RIVER RESEARCH AND APPLICATIONS

River Res. Applic. **21**: 977–989 (2005)

CATCHMENT-SCALE CONTROLS ON GROUNDWATER–SURFACE WATER INTERACTIONS IN THE HYPORHEIC ZONE: IMPLICATIONS FOR SALMON EMBRYO SURVIVAL

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ABSTRACT

The spatial and temporal variability of groundwater–surface water (GW–SW) interactions in the hyporheic zone were investigated in a semi-pristine upland salmon spawning catchment (Girnock Burn) in the Cairngorm Mountains, northeast Scotland. Stream and hyporheic water quality (200–300 mm depth) were monitored fortnightly at 16 spawning locations distributed throughout the catchment. Hydrochemical tracers were used to assess local GW–SW interactions. Stratified streambed incubators (50–300 mm) provided information on salmon embryo mortality at a sub-set of ten locations. Hyporheic water quality varied both temporally and spatially according to local GW–SW interactions. It was possible to categorize sites into three broad typologies reflecting local stream–aquifer interactions: (1) groundwater-dominated; (2) surface water-dominated; and (3) sites exhibiting transient water table features. Groundwater upwelling occurred in areas where low permeability glacial moraine features caused substantive valley constriction. These locations were also conducive to accumulation of spawning grade gravels and consequently were utilized heavily by spawning salmon. Long residence groundwater was typically characterized by low dissolved oxygen (DO), of sufficiently low quality to be detrimental to salmon embryo survival. At sites dominated by surface water, hyporheic DO remained high throughout and rates of embryo survival were correspondingly high. Survival rates were also high at sites where hydrochemical characteristics indicated a transient water table. This is probably attributable to the hydrological conditions which resulted in increasing DO concentrations towards hatch time when embryo oxygen demand is at its maximum. The degree to which the findings of this study are directly applicable to other catchments is currently unknown. However, similar effects have been observed elsewhere, and based on the information presented here, there are clear implications for fisheries managers who may wish to consider the use of surface incubation facilities to negate the effects of low DO groundwater upwelling where it dominates available spawning habitat. It is suggested that future research should aim to integrate across spatial scales and disciplines to obtain a better understanding of the ways in which hillslope and riparian zone hydrology affect GW–SW interactions, hyporheic zone processes and stream ecology. © Crown copyright 2005. Reproduced with the permission of Her Majesty's Stationery Office. Published by John Wiley & Sons, Ltd.

KEY WORDS: hydrology; hydrochemistry; oxygen; salmonid; ova; tracer; spawning

INTRODUCTION

Salmon deposit their eggs in open gravel structures in the streambed known as redds. Spawning activity tends to be located in areas with specific sedimentary and hydraulic characteristics which are well documented (Crisp and Carling, 1989; Kondolf and Wolman, 1993; Moir *et al.*, 2002). In Scotland, spawning can occur at any time between mid-October and early February, varying both within (Webb and McLay, 1996) and between catchments. In the Girnock Burn, eggs are typically buried in early November to depths of up to 0.3 m and are exposed to the hyporheic environment for approximately 5 months before hatch in early April. Embryo survival during the incubation stage is highly variable, though acknowledged to account for a major portion of total lifetime mortality (Peterson and Quinn, 1996). The controls on embryo survival are complex (Figure 1), but delivery of oxygen is widely acknowledged as being critical (Coble, 1961; Silver *et al.*, 1963; Sowden and Power, 1985; Peterson and

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Received 6 August 2004
Revised 16 December 2004
Accepted 17 January 2005

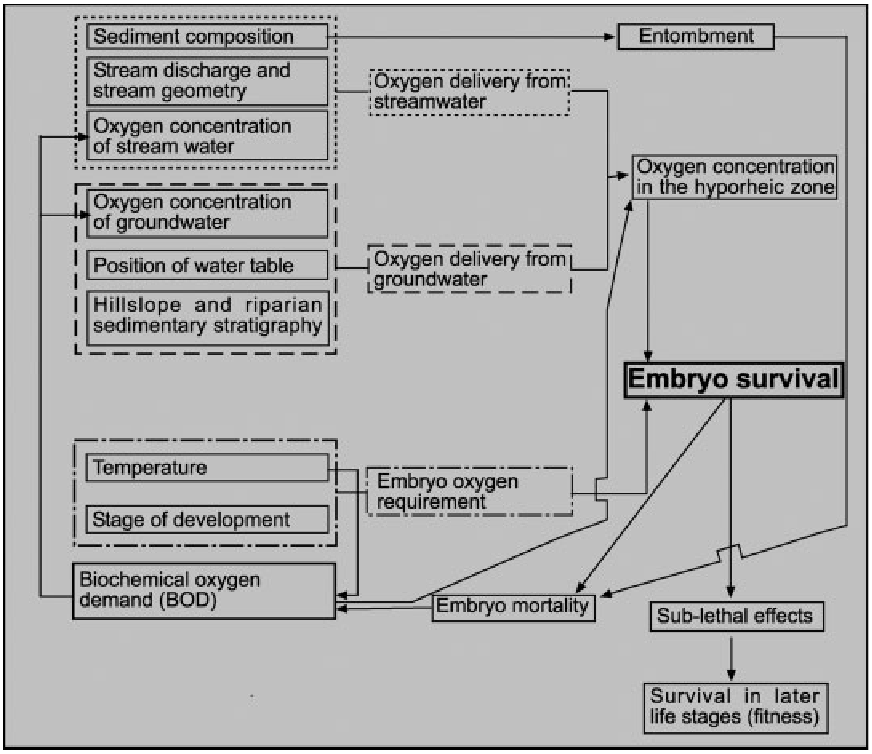

Figure 1. Conceptual diagram showing the complex interaction of processes that can influence salmon embryo survival. Hyporheic water quality is determined by the relative contributions of groundwater (– –) and surface water (- - - - -) which are in turn influenced by a variety of interacting physical and chemical processes. The oxygen requirement of embryos (– -) interacts with oxygen availability in the hyporheic environment to determine survival. The oxygen demand of embryos depends on a combination of metabolic rate and respiring mass which is influenced by embryonic stage and water temperature

Quinn, 1996; Rubin and Glimsater, 1996; Ingendahl, 2001 Malcolm *et al.*, 2003a). Investigations of in-redd survival have cited fine-sediment infiltration (Lisle and Lewis, 1992; Argent and Flebbe, 1999), sedimentary characteristics (Everest *et al.*, 1987; Chapman, 1988), washout (Vronskii and Leman, 1991), *in-situ* oxygen consumption (hyporheic respiration) and intrusion of de-oxygenated groundwater (Soulsby *et al.*, 2001; Malcolm *et al.*, 2003a) as causes of high mortality.

While local (micro-scale and reach-scale) controls on spawning site selection (Geist and Dauble, 1998; Moir, 1999; Moir *et al.*, in press) and embryo survival (Malcolm *et al.*, 2003a, 2004) are increasingly well understood, catchment-scale controls are less well known. However, it is catchment-scale controls such as geology and geomorphology that determine both the location of suitable spawning habitat (Moir *et al.*, 2004) and the stream–aquifer interactions that have the potential to influence embryo survival (Figure 1). This gap in available knowledge needs to be urgently addressed to make informed decisions at the catchment scale (i.e the scale at which most management plans are formulated) for sustainable fisheries management. This is particularly pertinent given recent declines in the fisheries resource (Youngson *et al.*, 2002).

The Girnock Burn is an extensively researched salmon spawning stream in the Dee catchment, northeast Scotland, where the dynamics of salmon populations (including spawner numbers and distribution and juvenile densities) have been monitored for almost 40 years by FRS (Fisheries Research Services) Freshwater Laboratory. Previous research in the catchment has described the spatial distribution of spawning locations (Moir *et al.*, 1998), the sedimentary characteristics of spawning gravels (Moir *et al.*, 2002), and the influence of hydrological variability on the distribution of spawning locations (Webb *et al.*, 2001; Gibbins *et al.*, 2002). In addition, recent investigations of egg mortality have revealed marked differences in survival to hatch depending on local groundwater–surface water (GW–SW) interactions at the reach scale (Malcolm *et al.*, 2004; Youngson *et al.*, in press). In some locations where surface water dominates the hyporheic zone, egg survival has been reported at near to 100% (Malcolm *et al.*, 2003a), while at spawning locations dominated by groundwater upwelling, survival has

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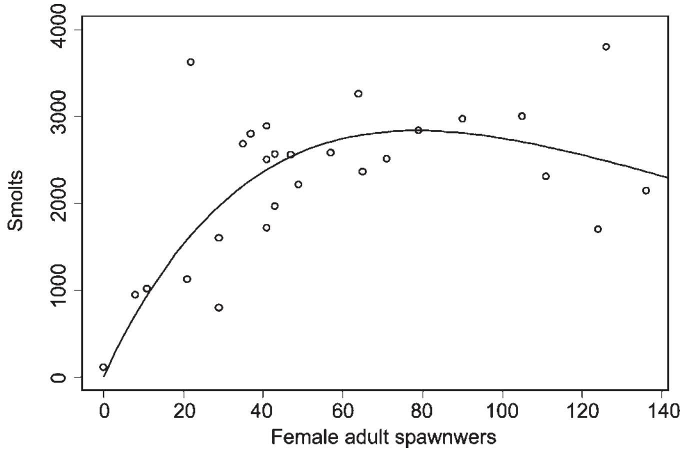

Figure 2. Stock–recruitment curve (Ricker curve) for the Girnock Burn from 1969 to 2001, where stock is the number of females caught ascending the stream each year and recruitment is the resulting number of smolts

been variable, but generally poor (Malcolm *et al.*, 2004). A high level of variability observed in the stock-recruitment curve (Figure 2), together with lower than anticipated fry densities, suggest that variable in-redd survival may be a problem in the Girnock Burn (Malcolm, 2002).

Whilst Soulsby and Boon (2001) and Moir *et al.* (2004) have drawn attention to catchment-scale geomorphological controls on spawning distributions, the extent to which these same processes influence in-redd survival through effects on GW-SW interactions are as yet unclear (Soulsby *et al.*, in press). This paper reports the finding of an investigation during the 2002–03 spawning season, which assessed the spatial distribution of in-redd water quality in the Girnock catchment and its implications for salmon embryo survival and recruitment to future populations. The detailed biological findings of this study are reported elsewhere (Youngson *et al.*, in press). This paper aims: (1) to elucidate the catchment-scale controls on in-redd water quality at spawning locations; (2) to assess the influence of groundwater-surface water interactions on in-redd water quality and; (3) to examine the implications for salmonid survival and management.

STUDY AREA

Glen Girnock is a semi-pristine upland catchment draining part of the Lochnagar massif into the Aberdeenshire Dee. The catchment ranges in altitude from approximately 230 m at the confluence with the Dee to 862 m at the summit of Caisteal na Caillich, draining an area of approximately 30.3 km^2 (Figure 3a). The catchment is underlain by a complex solid geology ranging from granite and diorite at higher altitudes to metamorphosed Dalradian rocks, primarily schists and gneisses, in the valley floor and sides (Figure 3b). A variety of glacial and fluvioglacial sediments overlie the solid geology, providing parent material for the soils. Podzols, gleys and peats are the dominant soil types, although there are also significant areas of brown forest soils in the more steeply sloping areas of the lower catchment (Soulsby *et al.*, 2005). The catchment receives approximately 1100 mm of precipitation annually, with up to 25% falling as snow (Warren, 1985). Temperatures have historically been highly variable. For example, during 1995 maximum and minimum temperatures of 31°C and −27°C respectively were recorded at Littlemill in the lower Girnock. Land use is dominated by heather (*Calluna*) moorland, though smaller areas of both commercial and semi-natural forest are found in the lower catchment. The Burn has a mean discharge of approximately 0.5 $\mathrm{m}^3\,\mathrm{s}^{-1}$. However, mean daily flow can vary between 0.02 $\mathrm{m}^3\,\mathrm{s}^{-1}$ in summer and over 23 $\mathrm{m}^3\,\mathrm{s}^{-1}$ during winter floods, representing a three-orders-of-magnitude variation in discharge. The majority of spawning activity in the Girnock Burn takes place in a few frequently and heavily utilized areas (Figure 3a). These are situated in the lower Girnock catchment close to the confluence with the River Dee, and in two main areas of suitable gravels in the upper catchment. Opportunistic spawning also takes place less frequently at locations where small lenses of gravel have collected. These locations are numerous, often transient and scattered throughout the catchment.

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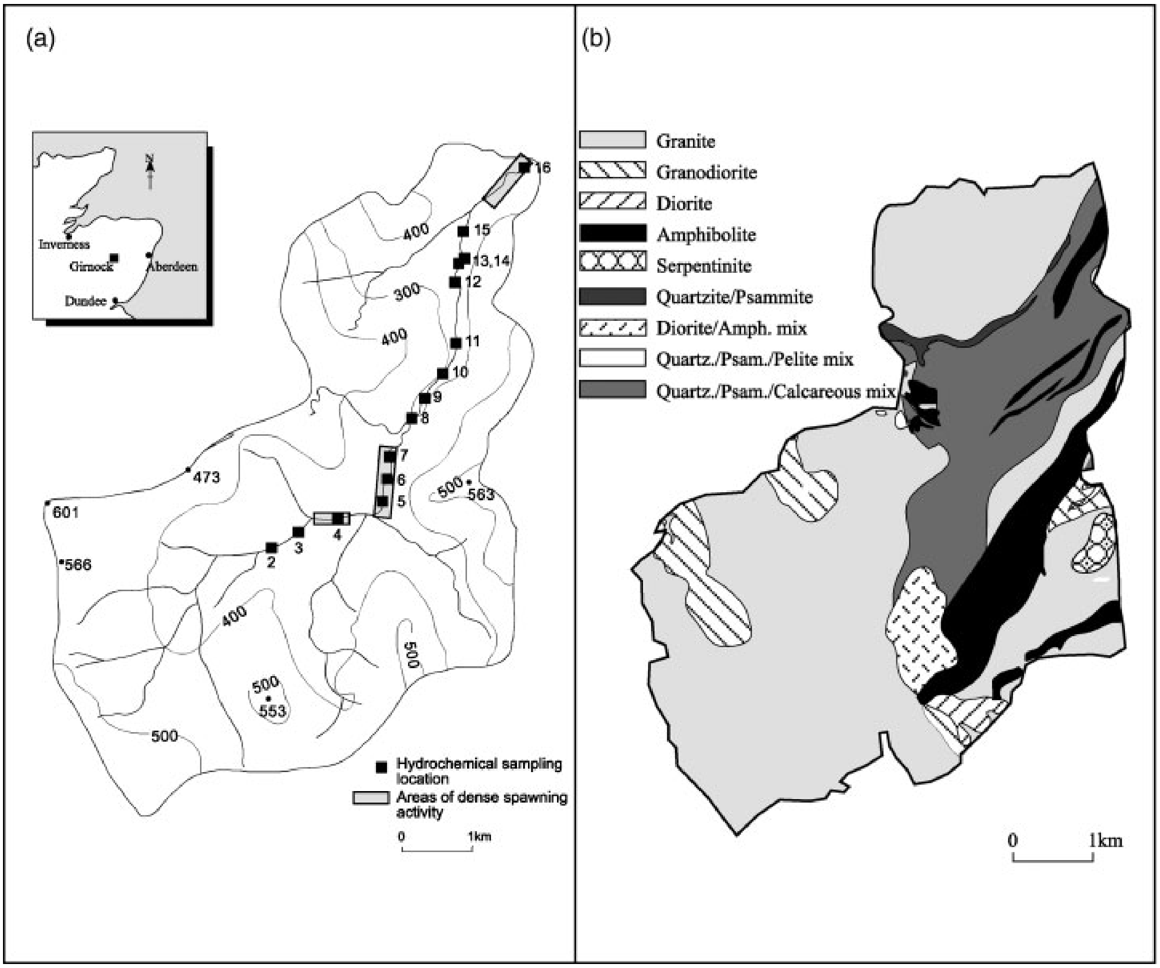

Figure 3. Maps of the Girnock Burn showing (a) topography, main spawning reaches and sampling locations, and (b) catchment solid geology (source information from BGS Solid Geology Base Map)

METHODOLOGY

Previous studies in the Girnock Burn and elsewhere have indicated that hydrochemical tracers provide a useful non-intrusive methodology for assessing the nature of groundwater-surface water interactions in upland catchments (e.g. Rodgers *et al.*, 2004). For this investigation a combination of techniques described by Soulsby *et al.* (2005) and Youngson *et al.* (2005) were used to obtain stream and hyporheic water samples from the Girnock Burn to characterize the spatial variability of stream and hyporheic water quality.

On 20 March 2002, a spatial survey of surface waters was carried out to investigate the variability of source water contribution to stream flow and the influence of geology and geomorphology on water quality at the catchment scale. Sixty water quality samples were collected in clean polyethylene bottles from sites on the Girnock main stem, tributaries and hillside springs. Samples were analysed for Gran alkalinity and electrical conductivity according to standard methods as discussed by Neal *et al.* (1999).

In September 2002, hyporheic water sampling tubes were inserted at 15 locations in the Girnock Burn (Figure 3a). The methodology is described in detail elsewhere (Youngson *et al.*, 2005); briefly, hyporheic samplers consisted of 1.5 m lengths of 0.4 mm i.d. Nalgene^{TM} tubing, perforated in the lower 100 mm and shielded with nylon mesh. Hyporheic sampling tubes were located to depths of 0.3 m, which is generally accepted as the maximum burial depth for salmon eggs in Scotland (DeVries, 1997); information was corroborated by excavations of natural redds in the field. All hyporheic sampling locations were located at sites where redds had been created in previous years by spawning

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salmon. Hyporheic sampling locations were distributed near-evenly throughout the stream network (0.5 km intervals), accounting for limitations imposed by patterns of spawning distribution (Figure 3a). The final choice of sampling locations covered the full geographical range of spawning sites and the range of geology and geomorphology that exists in the Girnock catchment. Redd locations were relocated in the field using a combination of redd maps, field notes and photographs of redd location taken at spawning time in previous years. Hyporheic sampling tubes were located at redd locations to an estimated accuracy of 0.5 m. Water samples were taken from surface and hyporheic water at each location approximately every 14 days. Water samples were analysed for dissolved oxygen (DO) and electrical conductivity in the field using a Hanna DO meter (HI9142) and Hanna conductivity meter (HI9033) respectively. Samples were returned to the laboratory for the analysis of Gran alkalinity by titration (Neal *et al.*, 1999). Samples were refrigerated and usually analysed within 48 hours. For consistency, the site nomenclature used in this paper is in agreement with that used by Youngson *et al.* (2005).

Ova survival and embryo performance were monitored at a sub-set of ten locations, which covered the range of variability observed in sub-surface water quality (Youngson *et al.*, 2005). DO measurements were converted from milligrams per litre percentage saturation using temperature measurements made in the field and atmospheric pressure data from the nearby Aboyne UK Meteorological Office synoptic station using the method described by Lee (1980), to allow comparison between sites with markedly different hyporheic temperatures.

RESULTS

Spatial variability

Surface water quality at the catchment scale (Figure 4, Table I) was strongly influenced by catchment geology (Figure 3b). Low-alkalinity stream water reflected granitic solid geology in the south (upper catchment) and west of the catchment. Areas of higher alkalinity stream water generally reflected the influence of base-rich solid geology in the east of the catchment. Similar, although more pronounced effects are likely for local groundwater quality, as longer residence times accentuate differences in the geochemistry and weathering rates of local geology (Soulsby *et al.*, 1998, 2005). The mean residence time of groundwater in the catchment is unknown, but work elsewhere in the Cairngorms suggests it is probably greater than 5 years (Soulsby *et al.*, 2000). Mean surface water alkalinity at the 15 spawning locations varied between 96 and 157 μeq l^{-1} during the spawning to hatch period. DO concentrations in surface water remained at or near saturation, with mean values ranging between 96.2 and 98.5% saturation for individual monitoring sites (Table I).

The spatial variability of hyporheic water quality greatly exceeded that of surface water (Table I). Mean DO concentrations varied between 28.3% (site 7) and 94.1% (site 16) saturation. Alkalinity and conductivity exhibited similar patterns of variability with mean concentrations varying between 102 (site 3) and 463 μeq l^{-1} (site 7), and 31.9 (site 3) and 83.2 μS cm^{-1} (site 7) respectively.

The spatial variability of stream and hyporheic water chemistry was increasingly apparent when plotted as downstream progression by site (Figure 5). Dissolved oxygen concentrations in surface water were consistently at or near saturation regardless of site (Figure 5a, b). Hyporheic oxygen concentrations varied markedly between sites and appeared independent of surface water concentrations. Sites 3, 9, 10, 12 and 16 exhibited similar oxygen concentrations to surface water, Sites 5, 7 and 11 consistently exhibited substantially depressed oxygen concentrations, while the remaining sites typically exhibited intermediate oxygen concentrations (Figure 5a, b).

Under high flow conditions surface water alkalinity typically exhibited a gradual increase with progression downstream, although more substantial increases were observed between sites 4 and 6 (Figure 5c) reflecting the influence of changing solid geology and tributary inflow. Under base flow conditions surface water alkalinity exhibited more of a pronounced stepped change between sites 5 and 6, with similar alkalinities between sites 2 and 4, 6 and 16 (Figure 5d). The spatial variability of hyporheic dissolved oxygen mirrored that of alkalinity. Low DO, indicative of chemically reduced conditions, was typically associated with high alkalinity, indicative of long residence times, suggesting that low dissolved oxygen in the hyporheic zone was associated with localized groundwater upwelling. Inter-site differences in hyporheic water quality were most apparent during high flow periods when differences between groundwater and surface water chemistry were most pronounced (Figure 5c). Variability was less marked during baseflow conditions, when groundwater contributions dominated surface water thereby reducing the chemical distinction between source waters (Figure 5d).

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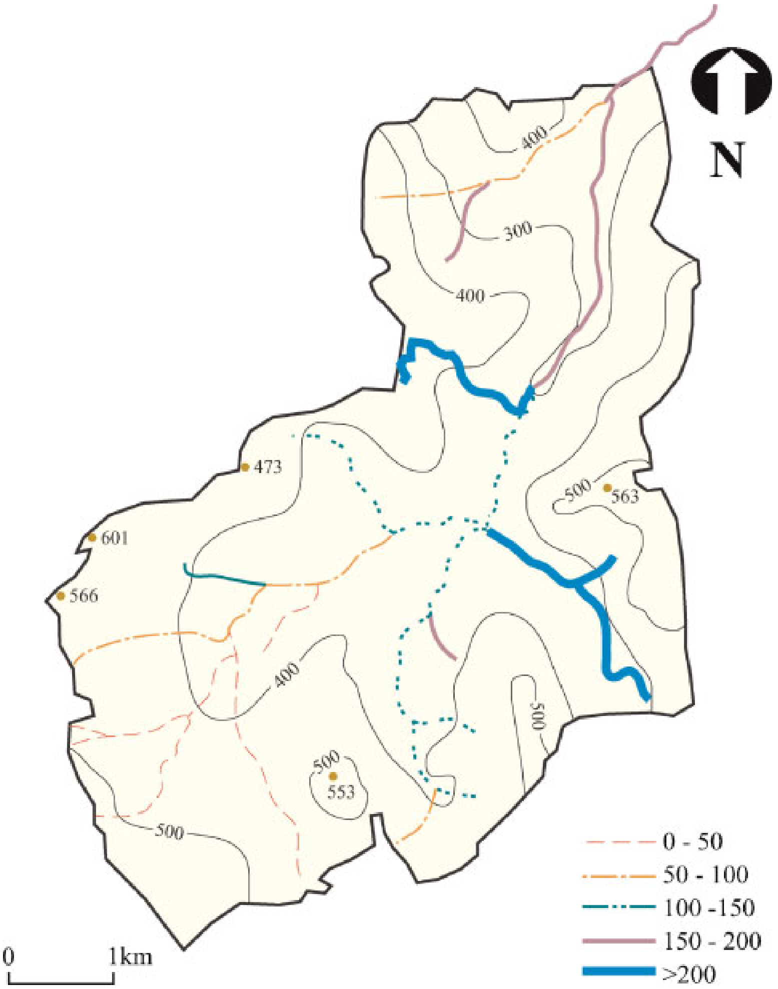

Figure 4. Spatial variability of surface water alkalinity (in μeq L^{-1}) in the Girnock Burn catchment. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Temporal variability

Despite complexity in the response of individual sites, it was possible to group sites according to three broad typologies reflecting local stream–aquifer interactions. These were: (1) groundwater-dominated sites; (2) surface water-dominated sites; and (3) sites exhibiting transient water table features. For clarity, Figure 6 shows temporal variability of stream and hyporheic water quality at a single site indicative of each of the three typologies.

At surface water-dominated locations, similarities in the chemical response of stream and hyporheic water indicated a common source (Figure 6a, b). Stream and hyporheic alkalinities closely tracked one another, both in terms of absolute values and patterns of variability (Figure 6a). Hyporheic DO concentrations were also in close agreement with those of surface water, remaining close to saturation throughout the monitoring period (Figure 6b).

At groundwater-dominated locations, stream and hyporheic water exhibited distinctly different chemistries reflecting the influence of different source waters in the hyporheic environment (Figure 6c, d). Hyporheic alkalinities were markedly higher than stream alkalinities indicating the influence of longer residence groundwater (Figure 6c). The temporal variability of hyporheic alkalinity reflected the influence of prevailing hydrological conditions and their effect on the relative contribution of groundwater and surface water to the hyporheic zone. During periods of high flow in late autumn and early winter, high stream stage ensured a substantial surface water contribution to the hyporheic zone. As winter base flows declined from late December through to March, surface water contributions to the hyporheic zone declined and groundwater contributions increased, indicated by

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Table I. Mean and standard deviation (SD) of stream (S) and hyporheic (H) water quality ($n = 9$) at 16 sampling locations in the Girnock Burn between 17 November 2002 and 05 March 2003

Site	Dissolved oxygen		Dissolved oxygen		Conductivity		Alkalinity	
	($\mathrm{mg\,l^{-1}}$)	SD	(% Saturation)	SD	($\mathrm{\mu S\,cm^{-1}}$)	SD	($\mathrm{\mu eq\,l^{-1}}$)	SD
2 S	12.7	1.0	96.3	5.8	30.3	5.2	96	58.5
2 H	11.1	1.3	86.4	7.0	36.0	10.9	155	83.9
3 S	12.8	1.3	97.2	6.5	32.0	5.2	104	54.9
3 H	12.1	1.3	92.6	7.3	31.9	4.8	102	55.3
4 S	12.8	1.3	97.2	6.3	31.9	4.8	102	56.4
4 H	8.0	2.2	61.0	14.5	51.0	9.1	280	77.4
5 S	12.8	1.3	97.7	6.6	34.4	6.1	110	61.9
5 H	6.7	1.5	49.7	10.7	63.9	18.6	473	191.2
6 S	12.7	1.1	97.3	4.7	36.2	7.3	136	70.8
6 H	8.8	1.1	69.6	8.9	62.2	16.6	401	164.2
7 S	12.7	1.2	97.2	5.6	36.7	7.1	143	64.0
7 H	3.6	0.7	28.3	6.2	83.2	9.9	463	103.0
8 S	12.6	1.2	96.9	5.9	38.4	7.3	143	69.7
8 H	9.8	1.3	77.2	6.6	52.3	4.9	304	59.7
9 S	12.6	1.1	97.1	5.0	38.1	5.8	148	60.8
9 H	12.1	1.0	93.6	5.4	39.4	6.4	173	66.9
10 S	12.7	1.0	97.8	5.0	37.9	6.9	145	63.4
10 H	11.6	0.8	90.8	4.3	35.6	6.2	149	60.7
11 S	12.6	1.0	97.2	4.9	38.0	6.8	149	64.0
11 H	7.3	1.8	59.4	12.2	53.8	3.0	235	77.9
12 S	12.6	1.0	97.2	3.9	39.5	6.7	154	63.5
12 H	11.6	1.0	91.8	4.9	38.6	5.5	186	66.0
13 S	12.7	1.1	98.1	6.5	39.3	7.0	153	62.9
13 H	9.3	1.0	71.7	5.8	41.4	6.7	197	81.3
14 S	12.7	1.1	98.5	6.3	39.3	7.0	155	62.2
14 H	10.8	1.1	84.1	4.1	38.8	6.3	159	57.6
15 S	12.6	1.0	97.6	4.0	40.1	7.6	157	64.1
15 H	10.2	0.8	80.0	8.1	42.3	6.1	191	56.5
16 S	12.5	1.1	96.2	3.3	44.3	6.2	145	61.0
16 H	12.2	1.1	94.1	4.1	42.7	5.3	157	60.3

increasing hyporheic alkalinity levels. Patterns exhibited by the alkalinity data were mirrored in the DO data, where concentrations declined over time in response to declining base flow and increasing groundwater contribution (Figure 6d).

The third typology denotes those sites that exhibited both groundwater- and surface water-dominated characteristics over time (generally sites of intermediate water quality). Figure 6e shows the temporal variability of stream and hyporheic alkalinity at one such location. The site initially behaved in a similar manner to other groundwater-dominated locations, with hyporheic alkalinity increasing in response to declining base flows and increasing groundwater contributions. However, following a prolonged period of predominantly dry weather, alkalinities began to decrease from 9 January onwards, indicating a reduction in groundwater contributions. This is consistent with a transient water table feature where prolonged periods of dry weather result in declining water table elevations and reduced streamward hydraulic head gradients (Vidon and Hill, 2004). Once again, patterns exhibited by alkalinity were mirrored in the DO data (Figure 6f). DO initially decreased in response to increasing groundwater contributions before increasing again as groundwater contributions declined.

Catchment-scale controls on GW–SW interactions

The spatial water quality survey identified areas where shallow hyporheic conditions were dominated by surface water, groundwater or intermediate conditions. Of the 15 locations monitored, groundwater upwelling was most

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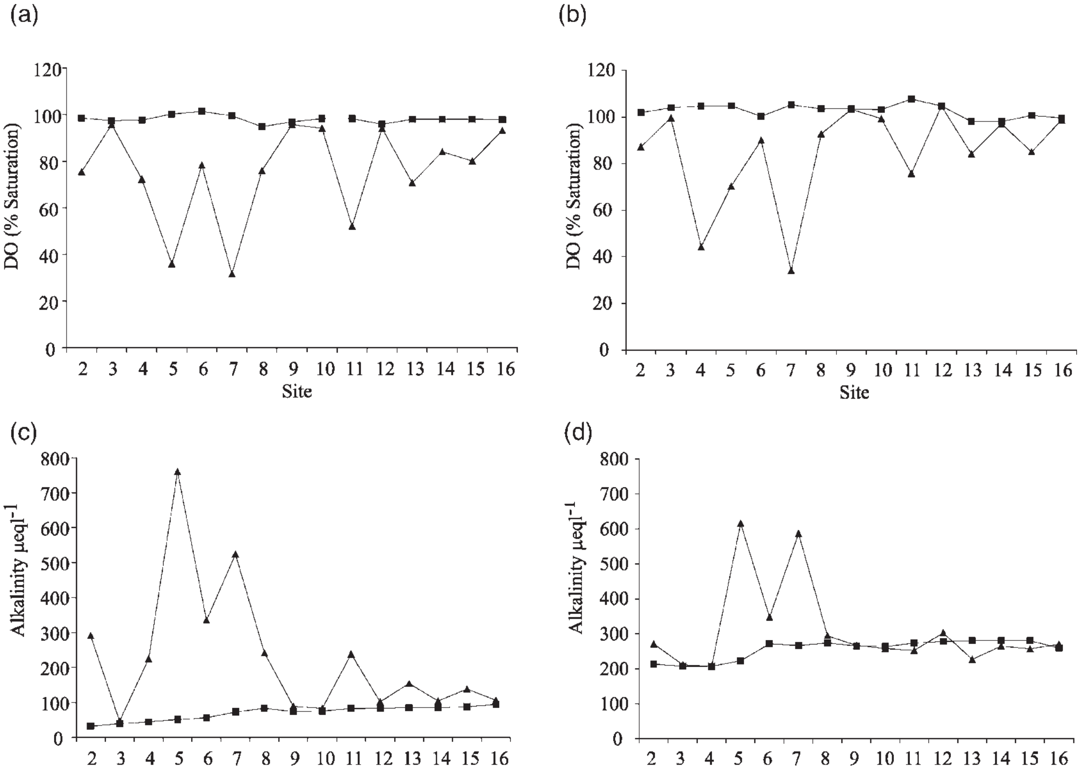

Figure 5. Spatial variability of DO (a, b) and alkalinity (c, d) in stream (-■-) and hyporheic (-▲-) water during low (b and d: 0.237 $m^3 s^{-1}$) and high (a and c: 0.914 $m^3 s^{-1}$) flow conditions

substantial at sites 5 and 7. In terms of importance to spawning, these sites are among the most intensively and consistently utilized locations in the Girnock Burn; for example in 1995, these two reaches accounted for *c*. 36% of all spawning activity. Figure 7 shows an aerial photograph annotated with the positions of sites 4–15. Sites 5 and 7 differ from other locations in that they were located immediately upstream of major valley constrictions resulting from substantial cross-valley moraine features characterized by poorly sorted and low permeability material. It is probable that these features have the effect of channelling down-valley groundwater movement towards the river channel where it discharges through the riverbed and banks.

Impact of GW–SW interactions on salmon embryo survival

Where groundwater upwelling dominates shallow hyporheic environments, DO concentrations can fall to critical levels for developing salmonid embryos (Malcolm *et al.*, 2003a, 2004; Youngson *et al.*, 2005). Paradoxically, the valley constriction and channel confinement associated with terminal moraine features that appear to facilitate groundwater upwelling, also have the effect of reducing upstream channel gradient, resulting in the accumulation of spawning-grade gravels. This results in the creation of sedimentary and hydraulic conditions suited to spawning by salmonids across a wide range of flows (Moir, 1999). Consequently, two of the most heavily utilized areas of suitable spawning gravel in the Girnock Burn (sites 5 and 7) are characterized by the poorest hyporheic water quality for developing salmonid ova.

Low DO caused by upwelling groundwater can have a variety of impacts on salmonid embryo permanence. The full range of effects is discussed elsewhere (Youngson *et al.*, 2005); this paper will simply consider mortality. Table II shows embryo survival rates at depths of between 50 and 300 mm at a sub-set of ten locations chosen to represent the range of hyporheic water quality available in the Girnock Burn. Estimates of embryo survival are likely to be conservative as ova were excavated shortly before hatch, while oxygen demand would have continued to increase up until hatch time (Figure 1). Survival was generally good across the ten sites investigated. High mortality at the

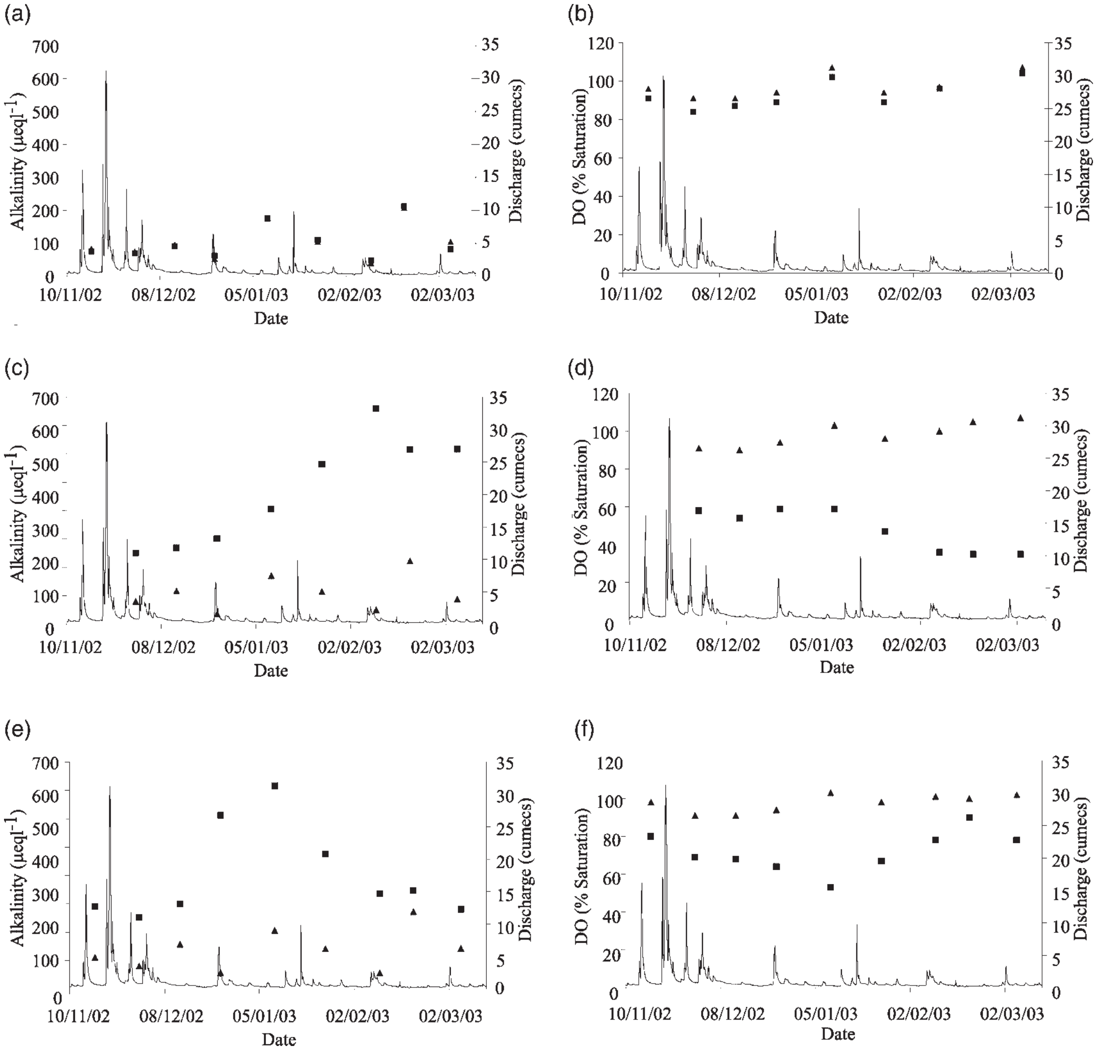

Figure 6. Temporal variability of stream (▲) and hyporheic (■) water quality at sites characterized by surface water dominance (a, b: site 3), groundwater dominance (c, d: site 5) and transient water table features (e, f: site 6)

shallowest depths probably resulted from mechanical shock and scour effects as opposed to the effects of water quality. Total mortality was observed at 300 mm at site 13 emphasizing the increasing influence of groundwater with depth. At site 7, mortality was observed at depths of between 100 and 300 mm, with survival only at 50 mm. No survival data were available for site 5, but given the similarity of conditions between sites 5 and 7 it is reasonable to assume that mortality rates would have been similar. A range of sub-lethal effects likely to affect survival later in life was observed at sites exhibiting intermediate water quality characteristics (Youngson *et al.*, 2005).

DISCUSSION AND CONCLUSION

Groundwater–surface water interactions exhibited marked spatial and temporal variability across the Girnock Burn catchment. The spatial distribution of groundwater upwelling appeared to be strongly influenced by catchment geomorphology, in particular valley constriction and channel confinement by low-permeability glacial moraine features. It is suggested that these features channel groundwater movement from a predominantly down-valley orientation towards the stream channel where it discharges through the banks and bed of the stream. These

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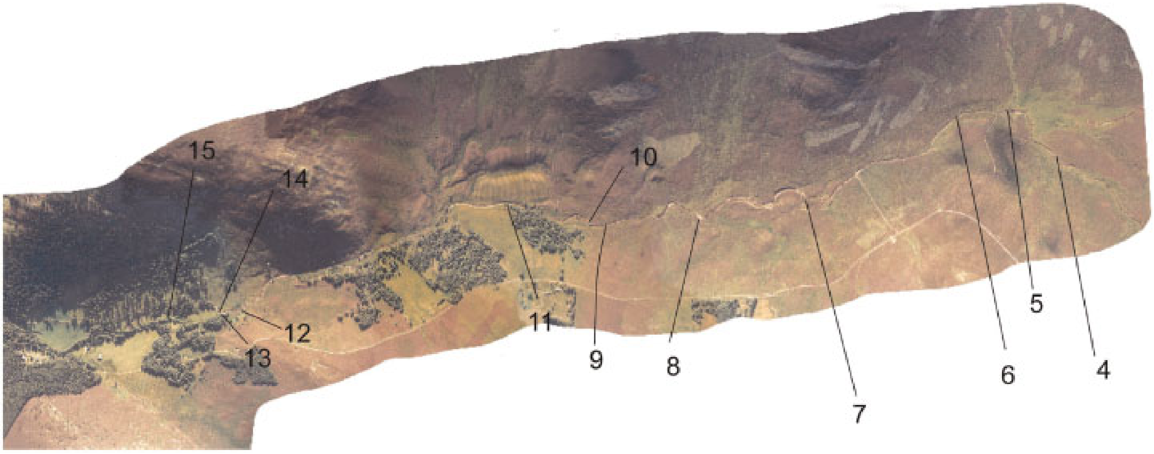

Figure 7. Aerial photograph of the Girnock Burn showing the position of sampling locations relative to catchment geomorphology. Sites 5 and 7 are located immediately upstream of moraine features that cause valley constriction with reduced channel slope upstream, channel incision through the moraine and increased gradient downstream. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Table II. Percentage of ova ($n = 20$) surviving to the eyed stage at a sub-set of ten sampling locations

Depth below streambed (mm)	Site									
	2	3	4	6	7	9	10	12	13	16
50	0	0	100	65	100	0	0	100	0	0
100	100	95	100	100	0	95	100	100	100	100
150	100	95	100	100	0	100	100	100	100	100
200	100	100	100	100	0	100	100	100	100	100
250	100	95	90	100	0	100	100	95	100	100
300	100	95	100	0	0	95	100	100	0	100

observations are in agreement with those of Baxter and Hauer (2000) who observed groundwater upwelling in association with ‘Geomorphic knickpoints’ (p. 1477). These knickpoints were associated with geological (bedrock) or geomorphological (terminal moraines) valley constriction.

Temporal variability in hyporheic water quality reflected gross changes in the relative contribution of groundwater and surface water at individual sites. This reflected interactions between stream stage and water table elevation, which in turn is influenced by riparian and sub-surface geomorphology and sedimentary structure (Williams, 1993; Wondzell and Swanson, 1996; Brunke and Gonser, 1997; Boulton *et al.*, 1998; Sophocleous, 2002; Malcolm *et al.*, 2003b, 2004; Vidon and Hill, 2004). At groundwater-dominated locations, the influence of surface water was highest at high stream stage; groundwater contributions increased in response to declining base flows in association with stable water table elevations. Where the water table subsequently declined (at transient water table locations) then so too did the groundwater contribution, leading once more to surface water dominance and increased DO concentrations. Hyporheic water quality at surface water-dominated locations reflected surface water quality. DO at these locations was consistently high throughout the study.

Because long residence groundwater in the Girnock Burn is associated with low oxygen conditions, reaches characterized by groundwater upwelling were also characterized by low rates of salmon embryo survival (Malcolm *et al.*, 2004, Youngson *et al.*, 2005). Paradoxically, the physical features that generate suitable spawning habitat (Moir, 1999) are also responsible for groundwater upwelling. The consequence of this is that two of the most consistently and heavily utilized spawning locations in the Girnock Burn (Webb *et al.*, 2001) are also two of the poorest locations in terms of interstitial water quality and thus embryo survival/performance (Youngson *et al.*, 2005).

Inter-annual variability in hydrological conditions has the potential to impact on salmon embryo survival through effects on spawning distributions and hyporheic water quality. Although there is some information

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available on the effects of changing hydrological conditions on salmon spawning distributions (Webb *et al.*, 2001; Gibbins *et al.*, 2002), little is known about the effects on hyporheic water quality. Because of the complexity of interactions between groundwater and surface water, inter-annual differences in groundwater recharge as well as the timing, frequency and magnitude of hydrological events have the potential to substantially alter hyporheic water quality with subsequent impacts on salmon embryo survival. Taken together, it is possible that these two factors may explain some of the variability observed in stock recruitment curves in the Girnock Burn and elsewhere (Malcolm, 2002; Prevost *et al.*, 2003; Jonsson *et al.*, 1998).

Historically, the numbers of adult female salmon returning to the Girnock was substantially in excess of those required to fully stock the stream system. However, in recent years, declining adult returns (Youngson *et al.*, 2002) have meant that there are no longer sufficient adult females to fully stock the system, a familiar situation across Scotland and elsewhere in Europe (ICES, 2004). Under this scenario, it is important to minimize mortality effects at all stages of the life cycle in order to maximize output from the freshwater environment. Where it can be demonstrated that embryo mortality is a substantial loss, fisheries managers may wish to consider the use of incubation facilities to avoid the impacts of low DO groundwater.

Although this study was particular to the Girnock Burn, much of the information presented here will be applicable elsewhere. Groundwater is common to all catchments, is often chemically reduced, and its distribution of entry to stream channels is uneven at all relevant spatial scales. GW–SW interactions are known to vary with changes in valley width (as demonstrated in the present study) and depth to bedrock (Stanford and Ward, 1993; Baxter and Hauer, 2000; Malard *et al.*, 2002), streambed permeability (Harvey and Bencala, 1993; Vallett *et al.*, 1996; Brunke and Gonser, 1997), local geomorphology (Vaux, 1962, 1968), streambed obstacles (Worman *et al.*, 2002), and preferential flowpaths, for example through abandoned stream channels or coarse fluvioglacial deposits (Curry and Devito, 1996; Wondzell and Swanson, 1996). However, regardless of the exact mechanism, the intrusion of low DO groundwater to spawning gravels has the potential to substantially restrict juvenile salmonid recruitment.

The variety of stream–aquifer interactions illustrated in this study has been demonstrated at larger spatial scales, inferred on the basis of detailed hillslope process measurements (Vidon and Hill, 2004). Elsewhere, studies have considered hillslope–riparian interactions in detail, without fully making the link to hyporheic-zone processes and stream–aquifer interactions (e.g. McGlynn *et al.*, 1999, 2002). A number of other studies have looked at hyporheic processes at small spatial scales and tried to infer stream–aquifer interactions (e.g. Hendricks and White, 1991; Malcolm *et al*., 2003b, 2004), and some studies have looked at the effect of hyporheic processes and water quality with reference to various aspects of stream ecology including fish (Sowden and Power, 1985; Geist, 2000; Geist *et al.*, 2002; Malcolm *et al.*, 2003a), invertebrates (Boulton and Foster, 1998; Fowler and Death, 2001) and nutrient processing. However, to date, no studies have attempted to link hillslopes, riparian areas, drift and solid geology aquifers, hyporheic-zone processes and stream ecology in a single study. To improve understanding of the processes controlling GW–SW interactions, hyporheic-zone processes and the links to stream ecology, scientists need to focus on working at the boundaries between disciplines that include hydrogeology, geomorphology, hydrology, hydrochemistry and ecology.

ACKNOWLEDGEMENTS

The authors would like to thank the British Atmospheric Data Centre for atmospheric pressure data, colleagues at FRS FL for assistance with fieldwork, and Maureen Lamb at the University of Aberdeen for expert Gran alkalinity titration.

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