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The magnitude and significance of sediment oxygen demand in gravel spawning beds for the incubation of salmonid embryos

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Abstract

Globally, salmon populations are under pressure and in those where numbers are severely depleted, density independent factors such as the accumulation of fine sediment and subsequent mortality of incubating embryos are critical factors in their conservation. Although progress has been made in identifying the processes by which fine sediment can lead to embryo mortality, this has focussed on the physical blockage of gravel pores. This paper presents new knowledge on the role of sediment-associated organic matter in controlling the supply of dissolved oxygen to incubating salmon embryos within gravel river beds. We report a new approach to the measurement of sediment oxygen demand (SOD) from interstitial sediments accumulated within salmon redds and demonstrate this across a range of salmon river types. The effects of varying SOD on dissolved oxygen supply to incubating salmon embryos are quantified for the first time, using the physically based Sediment Intrusion and Dissolved Oxygen (SIDO-UK) model. The results reveal the importance of the mass of accumulating sediment and sediment consumption rates (sediment oxygen consumption [SOC]), which constitute the overall SOD over time for a particular sediment sample. Higher SOC result in reductions in dissolved oxygen that are deleterious to salmonids; however, these are subordinate to the effects of sediment mass. Larger quantities of sediment accumulating within the redd not only create a higher SOD but also physically block the pores within the gravels, leading to a more drastic decline in oxygen supply through the combined effects of reduced seepage velocity and dissolved oxygen concentration. We seek to generalize the results by exploring the influence of catchment characteristics on field measures of SOD and SOC. This work makes a significant and novel contribution to improving our fundamental understanding of hyporheic processes within salmonid spawning gravels whilst providing resource managers with evidence of the deleterious effects of sediment-associated organic matter on salmon recruitment.

KEYWORDS

modelling, organic matter, salmon spawning habitat, sediment oxygen consumption (SOC), sediment oxygen demand (SOD)

1 | INTRODUCTION

There have been large-scale declines in many migratory salmonid populations in recent decades. Given the challenges faced in managing marine environments, fisheries management has often focused on maximizing production in freshwater. In North America, the declines of both Atlantic and Pacific salmon runs because human occupation has resulted in the extirpation of salmon from river catchments and driven a multibillion US\$ industry in habitat restoration (Palmer et al., 2005; Sear, DeVries, & Greig, 2008). In Europe, a similar pattern has

been observed, resulting in specific legislation to protect and restore the habitat of Atlantic salmon (Sear, 2010; WWF, 2001). Scientists have concluded that improved understanding of the factors leading to salmonid decline is essential to establishing a sustainable resource (Beechie et al., 2010). There is a consensus based on a growing evidence base that contributory factors include the simplification, modification, and decline in the quality of freshwater habitats (Parrish, Behnke, Gephard, McCormick, & Reeves, 1998; Sear, 2010; WWF, 2001). These identify embryo development within the river bed as the most critical life stage, during which mortality is typically high (Quinn, 2005). Key to

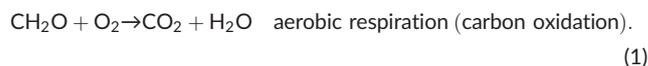
understanding the reasons for high mortality and thus improved resource management lies in being able to identify those factors that control the development of the incubating embryo (Quinn, 2005). Increasingly, this requires improved understanding of the bio-geochemical processes that affect the supply of oxygen to incubating embryos within the stream bed (Greig, Sear, & Carling, 2007a).

Critically, although not exclusively, embryo mortality is dependent on the supply of dissolved oxygen (DO), essential macronutrients and micronutrients, and the removal of potentially toxic metabolic by-products via the water within the hyporheic zone (Chapman, 1988; Greig et al., 2007a). The most frequent factor cited as contributing to the decline in productivity of spawning habitat is the intrusion and accumulation of fine sediment and associated organic matter (OM) into salmonid redds (Sear, Frostick, Rollinson, & Lisle, 2008). Hypotheses to explain these findings are based on the theory that to support the oxygen consumption of incubating embryos, the rate of oxygen supply to the boundary layer surrounding the egg must be greater than the rate of consumption of oxygen within the egg (Daykin, 1965; Greig et al., 2007a). Based on this theory, the effect of fine sediment accumulation within the spawning gravels post redd cutting can be articulated in four hypotheses: (a) sediment blocks interstitial pores reducing flow velocities and hence the rate of supply of oxygen (Olsson & Persson, 1988; Sear et al., 2008; Stuart, 1953); (b) sediment blocks the micropores on the surface of eggs resulting in a reduction in the uptake of oxygen by incubating embryos (Greig, Sear, & Carling, 2005a); (c) sediment-associated pollutants are toxic to fish eggs (Ballantine, Walling, Collins, & Leeks, 2009); and (d) sediment consumes oxygen, through the oxidation of OM and nitrogenous compounds, reducing concentrations in the egg zone (Chevalier, Carson, & Miller, 1984; Greig, Sear, Smallman, & Carling, 2005b). Sediment oxygen demand (SOD) in gravel-bed rivers has to date been poorly quantified (only two reported field measurements—Theurer & Theurer, 1986; Greig, 2004) yet has been identified by Malcolm, Greig, Youngson, and Soulsby (2008) as a key area for further research. Moreover, the magnitude of the effect of SOD in reducing the oxygen available to support embryo development has yet to be quantified. This paper addresses these critical gaps by the following: (a) using a novel methodology to provide measurements of the SOD of fine sediment accumulated within salmon spawning redds from a range of different river catchments (e.g., groundwater dominated, large lowland gravel-bed pool-riffle rivers, and steep upland pool-riffle streams) and (b) using a numerical model of the oxygen budget within a spawning redd to quantify the effect of SOD on the supply of oxygen to Atlantic salmon embryos. In addition, the aims of the paper are threefold: first, to provide new field data on the SOD and SOC of fine sediments intruded into salmon redds; second, to extend the field data using a physically based oxygen model to explore the magnitude of the impact of varying SOD and SOC on oxygen supply to incubating salmonids; and third, to generalize the field data by evaluating the relationship between measured SOD and SOC and wider catchment characteristics.

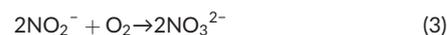
1.1 | SOD

SOD is the loss of DO from the water column through biological and chemical oxidation processes occurring within the sediment (Hondzo

& Steinberger, 2008). SOD is often said to be composed of three elements: (a) biological oxygen demand (BOD); (b) nitrogen oxygen demand; and (c) chemical oxygen demand. BOD is the decomposition of OM that accumulates in the subsurface gravels by microorganisms. This process occurs by carbon oxidation (Equation 1) and is thought to occur at the sediment–water interface where the sediment is coated with a microbial biofilm (Lundkvist, Grue, Friend, & Flindt, 2007). The rate of this process is believed to peak between 10 and 14 days and is shown by Line (a) in Figure 1.



Nitrogen oxygen demand is the oxidation of nitrogen containing compounds, such as ammonium (often found in fertilizers) and inorganic sediments. The process of nitrification converts ammonium to nitrite (Equation 2) followed by nitrate (Equation 3) through oxidation by nitrifying bacteria (Gaudy & Gaudy, 1980). This process is delayed and usually peaks on about Day 25 (Line b in Figure 1).



Chemical oxygen demand as defined in this instance, in contrast to the typical wastewater description, accounts for the oxidation of only the inorganic substances, for example, iron sulphite. These are often rapidly oxidized but are typically a minor contribution to total SOD, except in rivers with high industrial effluent discharges (Cox, 2003).

There are two separate processes that consume oxygen within the egg zone of a salmon redd: (a) the decay of sediment-associated OM transported into the pores between framework gravels and (b) the respiration of salmon eggs and, after hatch, salmon alevin (Theurer & Theurer, 1986).

The dominant controls on SOC are as follows: (a) temperature; (b) intragravel flow velocity; and (c) organic content both in the solid matrix and entrained in the pore water. The rates of biological processes, for example, respiration, are temperature dependent (Di Torro, 2001). It is widely accepted that a 10 °C rise in temperature results in a

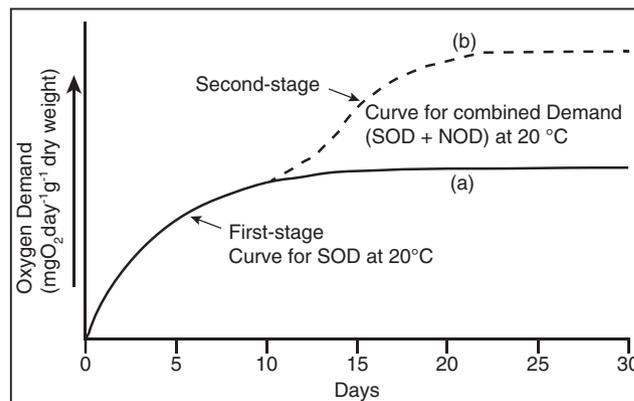


FIGURE 1 Theoretical graph showing how sediment oxygen demand (SOD) of sediment changes over time in a standard 30-day test at 20 °C

doubling of SOC (McDonnell & Hall, 1969). SOC increases linearly with velocity at speeds less than 10,800 cm/hr (such as found within the pores of redds; Josium & Stefan, 1999; Nakamura & Stefan, 1994), whereas at higher velocities, SOC is independent.

SOC is also reliant upon the types of OM. Labile carbon is highly bioavailable and decays rapidly, whereas refractory carbon is more resistant to decay (Cole & Wells, 2008; Otten, Gons, & Rijkeboer, 1992). Furthermore, particulate and dissolved OM (that which passes through a 0.45- μm filter) decay at different rates (Jewell & McCarty, 1971; Yoshimura, Gessener, Tockner, & Furumai, 2008). Particle size is also important, as this influences the surface area subject to decomposition (House, 2003). SOC rate is independent of the DO concentration over 2 mg/L (Chevalier & Murphy, 1985; Edwards & Rolley, 1965).

Along with the controls on SOD being complex, the other reason why few values exist for SOD is that there is currently no standard method for measuring it (Miskewitz, Francisco, & Uchirin, 2010). SOD can either be assessed in situ in the field or from samples taken and analysed in laboratories (Table 1). This makes the comparison between different studies difficult (Chau, 2002). For example, Patterson, Epstein, and McEvoy (1975) found that values for the same sediment differed by 10 times between field and laboratory measurements. It is thought that in situ measurements are favoured, as they most accurately represent the natural ambient conditions and errors are not introduced by transferring to the laboratory. However, field measurement within spawning gravel substrates is extremely difficult, especially in terms of the amount of time that experiments can proceed. Typically, benthic SOD chambers are deployed on the bed surface for period of a few minutes, and the SOD extrapolated from this data (Doyle & Lynch, 2005). The only reported measurements from within salmonid redds involved the use of freeze coring to recover bulk sediments, followed by laboratory incubation of the previously separated fine sediments within an incubator (Chevalier & Murphy, 1985; Greig, 2004; Theurer & Theurer, 1986).

1.2 | Modelling SOD in a salmon redd

The SIDO (Alonso, Theurer, & Zachman, 1996) and SIDO-UK models (Carling, Sear, Greig, & Whitcombe, 2003; Sear, 2010; Pattison, Sear, Collins, Jones, & Naden, 2014) are physically based and deterministic, representing the 1D channel hydraulics through the St. Venant equations, sediment transport with the Einstein-Brown bedload

transport equation and suspended sediment transport via the Rouse number (see Alonso et al., 1996 for a detailed review). Sediment accumulation within the salmon redd is simulated on a daily time step in relation to the near bed concentration of suspended sediment. Sand, silt, and clay-sized particles are deposited within each cell of the egg zone in a salmon redd (for full details of the process, see Alonso et al., 1996). The flow of water and oxygen through the redd are represented using the Darcy equation and through the process of convection. SOD is related to the amount of silt and clay that has accumulated within a salmon redd according to the model developed by Theurer and Theurer (1986):

$$\Delta SOD = SOD\Delta M_f \quad (5)$$

where ΔSOD is the sediment oxygen demand transported through, or accumulated in, the redd (mg/L), SOD is the ultimate SOD (defined by the SOD value measured over a 20-day period) in $\text{mgO}_2\text{g}^{-1}$ dry wt. sediment, and M_f is the mass of fines (silt and clay) added to the redd (g/L).

SOC follows a classic decay pattern over time, expressed by the following relationship:

$$SOC = SOD (1 - e^{-kt}) \quad (6)$$

where k is the deoxygenation constant (day^{-1}) and t is the time (day) (Theurer & Theurer, 1986).

The SOD remaining at the end of each day is equal to the amount at the beginning of the day plus the amount added during the day, less the amount consumed during the day, according to the following:

$$SOD_i = SOD_{i-1} + SOC - \Delta SOR \quad (7)$$

where SOD_i is the sediment oxygen demand at the end of the current day, SOD_{i-1} is the sediment oxygen demand at the end of the previous day, ΔSOR is the additional SOD caused by the current day addition of silt and clay fine sediment to the control volume (note that the consumption rate is based upon the amount present at the midpoint of the period), and SOC is the sediment oxygen consumption for the current day. All units are in milligrams per litre (Alonso et al., 1996).

DO concentration affects SOD according to the following:

$$DO(f) = (DO/DO_{ref})^{0.3} \quad (8)$$

where $DO(f)$ is the dissolved oxygen correction factor, DO is the dissolved oxygen of water in a grid cell within the redd domain, and

TABLE 1 Sediment oxygen consumption (SOC) values reported from field sites measured using in situ or laboratory methods

Location	SOC	Substrate	Method	Reference
Klamath River	1.58–1.84 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$	Silts/sands	In situ	Doyle and Rounds (2003)
River Hiz	1.75–3.25 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$	Silts/clays	Laboratory	Edwards and Rolley (1965)
Xindian River	4.39–5.35 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$	Silts/clays	In-situ	Liu and Chen (2011)
Suwannee River	0.1–2.3 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$	Sands	In-situ	Utley, Vellidi, Lowrance, and Smith (2008)
River Tucannon	0.13–0.59 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$	Gravel	Laboratory	Alonso et al. (1996)
River Test	0.94 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$	Gravel	Laboratory	Greig et al. (2005a)
River Blackwater	0.41 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$	Gravel		
River Ithon	0.58 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$	Gravel		
River Aran	1.19 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$	Gravel		

Note. Only two sites report values from spawning gravels.

DO_{ref} is the saturated dissolved oxygen at reference temperature and sea level (mg/L; after Alonso et al., 1996).

Oxygen in the water within the interstices in the redd is consumed by both the oxygen consumption of the infiltrated sediment-associated OM and the incubating salmon eggs. The egg oxygen consumption (EOC) depends upon the number of eggs and their rate of respiration, which varies according to the stage of embryo development (Chevalier et al., 1984). EOC is given by the following equation:

$$EOC = \frac{4\pi r^2 (D_0 - D_{oe})}{\frac{1}{k} + \left(\frac{\delta}{D_c}\right)}, \quad (9)$$

where r is the egg radius (cm), D_0 is the concentration of oxygen of the surrounding water (mg/cc), D_{oe} is the concentration of oxygen within the egg (mg/cm³), k is the mass transfer coefficient (cm/s), δ is the egg membrane thickness (cm), and D_c is the diffusion coefficient of water through the egg membrane (cm²/s). Parameter values for Atlantic salmon and brown trout are used in SIDO-UK, including the number of eggs, average radius, and membrane thickness. The equations controlling hatching time are from Crisp (1981).

The overall rate of oxygen consumption at any model node (n) is given by:

$$f_{jk}^n = (SOD)_{jk}^n - (EOC)_{jk}^n \delta^*(j - J_e)(k - K_e) \quad (10)$$

in which δ^* is the Dirac delta function and (J_e , K_e) indicates any cell in the model domain belonging to the egg zone (Alonso et al., 1996). EOC and SOD depend on water temperature (which controls stage of embryo development and hence EOC) and mass of ingressing fines, respectively. EOC and SOD are computed on the same time basis and are assumed to be uniformly distributed over a day period (Alonso et al., 1996).

Embryo survival is modelled at the end of every day by matching the DO requirements of the individual eggs for a given degree day development stage (Hamor & Garside, 1976) against the DO supply calculated for each model cell containing eggs. When DO supply falls below the oxygen demand, the number of eggs surviving in a cell is assumed to be zero. The oxygen consumption of dead eggs is set to EOC at time of death (Alderdice, Wickett, & Brett, 1958).

Full details of the SIDO model process representation can be found in Alonso et al. (1996), Theurer and Theurer (1986), and Pattison et al., (2014).

2 | METHODS

Because estimates of SOD within spawning gravels are rare, field investigations were undertaken to acquire samples of fine sediments intruded into artificial redds using methods developed by Greig et al. (2005a). Sites were chosen to ensure a representative sample of salmon spawning habitats from England and Wales that are typical of wider salmonid river types (e.g., pool-riffle, cobble-gravel grainsize, hard rock to soft rock, headwaters to main rivers, and freshet—groundwater dominated; Raven, Boon, Dawson, & Ferguson, 1998). We included the original four sites used by Greig et al. (2005b), together with additional field sites in rivers draining different lithology (e.g.,

Rede—sandstone/limestone and Itchen—chalk groundwater dominated rivers), and to provide duplication of river types (e.g., Lugg similar to Ithon/Aran) and (Test similar to Itchen). Summary data on all sites are provided in Table 2 and mapped in Figure 2. In all cases, the sites chosen were known spawning grounds for either Atlantic salmon and/or brown trout.

At each site, two artificial salmon redds were constructed according to the methods outlined in Greig et al. (2005b) and Greig, Sear, and Carling (2007b). A single sedimentation basket was inserted into each redd to a depth of 20 cm, which is typical of egg burial depths of Atlantic salmon in UK rivers (Crisp & Carling, 1989). One month after insertion, the baskets were extracted using a preinstalled outer bag to retain the ingressed fine sediments (Greig et al., 2005a) and the sediment samples stored in a cool box (c.4°C) and transported to the laboratory within 24 hr of sampling.

2.1 | Laboratory procedure

The sediment samples collected for SOD measurements were processed following the procedures detailed in Collins et al. (2017, this volume). Samples were wet sieved using river water, and the <63- μ m fraction retained, as previous experience has shown that the highest SOD corresponds to this grain size fraction (Bateman, 2012). Duplicate 200-mL aliquots of the wet-sieved slurry were subsampled and transferred into 1-L amber Duran flasks. When all of the bed sediment samples were processed, the flasks were placed in a Gallenkamp temperature controlled orbital incubator set to the average water temperature for the sample river. A shaker speed of approximately 100 rpm was used to ensure adequate mixing of the sediment samples during the experiment and to mitigate the formation of oxygen gradients within the liquid. The flasks were sealed with tops in which were inserted a calibrated Q-OX MediceL oxygen sensor (Shawcity Technology Ltd, error < 1% signal) connected to a Delta-T2 data logger. The flask contents were allowed to acclimate to operating conditions (approx. 1 hr) prior to commencing data logging. Oxygen concentration in the bottle headspace was sampled at 1-min intervals and logged every 10 min for the 25-day duration of the experiment. In order to correct for each individual oxygen probe, a blank experiment was run for 25 days using 200 mL of ultrahigh pure water. At the end of the 25-day measurement period, the dry weight equivalent of sediment in each test vessel was determined by filtering the slurry through dried, pre-weighed GFC filters. The filters were subsequently oven dried for 2 hr at 100 °C, cooled in desiccators, and weighed until constant values were achieved.

The output from the Q-OX MediceL probes was converted into a mass of oxygen in the head space. The SOC rate was calculated from the mass of oxygen consumed in the flask over time:

$$SOC = \frac{(m_1 - m_2)}{t}, \quad (11)$$

where SOC is the sediment oxygen consumption rate in mgO₂ day⁻¹, t is time in days, and m_1 and m_2 are the mass of oxygen at Times 1 and 2 in the head space. All values were blank corrected. The final values were corrected using a Q10 (or Van't Hoff) equation to normalize the SOC estimates to 20 °C:

TABLE 2 Mean and standard deviation (italics>) of the physical characteristics and sediment oxygen demand (SOD) from a range of salmonid rivers

River	%Silt	%Clay	Mass organic (g)	% Organic	SOD ₅ (mgO ₂ /g)	SOC ₅ (mgO ₂ /g/day)	SOD ₂₀ (mgO ₂ /g)	SOC ₂₀ (mgO ₂ /g/day)	SOD ₂₀ 20t mgO ₂ /g
Blackwater	77.98	19.06	0.029	15.30	1.33	0.27	4.41	0.22	8.26
	<i>8.14</i>	<i>4.13</i>	<i>0.025</i>	<i>11.89</i>	<i>1.49</i>	<i>0.30</i>	<i>4.14</i>	<i>0.21</i>	<i>7.76</i>
Axe	80.92	19.08	0.035	30.75	20.02	4.00	8.76	0.44	16.43
	<i>6.95</i>	<i>6.95</i>	<i>0.030</i>	<i>30.24</i>	<i>6.94</i>	<i>1.39</i>	<i>8.26</i>	<i>0.41</i>	<i>15.49</i>
Esk	81.94	18.06	0.007	4.95	6.21	1.24	27.44	1.37	51.45
	<i>2.98</i>	<i>2.98</i>	<i>0.004</i>	<i>3.73</i>	<i>4.83</i>	<i>0.97</i>	<i>23.80</i>	<i>1.19</i>	<i>44.63</i>
Lod	ND	ND	ND	ND	1.18	0.24	1.53	0.08	2.86
	ND	ND	ND	ND	1.48	0.30	ND	ND	ND
Lugg	88.72	11.27	ND	7.26	1.16	0.23	4.10	0.20	7.69
	<i>1.71</i>	<i>1.71</i>	ND	<i>0.00</i>	<i>0.95</i>	<i>0.19</i>	<i>3.59</i>	<i>0.18</i>	<i>6.73</i>
Ithon ^a	92.31	7.69	0.251	11.00	2.43	0.49	6.23	0.31	11.68
	<i>1.44</i>	<i>1.44</i>	<i>0.033</i>	<i>0.00</i>	<i>1.44</i>	<i>0.29</i>	<i>1.99</i>	<i>0.10</i>	<i>3.74</i>
Aran ^a	91.82	8.18	0.294	9.00	4.10	0.82	12.65	0.63	23.73
	<i>2.12</i>	<i>2.12</i>	<i>0.206</i>	<i>0.76</i>	<i>2.20</i>	<i>0.44</i>	<i>10.90</i>	<i>0.55</i>	<i>20.44</i>
Rede	84.50	15.50	0.003	1.80	35.13	7.03	20.80	1.04	39.00
	<i>3.81</i>	<i>3.81</i>	<i>0.002</i>	<i>1.39</i>	<i>27.24</i>	<i>5.45</i>	<i>8.47</i>	<i>0.42</i>	<i>15.88</i>
Towy	84.51	15.49	0.004	3.42	5.31	1.06	13.14	0.66	24.63
	<i>3.62</i>	<i>3.62</i>	<i>0.002</i>	<i>2.43</i>	<i>2.66</i>	<i>0.53</i>	<i>5.21</i>	<i>0.26</i>	<i>9.77</i>
Itchen	ND	ND	0.082	12.58	24.00	7.52	29.83	1.74	55.93
	ND	ND	<i>0.008</i>	<i>2.22</i>	<i>8.46</i>	<i>8.30</i>	<i>10.05</i>	<i>0.89</i>	<i>18.84</i>
Frome	84.40	15.60	0.093	35.40	4.57	0.91	24.81	1.24	46.51
	<i>4.85</i>	<i>4.85</i>	<i>0.056</i>	<i>19.46</i>	<i>2.58</i>	<i>0.52</i>	<i>14.31</i>	<i>0.72</i>	<i>26.84</i>
Test ^a	96.69	3.31	0.419	20.00	3.23	0.65	10.06	0.50	18.86
	<i>0.28</i>	<i>0.28</i>	<i>0.000</i>	<i>0.00</i>	<i>0.76</i>	<i>0.15</i>	<i>1.90</i>	<i>0.10</i>	<i>3.57</i>

Note. ND = No Data; Underlined names are groundwater-dominated chalk streams. All others are run-off-dominated gravel-bed rivers.

^aData from Greig (2004).

$$\text{SOC}^{20} = 1.065^{(20-T)} \cdot \text{SOC}^T \quad (12)$$

where SOC²⁰ is the rate at 20 °C and *T* is the water temperature during measurement in degrees Celsius (Doyle & Lynch, 2005; Thomann & Mueller, 1987). This correction applies to temperatures of 10 °C or more, which was the incubation temperature used in the experiments. The resulting rates were used to calculate the total mass of oxygen consumed over 0–5 days (SOC₅) and 0–20 days (SOC₂₀), respectively. These values were divided by the dry mass of sediment used in each flask to give SOD values in mgO₂g⁻¹ dry sediment. Five days is a standard time period used to observe the oxygen demand of organic effluents and sewage wastes on water. A 25-day time period is considered by convention to be an adequate time for the complete biochemical oxidation of organic material within water samples, sometimes known as the total BOD (Delzer & McKenzie, 2003). It was considered that the 5- and 20-day periods used in the measurement of SOD are significant to incubating fish embryos since these rates provide a more accurate account of oxygen consumption by channel bed sediment over the embryo incubation period. It is critical to understand the longer term SOC of river channel bed sediments given the propensity for sediment retention in UK lowland rivers (e.g. Naden et al., 2016) and the need to take into account the oxygen demand imparted by deposited sediment-associated OM (Sear et al., 2008).

2.2 | SIDO-UK modelling

A previously calibrated SIDO-UK model for the Ithon (Pattison et al., 2014) was used to assess the SOD effect upon Atlantic salmon eggs. The effect of SOD is reliant upon the mass of accumulated fines, which is the variable used to calibrate the model. The mean error on the final accumulated mass was 2.5%, and the simulated percentage was within the range of the two field observations given by the retrievable baskets.

First, a sensitivity analysis of SIDO-UK to the two parameters that control the rate of oxygen consumption by the fine sediment, SOC and *k*, was carried out. SOC is the oxygen consumption rate at Day 20 at 20 °C, whereas *k* is the deoxygenation decay constant. *k* is calculated via the following equation:

$$k = \frac{\sum t_i \ln \left(1 - \frac{\text{SOC}_i}{\text{SOD}} \right)}{\sum (t_i^2)}, \quad (13)$$

where SOC_{*i*} is the sediment oxygen consumption rate at time *t* at node *i* in the model and SOD is the sediment oxygen demand at 20 °C.

k values were calculated from the measured SOC rate and overall SOD data for the 12 catchments, using SOC rates at time 0–5 and 5–15 days, and SOD over 20 days. SOC is calculated by Equation 8. Figure 3 shows the relationship between SOD, *k* and SOC. The SOC

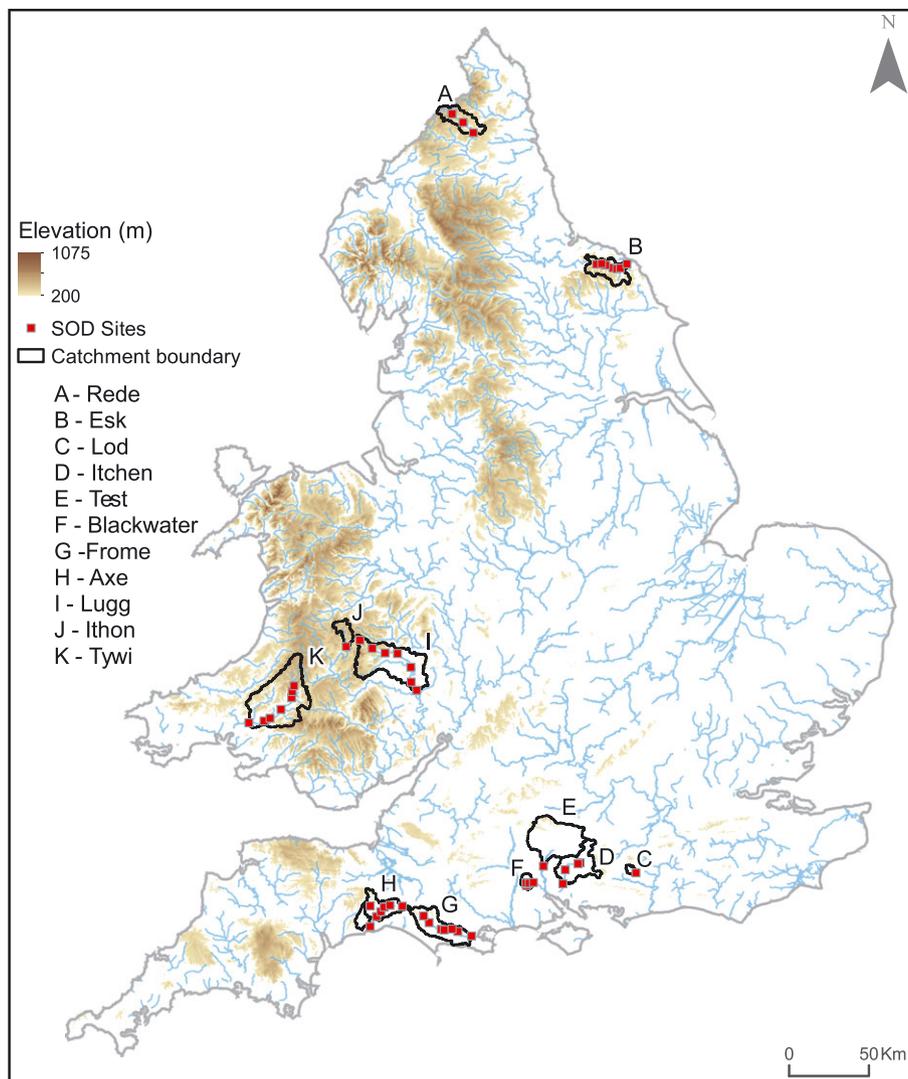


FIGURE 2 Location of study sites and catchments. Sites cover a range of salmon river types, from lowland, chalk groundwater dominated gravel rivers to headwater gravel-cobble bed streams in upland catchments draining impermeable igneous geology [Colour figure can be viewed at wileyonlinelibrary.com]

rates decline over time, with the rate (gradient) dependent upon the k (deoxygenation decay constant) parameter. The overall magnitude of SOC rate is controlled by the overall SOD parameter. The literature (Alonso et al., 1996; Bateman, 2012; Greig, 2004; Greig et al., 2005a) was used to define the range of the parameters, with SOD ranging from 1 to 90 $\text{mgO}_2\text{g}^{-1}$ (1, 5, 10, 15, 20, 30, 40, 50, 60, 70, 80, 90 $\text{mgO}_2\text{g}^{-1}$), and k from 0.0001 to 0.2 (0.0001, 0.0005, 0.001, 0.005, 0.01, 0.05, 0.1, 0.15, 0.2). Overall, 108 simulations were run within this parameter space using the Ithon as a case study. The SIDO-UK model has not been specifically validated in terms of the effect of fine sediment on DO for the Ithon, but a previous study (Sear et al., 2014) found that for the Rede, the SIDO-UK model predicted DO concentrations within the range of field measurements. Experimental data from all the study rivers were then used to calculate corresponding values for SOD and k (Equation 13) and then plotted within the parameter space for the Ithon to identify which rivers were more/less sensitive to the effect of SOD. The average set of values for each catchment were calculated to show the range of values in the UK. The influence of mass of fines upon the sensitivity to SOD and k was assessed by

looking at different times (Days 62, 76, and 100) through the simulation. Key outputs such as SOC rate, DO, and % eggs whose oxygen demands are met by the oxygen available, were assessed.

Scenarios representing the average values of SOD and k decay constants (Table 3) from various UK catchments were then compared using the calibrated Ithon SIDO-UK model, as calibrated models were unavailable for all catchments. This allowed the effect of SOD alone to be identified, as the time series of sediment inputs, blocking effect of sediment on intra-gravel flow velocity, supply of DO and egg survival, were kept constant between simulations. Thus, any variations predicted were due to changes in SOD.

2.3 | Statistical analysis

In order to understand catchment influences on SOD and SOC, relationships between catchment, site and sediment characteristics, and SOD and SOC were explored using ordination. Principal component analysis was used to describe variation in catchment land use (% cover from Land Cover Map) and environmental characteristics among the

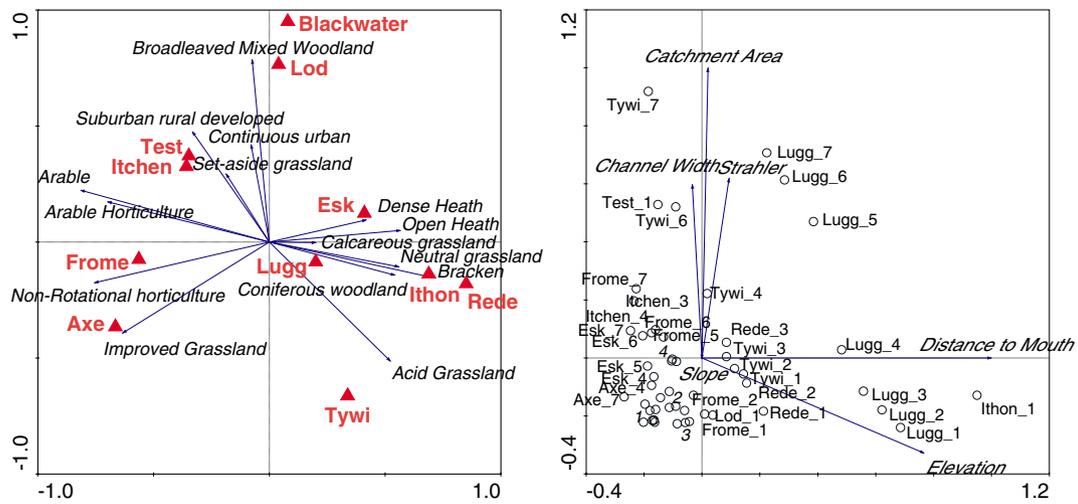


FIGURE 3 Variation in (a) land use, as percentage cover, among the study catchments (centroids shown as ▲) and (b) characteristics of field sites used (sites shown as ○) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Average sediment oxygen demand (SOD) and *k* values for different UK gravel-bed rivers (with standard deviations where sample size permitted)

River	No. of samples	SOD ₂₀	<i>k</i>
Blackwater	1	16.3	0.046
Axe	1	39.5	0.046
Esk	1	14.0	0.070
Lod	1	2.9	0.186
Lugg	2	5.9 ± 3.6	0.026 ± 0.004
Ithon	4	11.7 ± 3.7	0.041 ± 0.012
Aran	8	23.7 ± 20.4	0.042 ± 0.011
Rede	1	46.3	0.131
Towy	6	23.3 ± 10.9	0.040 ± 0.013
Itchen	7	60.4 ± 15.0	0.062 ± 0.018
Frome	4	57.6 ± 25.1	0.038 ± 0.006
Test	2	18.9 ± 3.6	0.037 ± 0.001

field sites. To understand better the relationship between measured SOD and SOC and wider catchment characteristics, redundancy analysis was first used to establish relationships between catchment land use and sediment characteristics, and the significance of explanatory variables tested with forward selection using Monte Carlo permutation tests ($n = 999$ permutations, $p < .05$ with Bonferroni correction for number of variables included). As only the first two axes were significant, to enable visualization of relationships between catchment land use, sediment composition and SOD, contours of variation in SOD₅ and SOD₂₀ were then superimposed on the relationship passively (i.e. without influencing the underlying ordination) based on measured SOD₅ and SOD₂₀ of the sediment samples and smoothed using loess.

3 | RESULTS

The principal aim of the work was to quantify the effect of SOD on the oxygen supply to salmon embryos.

The land use in the catchment and the physical characteristics of the interstitial sediments varied markedly among the study catchments (Figure 4). It should be noted that land use was % cover of the catchments leading to a separation of intensive and extensive land uses. Similarly, the SOD of silt/clay material in salmon redds sampled within the same spawning season (Dec 2010 - March 2011), was highly variable between different rivers (Figure 5).

The sensitivity of redd abiotic conditions and egg survival to SOD are shown in Figure 6. The effect of SOD is complex and is dependent on the ultimate SOD rate, the rate of decay over time and the mass of sediment added. The mass added is further complicated by residual SOD effects from sediment added in previous time steps. Figure 6a shows the SOC rate at different time steps, as mass added at that time step decreases from left to right, but total infilled sediment increases. As the mass added increases, the SOC rate increases. The black dots show the average SOD over the simulated time period and *k* values for the UK catchments, with the Itchen having the highest SOD value, and the Lod having the highest *k* value. The Rede was the most sensitive to SOD, as it had a higher than average SOD value and the second

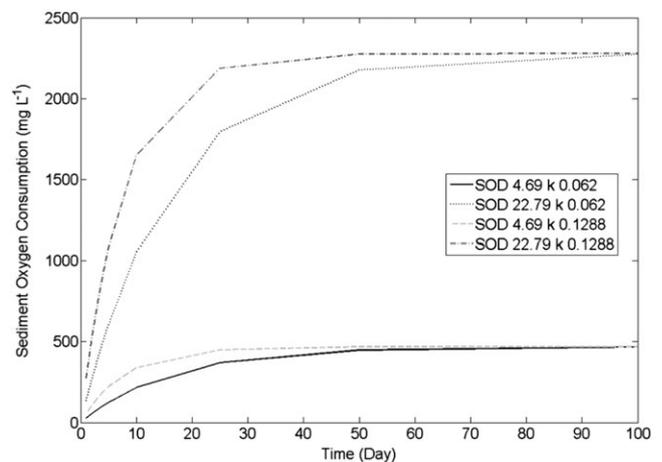


FIGURE 4 Sensitivity of sediment oxygen consumption to sediment oxygen demand (SOD) and *k* coefficients

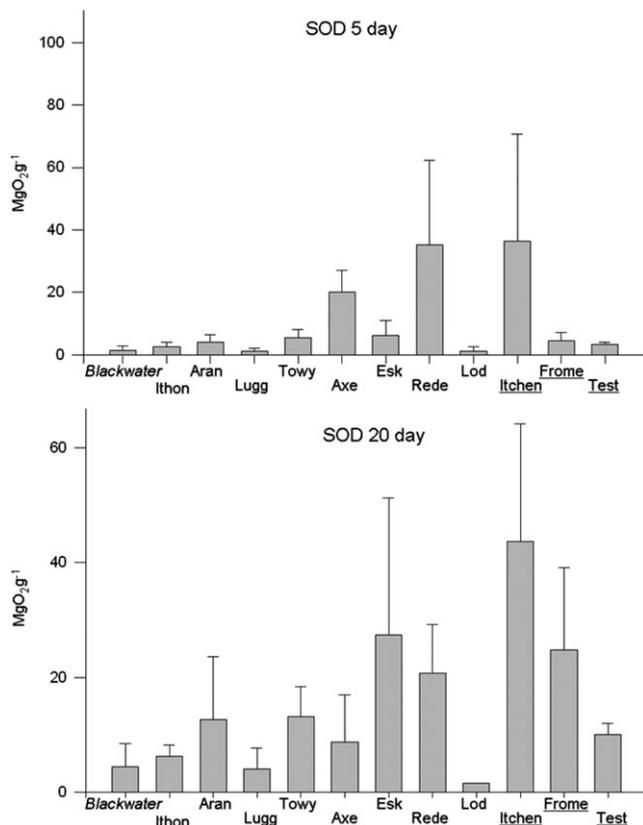


FIGURE 5 Variation in SOD₂₀ and SOD₅ across the study catchments. Itchen, Frome, and Test are all groundwater-dominated rivers with high instream biomass. Blackwater is a seminatural woodland stream. The Lod represents only one sample

lowest k value. This means that ultimate SOD started high and decayed slowly. The effect of this on DO was more complex, as this was dependent upon previous time steps. Therefore, the most influential factor here was the whole time series, rather than the discrete time steps. As the total mass of sediment in the redd increased, the DO decreased. However, this effect can be attributed singly to the SOD as everything else was kept constant. The UK catchments at Day 62 (just after the first sediment input) were insensitive (<5% from baseline) to SOD in terms of the DO concentration. At Day 76, four catchments (Rede, Itchen, Frome, and Axe) had a value >10% from the baseline value, with the Rede having the highest value of ~15% from baseline. By 100 days, all but the Lugg catchment had a value >10%, and the Rede had a value of ~25%. Finally, in terms of the sensitivity of egg survival to SOD, Figure 6c shows that there was up to a 4.5% difference in the percentage of eggs being satisfied with their oxygen demand over the range of SOD values found in the river sediments sampled.

Figure 7 shows the differences in egg incubation conditions between different UK rivers, which had different observed SOD rates. Figure 7a shows the SOC rate for the various rivers over the incubation period. SOC rate is a function of both the initial ultimate SOD and the decay rate k . Of the 12 UK catchments included in this study, influence of SOC was highest in the Rede, where the maximum rate was 1.5 mg/L at Day 66. The Itchen also experienced a high effect of SOC, whereas the influence of SOC was very small in the Lugg. Figure 7b and 7c shows how SOC controls the DO concentration.

Small amounts of fine sediment seemed to make no difference to the DO and did not have a significant impact until the SOC rate was greater than ~0.2 mg/L. In addition to the consumption of oxygen by the sediment and eggs, DO concentration is influenced by the blocking effect of sediment and hence, a reduction in the supply of oxygen rich water through sufficient intragravel flow velocities. This effect was constant in all simulations, but the effect of SOC alone was isolated in Figure 7c by subtracting a baseline scenario with no SOD influence ($SOD = 0, k = 0$). The greatest effect of SOC was seen at Day 79, where for the Rede, the DO concentration was reduced by 2.03 mg/L due to the SOC effect alone. Figure 7d and 7e shows how this impacted upon the percentage of eggs satisfied in terms of their oxygen demand. Overall, SOC alone made little difference to the percentage of eggs surviving to hatch, with the largest effect seen for the Rede, where the number of eggs hatching was reduced by 1.53%. However, SOC had more of an effect on the timing of egg mortality or possible sublethal effects. Eggs in the Rede hatched 2 days later due to the SOC effect alone, whereas in all other rivers, except the Lod and the Lugg, it was a day later. Furthermore, the timing of when eggs were not being satisfied in terms of oxygen could be different by up to 3 days, and the magnitude of the change caused by SOC alone could be ~21%.

Redundancy analysis indicated that catchments with a high cover of arable land (as arable horticulture, arable cereals or nonrotational horticulture) tended to have more organic river sediments, both in terms of % organic and mass of OM (Figure 8). Arable horticulture was also associated with high % silt in the sediment, as was calcareous grassland. It should be noted that the % cover data resulted in a tendency to exclude extensive land uses from the model, as they were negatively associated with the intensive land use types included (see Figure 3) and added no further explanatory power. SOD₅ tended to be higher in sediments with higher organic content, and those sediments with higher % clay (and to a lesser extent % silt): these comprised sites with more arable land in their catchments (Figure 8a). However, SOD₂₀ demonstrated a slightly different pattern, being highest in sediments with a high % silt and mass of OM, from catchments with more calcareous grassland and arable horticulture: in contrast to SOD₅, sediments with a high % clay had relatively low SOD₂₀ (Figure 8b).

4 | DISCUSSION

The SOD values reported from the different rivers show strong site and catchment variability. Reasons for this are likely to be a function of the type of OM (Lundkvist et al., 2007); the quantity of OM (Thomann & Mueller, 1987); and particle size (House, 2003). These might be expected to vary with the catchment type. Although the data show some differences between broad catchment types (seminatural woodland < upland < mainstem < chalk), within these, there are considerable site-specific differences in SOD. These are possibly the result of differences in OM content (Tank, Rosi-Marshall, Griffiths, Entekin, & Stephen, 2010), proportion of silt to clay or the type of OM and biological communities involved in the breakdown of OM within the redds (Yoshimura et al., 2008). **Our analysis indicates that higher SOD₅ appears to be associated with a higher organic content in the sediment**

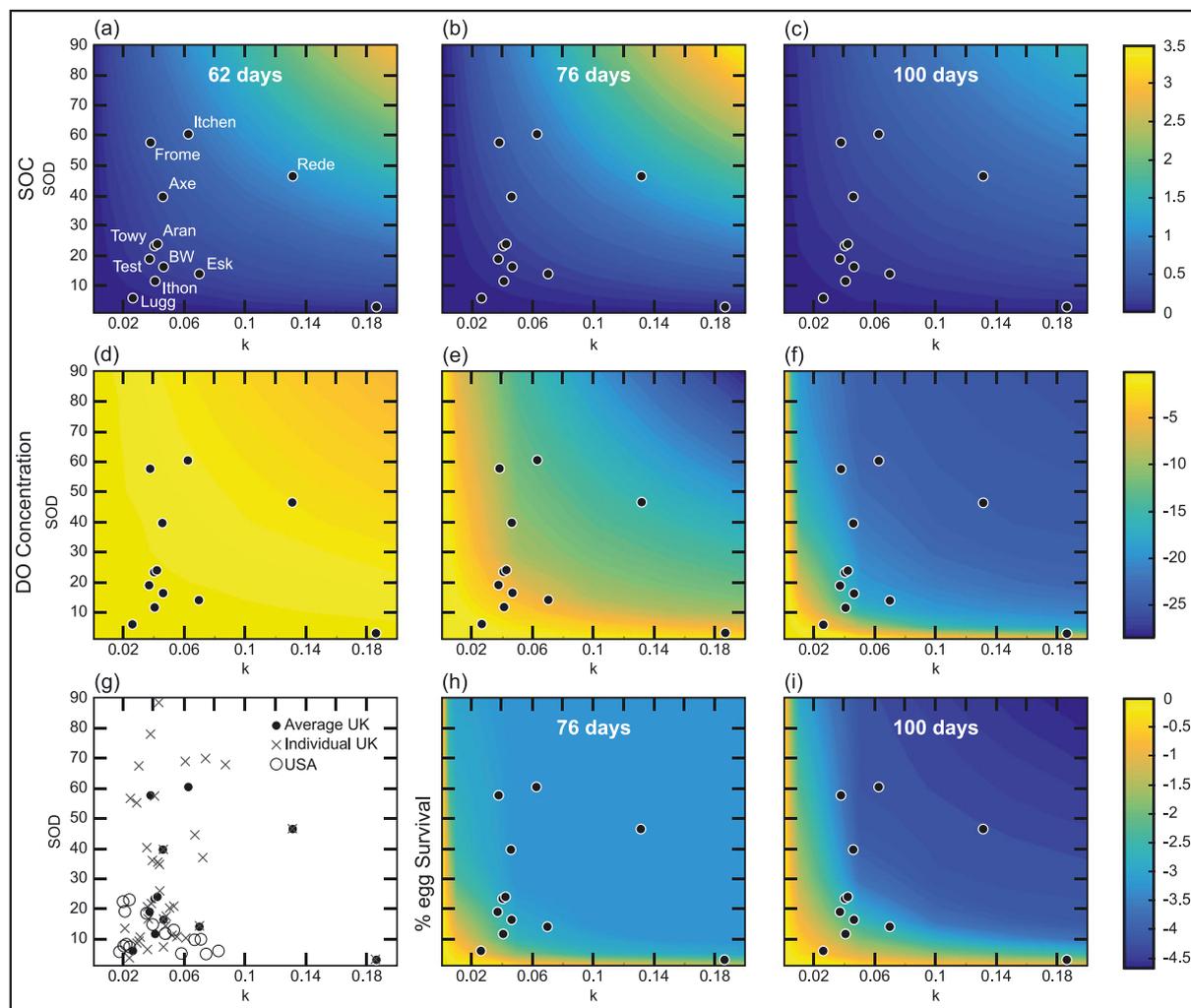


FIGURE 6 Sensitivity analysis of (a) sediment oxygen consumption (SOC); (b) dissolved oxygen (DO); and (c) % egg survival to different SOD and de-oxygenation rates, at different times within the SIDO-UK model River Ithon simulation [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

and more intensive land use, particularly a higher proportion of arable land (of all types), in the catchment, whereas SOD_{20} is more associated with arable horticulture and a high proportion of silt in the sediment. For groundwater dominated catchments (Frome, Itchen, and Test), higher SOD_5 may be a function of large instream biomass, emphasizing the need for OM source apportionment in future studies of SOD.

Our results support the assumption that SOD increases with increasing OM content (Thomann & Mueller, 1987), although some studies have found no relation between OM content and SOD (Caldwell & Doyle, 1995; Seiki, Izawa, Date, & Sunahara, 1994). In our analysis, there is no relationship between mass or proportion of OM and SOD_{20} (Figure 8). A similar result was found for SOD_5 . Similarly, the mass and proportion of clay within the samples showed no relationship with 20- or 5-day SOD (Figure 8). It was beyond the scope of this study to explore the specific OM composition, but the results indicate that the variations in SOD between catchments and between samples from the same catchment are most likely the result of differences in the OM composition (Tank et al., 2010; Yoshimura et al., 2008). The source and size of OM is known to influence the rate of microbial decomposition and the respiration of these biological communities (Tank et al., 2010; Yoshimura et al., 2008). FPOM (<100 μm), which comprised much of the organic material in our sediment samples, is

mostly made up of amorphous OM (Wotton, 2007). It originates from direct inputs from the terrestrial environment (Ward, 1986), fragmentation, and maceration of CPOM (Ward, 1984), and aggregation of colloidal (Wotton, 1990) or dissolved OM (Petersen, 1986). Although Yoshimura et al. (2008) found that the oxygen demand of FPOM was less than CPOM due to the increased concentration of refractive carbon (lignin), Bateman (2012) found higher rates of SOD in <63- μm particles. Yoshimura et al.'s (2008) experiments were based on organic sources derived from wood and leaf fragments. In agricultural catchments, additional sources are likely to come from soil erosion, animal and human waste, and autochthonous sources such as invertebrate faecal pellets, fish carcasses, and aquatic plant fragments (Collins et al., 2014; Richardson, Bilby, & Bondar, 2005). Research is required to determine the active components of oxygen demand within fine sediments of different river systems and to establish the sources of these materials. A limitation of the SIDO-UK and SIDO modelling platform in relation to sources of SOD include the lack of representation of oxygen consumption from biofilms covering larger framework clasts (although it will be included in empirical values of SOD for interstitial fines), other organisms (e.g., invertebrates and diatoms), and the SOD arising from larger particles that comprise a higher proportion of the infiltrated fines than that currently represented. Additional research is required to

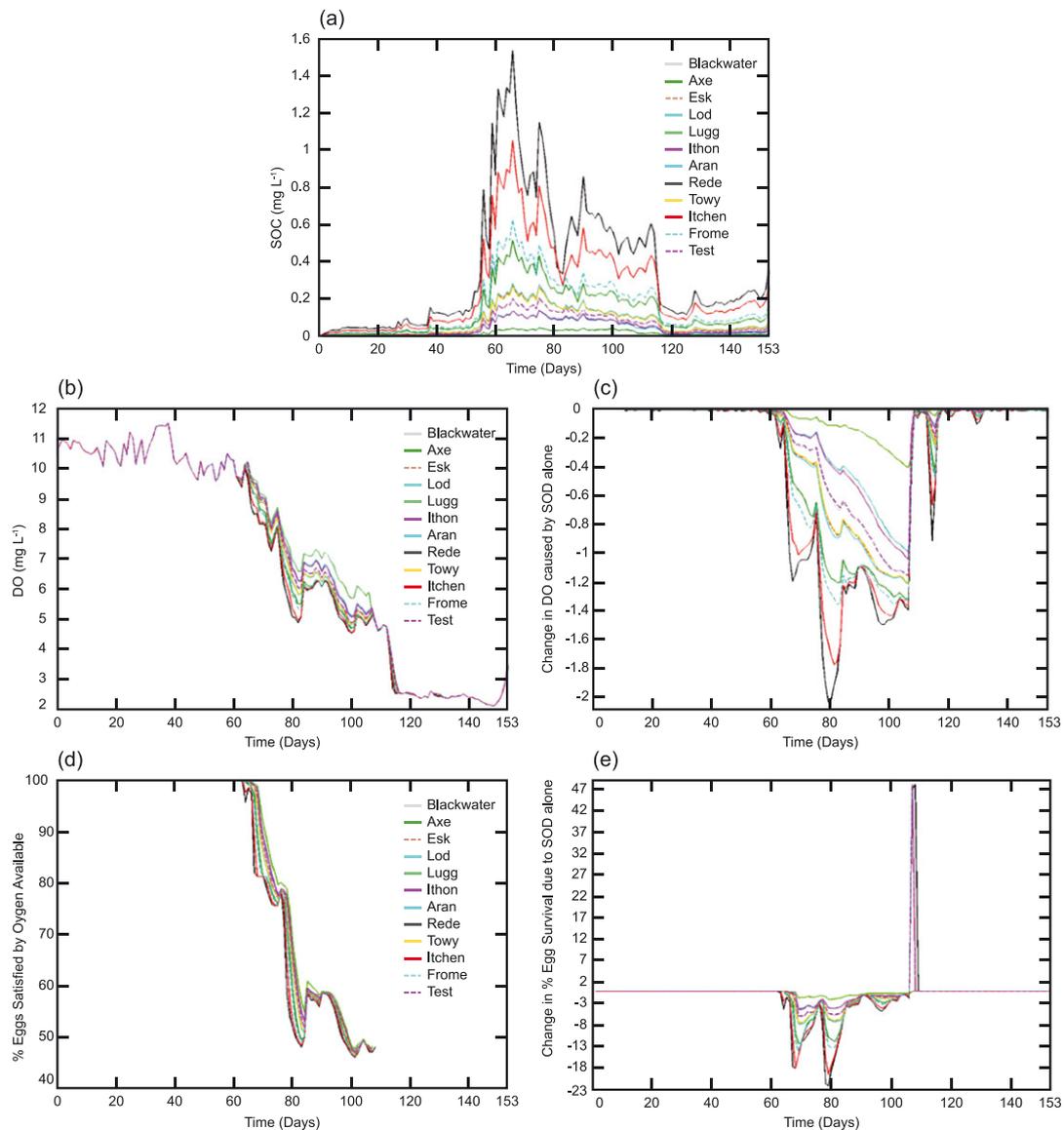


FIGURE 7 Time series of (a) sediment oxygen consumption (SOC); (b) absolute dissolved oxygen (DO); (c) DO reduction caused by SOC alone; (d) egg survival; and (e) change in egg survival caused by SOC alone; for a range of different river types sampled in this study. SOD = sediment oxygen demand [Colour figure can be viewed at wileyonlinelibrary.com]

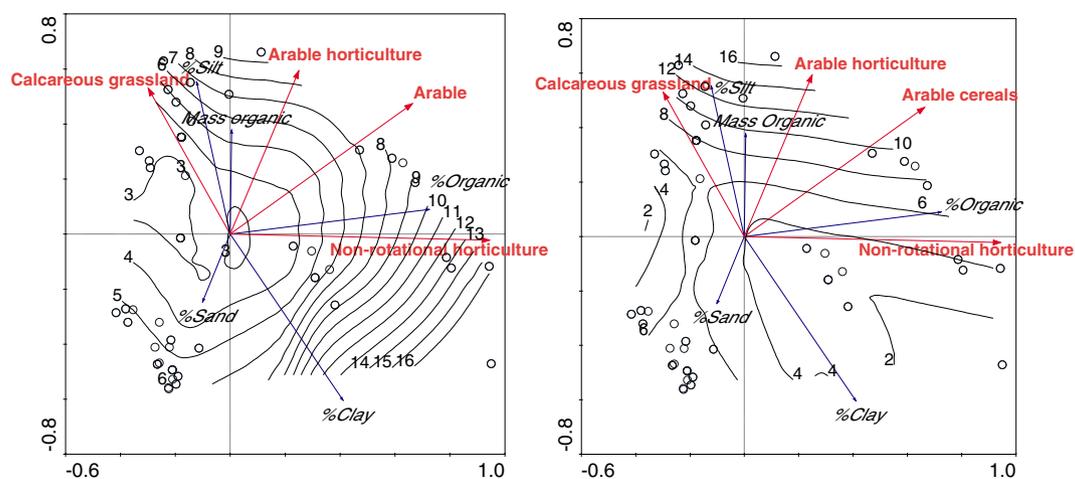


FIGURE 8 Results of redundancy analysis (RDA) showing that catchment land use cover is significantly associated with variation in sediment characteristics, with contours of (a) SOD₅ and (b) SOD₂₀ of sediment samples. Sample sites shown as (O) [Colour figure can be viewed at wileyonlinelibrary.com]

identify the magnitude of these different sources in relation to the spawning timing of salmonids.

SIDO-UK and SIDO are 2-dimensional process-based models that seek to couple explicitly, the surface hydrodynamics and sediment transport processes to subsurface hyporheic flows, sedimentation, and DO processes using a mass balance approach to establish the interaction between incubating salmonid embryos and the supply rate of DO, thus predicting when embryo mortality occurs. SIDO and SIDO-UK are still the only models that incorporate all the key processes within a salmonid spawning redd environment, though Sear et al. (2014) highlight the limitations in applying these models to spawning substrates strongly influenced by upwelling groundwater. Although more complex 2D and 3D hyporheic flow models have been developed (e.g., Cardenas, Ford, Kaufman, Kessler, & Cook, 2016 and Tonina & Buffington, 2009) that represent turbulent exchange processes at the streambed, hyporheic flows through complex 3D topography and include upwelling groundwater, to date, they are not capable of fully representing fine sedimentation processes, SOD, and biological processes of salmonid incubation. Similarly, Wu (2000), for example, present more complex models of fine sediment accumulation, but in this case, fines are typically defined by sand sizes rather than silts and clays that are critical for salmonid survival, and they do not explicitly model SOD or embryo survival. Notwithstanding these limitations, there is clearly scope for improving process representation within the hyporheic zone, including better representation of sources and sinks of DO, and improved representation of flow and DO fluxes building on more recent hyporheic modelling frameworks.

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