrogen dynamics in the hyporheic zone of reference and human-altered southwestern U. S. streams. – Fundam. Appl. Limnol. **176:** 391–405.

Czerkies, P., Kordalski, K., Golas, T., Krysinski, D. & Luczynski, M., 2002: Oxygen requirements of whitefish and vendace (Coregoninae) embryos at final stages of their development. – Aquaculture **211:** 375–385.

Davis, J. C., 1975: Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. – J. Fish. Res. Board Can. **32:** 2295–2332 .

DeVries, P., 1997: Riverine salmonid egg burial depths: review of published data and implications for scour studies. – Can. J. Fish. Aquat. Sci. **54:** 1685–1698.

Elliot, J. M. & Hurley, M. A., 1998: An individual-based model for predicting the emergence period of sea trout fry in a lake district stream. – J. Fish Biol. **53:** 414–433.

Everest, F. L., Beschta, R. L., Scrivener, J. C., Koski, K. V., Sedell, J. R. & Cederholm, C. F., 1987: Fine sediment and salmonid production: a paradox. – In: Salo, E. O. & Cundy, T. W. (eds): Streamside Management: Forestry and Fishery Interactions. – University of Washington, Institute of Forest Resources, Contribution No. 57, pp. 98–142.

Fritz, B. G. & Arntzen, E. V., 2007: Effect of rapidly changing river stage on uranium flux through the hyporheic zone. – Groundwater **45:** 753–760.

Gooseff, M. N., Hall Jr., R. O. & Tank, J. L., 2007: Relating transient storage to channel complexity in streams of varying land use in Jackson Hole, Wyoming, – Water Resour. Res. **43:** W01417 doi:10.1029/2005WR004626.

Gooseff, M. N., Wondzell, S. M., Haggerty, R. & Anderson, J., 2003: Comparing transient storage modelling and residence time distribution (RTD) analysis in geomorphically varied reaches in the Lookout Creek basin, Oregon, USA. – Adv. Water Resour. **26:** 925–937.

Greig, S. M., Sear, D. A. & Carling, P. A., 2007: A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. – Hydrol. Process. **21:** 323–334.

Groves, P. A. & Chandler, J. A., 2005: Habitat quality of historic Snake River fall Chinook salmon spawning locations and implications for incubation survival. Part 2: intra-gravel water quality. – River Res. Appl. **21:** 469–483.

Hamor, T. & Garside, E. T., 1976: Developmental rates of embryos of Atlantic salmon, *Salmo salar* L., in response to various levels of temperature, dissolved oxygen, and water exchange. – Can. J. Zool. **54:** 1912–1917.

Hancock, P. J., 2002: Human Impacts on the Stream-Groundwater Exchange Zone. – Environ. Manage. **29:** 763–781.

Harvey, J. W. & Wagner, B. J., 2000, Quantifying hydrologic interactions between streams and their subsurface hyporheic zones. – In: Jones, J. A. & Mulholland, P. (eds.): Streams and Ground Waters. – Academic Press, Orlando, pp. 3–43.

Harvey, J. W., Wagner, B. J. & Bencala, K. E., 1996: Evaluating the reliability of the stream tracer approach to characterize stream-subsurface water exchange. – Water Resour. Res. **32:** 2441–2451.

Jensen, D. W., Steel, E. A., Fullerton, A. H. & Pess, G. R., 2009: Impact of Fine Sediment on Egg-To-Fry Survival of Pacific Salmon: A Meta-Analysis of Published Studies. – Rev. Fish. Sci. **17:** 348–359.

Kalbus, E., Schmidt, C., Molson, J. W., Reinstorf, F. & Schirmer, M., 2009: Influence of aquifer and streambed heterogeneity on the distribution of groundwater discharge. – Hydrol. Earth Syst. Sci. **13:** 69–77.

Kasahara, T. & Hill, A. R., 2006: Hyporheic exchange flows induced by constructed riffles and steps in lowland streams in southern Ontario, Canada. – Hydrol. Process. **20:** 4287–4305.

Käser, D. H., Binley, A., Heathwaite, A. L. & Krause, S., 2009: Spatio-temporal variations of hyporheic flow in a riffle-step-pool sequence. – Hydrol. Process. **23:** 2138–2149.

Leek, R., Wu, J. Q., Wang, L., Hanrahan, T. P., Barber, M. E. & Qiu, H., 2009: Heterogeneous characteristics of streambed saturated hydraulic conductivity of the Touchet River, south eastern Washington, USA. – Hydrol. Process. **23:** 1236–1246.

Malcolm, I. A., Soulsby, C., Youngson, A. & Petry, J., 2003: Heterogeneity in ground water – surface water interactions in the hyporheic zone of a salmonid spawning stream. – Hydrol. Process. **17:** 601–617.

Malcolm, I. A., Soulsby, C., Youngson, A. F., Hannah, D. M., McLaren, I. S. & Thorne, A., 2004: Hydrological influences on hyporheic water quality: implications for salmon egg survival. – Hydrol. Process. **18:** 1543–1560.

Malcolm, I. A., Soulsby, C., Youngson, A. F. & Hannah, D. M., 2005: Catchment scale controls on groundwater – surface water interactions in the hyporheic zone: implications for salmon embryo survival. – River Res. Appl. **21:** 977–989.

Malcolm, I. A. Soulsby, C. & Youngson, A. F., 2006: High frequency logging technologies reveal state dependant hyporheic process dynamics: implications for hydroecological studies. – Hydrol. Process. **20:** 615–622.

Malcolm, I. A., Youngson, A. F., Greig, S. & Soulsby, C., 2008: Hyporheic influences on spawning success – In: Sear, D. & DeVries, P. (eds): Salmon Spawning Habitat in Rivers: Physical Controls, Biological Responses and Approaches to Remediation. – American Fisheries Society, Bethesda, Maryland, USA, pp. 225–248.

Malcolm, I. A., Soulsby, C., Youngson, A. F. & Tetzlaff, D., 2009: Fine scale spatial and temporal variability of hyporheic hydrochemistry in salmon spawning gravels with contrasting groundwater-surface water interactions. – Hydrogeol. J. **17:** 161–174.

Meyer, E. I., Niepagenkemper, O. & Molls, F., 2008: An experimental assessment of the effectiveness of gravel cleaning operations in improving hyporheic water quality in potential salmonid spawning areas – River Res. Appl. **24:** 119–131.

Moir, H. J., 1999: Characterisation of salmon spawning habitat in the Dee catchment, NE Scotland. – Unpublished PhD thesis, University of Aberdeen.

Moir, H. J., Soulsby, C. & Youngson, A., 1998: Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in Girnock Burn, Scotland. – Fish. Manage. Ecol. **5:** 241–254.

Packman, A. I. & Salehin, M., 2003: Relative roles of stream flow and sedimentary conditions in controlling hyporheic exchange. – Hydrobiologia **494:** 291–297.

Packman, A. I., Salehin, M. & Zamarella, M., 2004: Hyporheic exchange with gravel beds: basic hydrodynamic interactions and bedform-induced advective flows. – J. Hydraul. Eng. **130:** 647–656.

Peterson, N. P. & Quinn, T. P., 1996a: Persistence of egg pocket architecture in redds of chum salmon, *Oncorhynchus keta*. – Environ. Biol. Fishes. **46:** 243–253.

Peterson, N. P. & Quinn, T. P., 1996b: Spatial and temporal variation in dissolved oxygen in natural egg pockets of chum salmon, in Kennedy Creek, Washington. – J. Fish Biol. **48:** 131–143.

Petry, J., Soulsby, C., Malcolm, I. A. & Youngson, A. F., 2002: Hydrological controls on nutrient concentrations and fluxes in agricultural catchments. – Sci. Total Environ. **294:** 95–110.

R Development Core Team, 2009: R : A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rombough, P. J., 1988: Respiratory gas exchange, aerobic metabolism and effects of hypoxia during early life. – In: Hoar, W. S. & Randall, D. J. (eds): Fish physiology. Volume XI. The Physiology of Developing Fish. – Academic Press Limited, London, pp. 59–162.

Rubin, J. F. & Glimsater, C., 1996: Egg-to-fry survival of the sea trout in some streams of Gotland. – J. Fish Biol. **48:** 585–606.

Runkel, R. L., 1995: Simulation models for conservative and non-conservative solute transport in streams. – In: Osterkamp, W. R. (ed.): Effects of scale on interpretation and management of sediment and water quality. – Proceedings of the 1995 meeting of the International Association of Hydrological Sciences, Boulder, Colorado, July 3–14, 1995: IAHS publication no. **226:** 153–159.

Runkel, R. L., 1998: One-dimensional Transport with Inflow and Storage (OTIS): a solute transport model for streams and rivers. – USGS Water-Resources Investigations Report 98-4018, 73 pp.

Runkel, R., 2000: Using OTIS to model solute transport in streams and rivers. – USGS Fact sheet FS-138-99.

Sarriquet, P. E., Bordenave, P. & Marmonier, P., 2007: Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. – River. Res. Appl. **23:** 815–828.

Schmidt, C., Bayer-Raich, M. & Schirmer, M., 2006: Characterization of spatial heterogeneity of groundwater-stream water interactions using multiple depth streambed temperature measurements at the reach scale – Hydrol. Earth Syst. Sci. D. **3:** 1419–1446.

Soulsby, C., Youngson, A. F., Moir, H. J. & Malcolm, I. A., 2001a: Fine sediment influence on salmonid habitat in a lowland agricultural stream: a preliminary assessment. – Sci. Total Environ. **265:** 295–307.

Soulsby, C., Malcolm, I. & Youngson, A., 2001b: Hydrochemistry of the hyporheic zone in salmon spawning gravels: a preliminary assessment in a small regulated stream. – Regul. Riv. Res. Manage.**17:** 651–665.

Soulsby, C., Petry, J., Brewer, M., Dunn, S., Ott, B. & Malcolm, I. A., 2003: Identifying and assessing uncertainty in hydrological pathways: a novel approach to end member mixing analysis in a Scottish agricultural catchment. – J. Hydrol. **274:** 109–128.

Soulsby, C., Tetzlaff, D., van den Bedem, N., Malcolm, I. A., Bacon, P. J. & Youngson, A. F., 2007: Inferring groundwater influences on surface water in montane catchments from hydrochemical surveys of springs and streamwaters. – J. Hydrol. **333:** 199–213.

Soulsby, C., Malcolm, I. A., Tetzlaff, D. & Youngson, A. F., 2009: Seasonal and inter-annual variability in hyporheic water quality revealed by four years continuous monitoring in a salmon spawning stream. – River Res. Appl**.** **25:** 1304–1399.

Sowden, T. K. & Power, G., 1985: Prediction of Rainbow Trout Embryo Survival in Relation to Groundwater Seepage and Particle Size of Spawning Substrates. – Trans. Amer. Fish. Soc. **114:** 804–812.

Storey, R. G., Howard, K. W. F. & Williams, D. D., 2003: Factors controlling riffle-scale hyporheic exchange flows and their seasonal changes in a gaining stream: A three-dimensional groundwater flow model. – Water Resour. Res. **39:** 1034.

Stream Solute Workshop, 1990: Concepts and methods for assessing solute dynamics in stream ecosystems. – J. N. Amer. Benthol. Soc. **9:** 95–119.

Tonina, D. & Buffington, J. M., 2007: Hyporheic exchange in gravel bed rivers with pool-riffle morphology: Laboratory experiments and three-dimensional modeling, – Water Resour. Res. **43:** W01421, doi:10.1029/2005WR004328.

Vollmer, S., Ramos, F. S., Daebel, H. & Kuhn, G., 2002: Micro scale exchange processes between surface and subsurface water. – J. Hydrol. **269:** 3–10.

Wagner, B. J. & Harvey, J. W., 1997: Experimental design for estimating parameters of rate-limited mass transfer: analysis of stream tracer studies. – Water Resour. Res. **33:** 1731–1741.

Webster, J. R., & Ehrman, T. P., 1996: Solute dynamics. – In: Hauer, F. R. & Lamberti, G. A. (eds): Methods in stream ecology. – Academic Press, San Diego, California, USA, pp. 145–160.

Youngson, A. F., Malcolm, I. A., Thorley, J. L., Bacon, P. J. & Soulsby, C., 2005: Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development and causes mortality. – Can. J. Fish. Aquat. Sci. **61:** 2278–2287.

Zimmerman, A. E. & Lapointe, M., 2005: Intergranular flow velocity through salmonid redds: sensitivity to fines infiltration from low intensity sediment transport events. – River Res. Appl. **21:** 865–881.

Zuur, A. F., Ieno, E. N. & Smith, G. M., 2007: Analysing Ecological Data. – Springer, New York, USA. 680 pp.

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