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Impact of *Didymosphenia geminata* on hyporheic conditions in trout redds: reason for concern?

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Abstract. *Didymosphenia geminata* (Lyngbye) Schmidt (commonly called didymo) is an invasive diatom and of concern to fisheries managers in North America and more recently New Zealand. Didymo grows in thick mats in several river systems on the South Island of New Zealand, often smothering entire river beds. Salmonid eggs, deposited in gravel nests (redds), depend on constant water exchange across the riverbed to provide oxygen-rich water for development. Thick didymo mats might restrict the flow of oxygen-rich water into spawning gravels, resulting in increased egg mortality and reduced trout recruitment. The present study measured hyporheic hydraulic conditions in trout redds with varying didymo cover in the Clutha River catchment, South Island, New Zealand. Didymo cover had no significant effects on several hydraulic variables (flow into the substrate, hydraulic conductivity and hyporheic oxygen concentration). However, there was a significant difference in the potential surface water–groundwater exchange between sites, suggesting some effect of didymo on hydraulic conditions. Considering the limited number of replicates, the impact of didymo on trout redds in the Clutha River cannot be excluded. The present study highlights the need for further research on the possible effects of didymo on important surface water–groundwater exchange processes.

Additional keywords: didymo, spawning.

Introduction

Didymosphenia geminata (Lyngbye) Schmidt (hereafter didymo) is an invasive diatom alga first recorded from New Zealand in the Waiau River, South Island, in 2004 (Kilroy 2004). Initially restricted to the Mararoa and Waiau Rivers, Southland, the alga has spread rapidly throughout the South Island and is currently present in numerous river systems (Duncan 2007). Blooms of didymo can form thick, smothering mats, covering entire river beds. Concerns about the effects of didymo on salmonid populations have been voiced in British Columbia, Canada, the western USA (Kilroy 2004) and New Zealand (Hayes *et al*. 2006). In addition, owing to often extensive growth, didymo could potentially directly or indirectly affect hydraulic conditions in the streambed. For example, a thick cover of didymo could impede surface–groundwater exchange processes by forming a physical barrier at the streambed or increase the deposition of fine sediment, potentially reducing hydraulic conductivity (K_v).

Hyporheic conditions can be highly heterogeneous over a small scale (<10 m) (Malcolm *et al*. 2003*a*). Salmonids are known for their selectivity for suitable redd sites in terms of both substrate quality and hyporheic exchange (Geist and Dauble 1998; Rubin 1998; Zimmer and Power 2006). Currently, there is no exhaustive review of spawning site selection for salmonids available. However, from the literature it appears that the selection of suitable hydraulic conditions for redd sites differs between species and geographic locations (Power *et al*. 1999; Geist *et al*. 2002). In general, salmonid populations in colder areas (northern North America) select areas of local groundwater discharge that provide warmer water temperatures and prevent freezing (e.g. Lorenz and Eiler 1989), whereas populations further south often select areas of inflow into the hyporheic zone for the higher temperature and oxygen concentration of surface water (e.g. Baxter and Hauer 2000). In temperate New Zealand, spawning locations typically feature gravelly substrates that allow local inflow of river water into the substrate at the site of the redd construction (T. O. Bickel and G. P. Closs, pers. obs.); redds are typically found at the tail of pools or on river bends. This surface water–riverbed exchange guarantees sufficient oxygenation, which is essential for the development of trout eggs and larvae (Lapointe *et al*. 2004).

Initially, when trout create redds, the disturbance of the gravels clears didymo from the substrate (A. Horrel, pers. comm.), resulting in clear gravel patches in the streambed. However, depending on the growing conditions, didymo might overgrow the cleared redds within weeks. This thick cover of didymo over redds could interfere with the water inflow into the redds and disrupt the vital oxygen supply and lower the water temperature, which could consequently impact on egg development or the hatching success of fry, similar to the effects of sedimentation (Rubin 1998; Lapointe *et al*. 2004). Furthermore, the thick algal cover might decrease the oxygen concentration as a result of the increased oxygen demand of decaying organic matter (dead

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didymo) on the streambed. As didymo can virtually cover the entire riverbed, this could potentially have profound impacts on trout recruitment. However, as trout display a high selectivity in their choice of suitable redd sites, they might still select redd locations with sufficient water exchange in the gravel to avoid any potential impact of didymo on egg development.

The upper Clutha River system, South Island, New Zealand, is an important recreational trout fishery. Didymo coverage varies from being visually absent to smothering the entire riverbed (100% areal cover). The present study was initiated to investigate the possible effects of didymo on hydraulic conditions in redds and to encourage more detailed research into the ecological effects of didymo. Specifically, we hypothesised that didymo affects the potential hyporheic exchange at the microscale of individual salmonid redds, that is, it reduces the vertical hydraulic gradient (VHG) and hydraulic conductivity (K_V) of the substrate, and that didymo reduces available oxygen concentrations and water temperature in the redds as a result of changes in the hydraulic properties.

Materials and methods

We selected three sites in the Clutha River system (Fig. 1) with varying degrees of didymo cover. Didymo was virtually absent (no visible infestation) in the upper reaches (Deans Bank; 44°40′24″S, 169°11′10″E), whereas there was an intermediate cover (patchy growth of didymo, ~50% areal cover) in the middle reaches above Lake Dunstan (Maori Point; 44°49′56″S, 169°21′14″E). At Maori Point, didymo was restricted to the shallow margins of the river channel. Redds were located in an area affected by didymo, but not covered by didymo at the time of measurement, that is, didymo was cleared by spawning trout during redd construction. The smaller Clutha River tributary Fraser River (45°13′20″S, 169°19′22″E) was heavily infested with didymo, covering 100% of the riverbed (including the redds at the time of measurement). To prevent the spread of didymo between sites and to other systems, the Deans Bank site was sampled first; all gear was thoroughly cleaned with a detergent solution (household detergent, 5%) and air-dried after fieldwork.

Brown trout (*Salmo trutta* L., 1758) and rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) are present in both rivers; we did not establish which species excavated the redds. Hyporheic hydraulic conditions were measured in 4–6 redds at each site. The number of redds measured was limited mainly by the high discharge of the Clutha River during the spawning season, making most of the redds inaccessible. To establish if trout select suitable (in terms of hydrology) spawning locations, we measured five random spots in the vicinity of the redds (<2 m). Hence, we measured hyporheic conditions in three different 'treatment' types: control redds (no didymo), redds in didymo, and non-redd (random) sites in didymo. The treatment 'redds in didymo' contained redds from both Maori Point and the Fraser River because redds at both sites were located in an area affected by didymo. Sites were sampled once each in November 2006 (Deans Bank and Maori Point) and December 2006 (Fraser River); at the time of sampling, trout fry (both brown and rainbow trout) would have already emerged from the gravel.

River levels (discharge) were the same for the two Clutha River sites at the times of measurement (~250 $m^3 s^{-1}$). The upper Clutha River (median flow = 258 $m^3 s^{-1}$, minimum flow = 77 $m^3 s^{-1}$ and maximum flow = 1617 $m^3 s^{-1}$) flows through a wide alluvial plain and extensive sidebars are present in most locations. At both sites, the river flows through a main channel with limited gravel bars. The channel has a predominantly gravelly substrate with a low proportion of sands and silts with moderate compaction of the sediment matrix. In the sampled area, the Fraser River (median flow = 0.895 $m^3 s^{-1}$, minimum flow = 0 $m^3 s^{-1}$ and maximum flow = 105 $m^3 s^{-1}$) flows through a wide floodplain valley in a U-shaped channel cut into alluvial gravel, probably predominantly deposited by the Clutha River. The sediments are finer than the sediments at the Clutha sites, with a larger fraction of finer gravel and sands with low compaction of the sediment matrix. Trout redds are usually found at the tail of pools or on inner bends in both systems. The redds sampled in the present study were located at the tail of a pool at all sites (Fig. 1).

We quantified the surface water–riverbed exchange by measuring the VHG (cm cm^{-1}) and K_V (cm s^{-1}) in each of the redds and at random locations using minipiezometers (Lee and Cherry 1978; Baxter *et al.* 2003). Minipiezometers (1200 mm long, 28 mm inside diameter) were placed ~20 cm deep into the riverbed (~depth of the egg pockets in the redds), repeatedly cleared of water and left to settle before the measurements were taken (>1 h). The direction of the potential hyporheic exchange was expressed as the difference in the hydraulic head in the piezometer compared with the river surface level (Δh) divided by the depth from the riverbed surface to the first opening in the piezometer wall (Δl). These parameters were measured to the nearest millimetre using a metre-stick inside the piezometer and in a stilling well for the river level (Baxter and McPhail 1999; Baxter *et al.* 2003). If the water level in the piezometer is below that of the river (negative VHG values), then water is potentially downwelling from the river to the bed (Baxter and Hauer 2000). A modification of the falling-head slug test was used to determine the vertical hydraulic conductivity (K_V) as outlined in Baxter *et al.* (2003), which can be applied in highly permeable substrate and resulting fast water flow as was the case at the present study sites (the water levels in the piezometers would equilibrate usually within 10 s).

We measured the water temperature and oxygen concentration of the interstitial water with a YSI 85 Handheld Instrument (YSI Environmental, Baton Rouge, LA, USA) inside the piezometer and of random river water samples; as a result of instrument malfunction we could not measure the water parameters in the Fraser River. We assumed that the interstitial water was completely re-equilibrated by the time of measurement because of the high permeability of the streambed and strong inflow into the gravel at most sites.

A two-way ANOVA (site × treatment, both factors fixed) was used to test for significant differences in parameters between sites and treatment. Data were tested to meet the assumptions of normality and homoscedasticity for parametric tests by examination of residuals and the Levene's test. Least significant difference (LSD) tests were used for subsequent post-hoc pairwise comparisons. The hydraulic conductivity (K_V) data were square-root transformed to stabilise the variances. All statistics

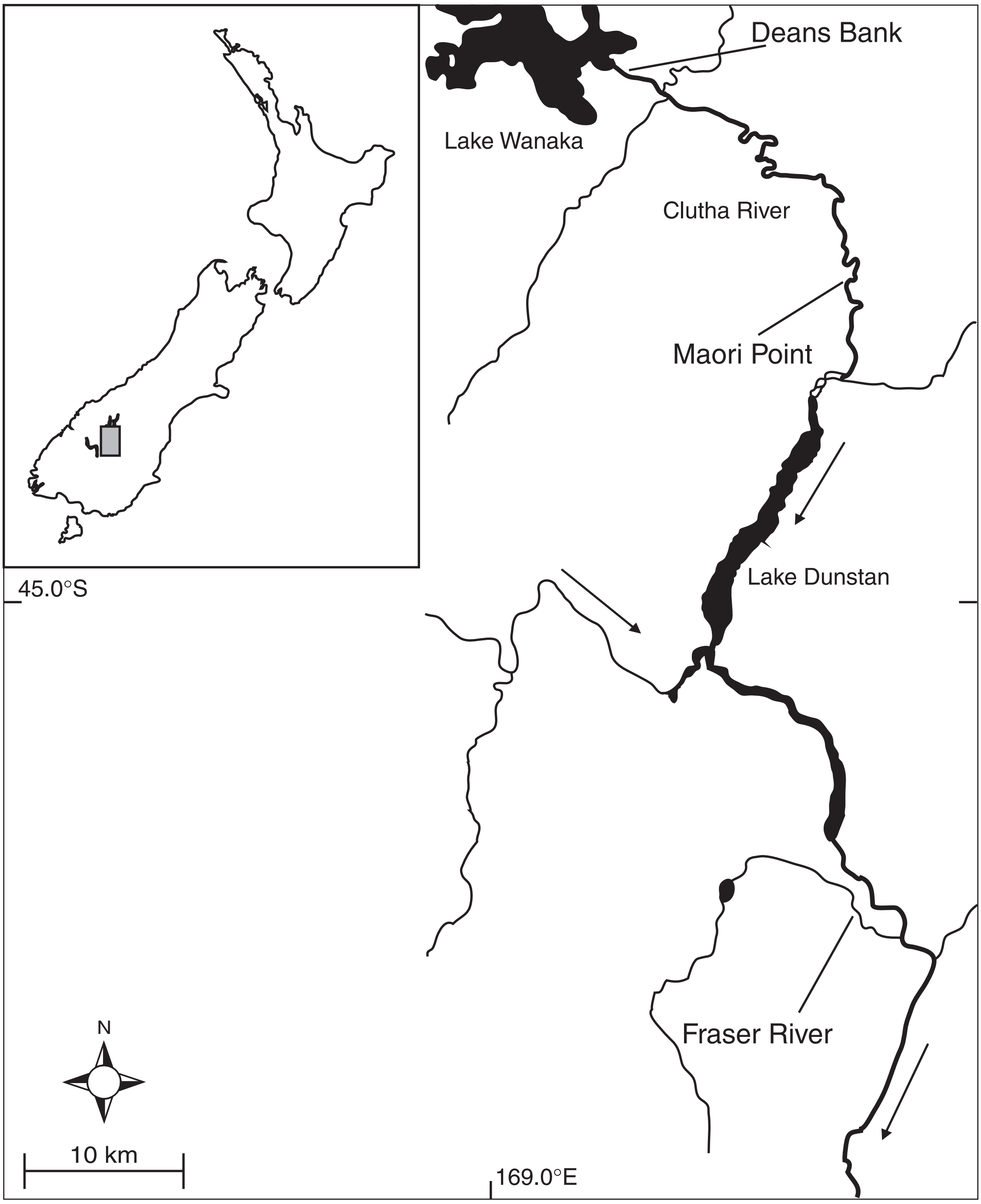

Fig. 1. The location of the study area, South Island, New Zealand, is indicated by the shaded area. Hydraulic parameters in trout redds were measured at three sites differing in the degree of didymo infestation: Deans Bank (didymo absent), Maori Point (intermediate infestation) and Fraser River (high infestation, 100% cover). Arrows indicate the direction of flow.

were analysed with SPSS 15.0 for Windows (SPSS, Chicago, IL, USA).

Results

The VHG measured at the three sites indicated an intermediate potential vertical exchange between the surface and the groundwater. The average direction of exchange was negative at all sites, that is, redds were located in downwelling areas. The VHG varied between control redds without didymo cover ($-0.009 + 0.004\,\mathrm{cm\,cm^{-1}}$ (mean + s.e.)), redds affected by didymo (Maori Point and Fraser River; $-0.003 + 0.008\,\mathrm{cm\,cm^{-1}}$) and random didymo-covered locations ($-0.012 + 0.007\,\mathrm{cm\,cm^{-1}}$) (Fig. 2*a*), but this variation

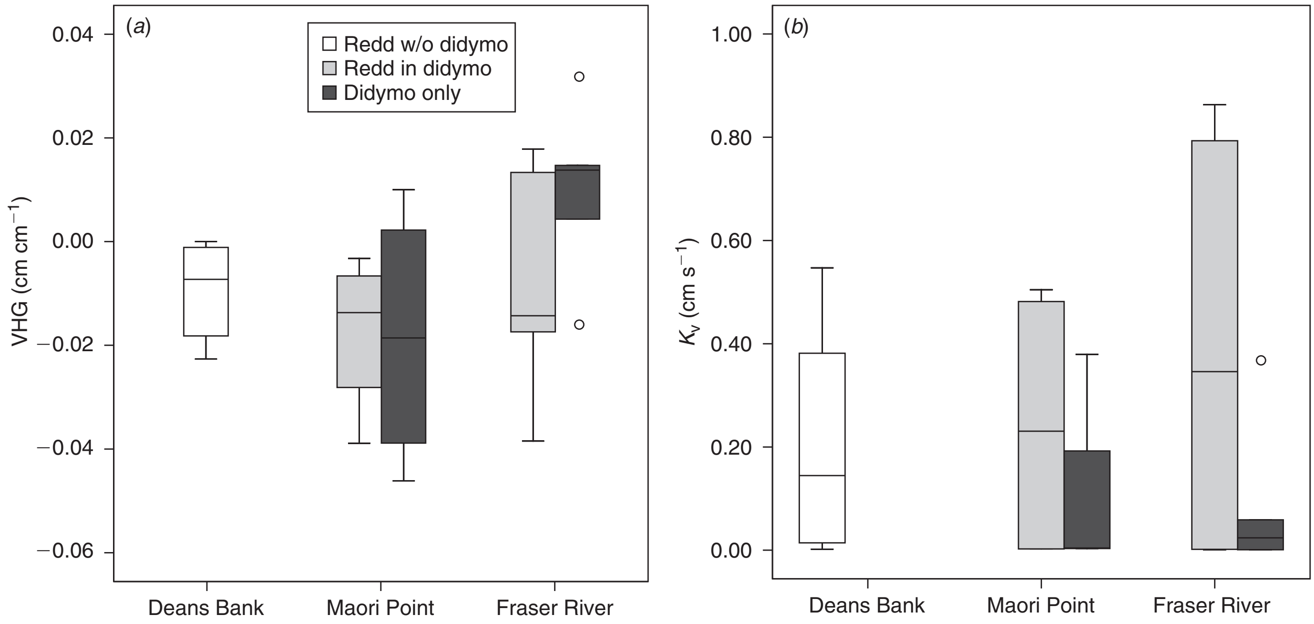

Fig. 2. Boxplot of (*a*) vertical hydraulic gradient (VHG; a measurement of surface water–riverbed exchange) and (*b*) hydraulic conductivity (K_v: permeability of the substrate) for redd and control areas (treatment) at the sites. Boxes represent the upper and lower quartile around the median (bar), and the whiskers show the spread of the data (95%). Shading of the boxes indicates control redds (white), redds with didymo cover (light grey) and random locations with didymo cover (dark grey). Circles indicate outliers.

Table 1. Results of a two-way ANOVA to test for differences in vertical hydraulic gradient (VHG) and hydraulic conductivity (K_v) (square-root transformed) between sites and treatment (both fixed)

	Source	d.f.	*F*	*P*	Observed power$_{\alpha=0.05}$
VHG	Site	1	4.626	0.045	0.533
	Treatment	1	0.897	0.355	0.147
	Site × treatment	1	1.114	0.305	0.171
	Error	19			
K_v	Site	1	0.189	0.669	0.070
	Treatment	1	2.110	0.163	0.281
	Site × treatment	1	0.125	0.728	0.063
	Error	19			

was not significant ($P = 0.355$, two-way ANOVA; Table 1). However, there was a significant difference between sites ($P = 0.045$; Table 1). The VHG was significantly higher in the Fraser River compared with the Clutha River at Maori Point (LSD, $P = 0.045$). There was no significant difference between the VHG in Fraser River and Deans Bank.

The K_v showed that the sediments at all sites provided good permeability for surface water–riverbed exchange processes. Hydraulic conductivity was similar at the three sites, Deans Bank ($0.206 + 0.09\ cm\ s^{-1}$ (mean + s.e.)), Maori Point ($0.169 + 0.082\ cm\ s^{-1}$) and Fraser River ($0.246 + 0.107\ cm\ s^{-1}$) (Fig. 2*b*; Table 1). However, hydraulic conductivity varied considerably with the degree of didymo cover (redd without didymo $0.206 + 0.091\ cm\ s^{-1}$, redd in didymo $0.330 + 0.116\ cm\ s^{-1}$ and didymo only $0.098 + 0.053\ cm\ s^{-1}$); however, this difference was not significant (Table 1).

Hyporheic oxygen concentration was suitable for salmonid embryo survival ($10.6 + 0.5\ mg\ L^{-1}$ (mean + s.e.)) and was similar to river surface water ($11.0 + 0.6\ mg\ L^{-1}$; $F_{2,25} = 0.364$, $P = 0.698$, observed power$_{\alpha=0.05} = 0.102$). Only one redd had a hyporheic oxygen concentration that could be seen as critical for salmonid embryo survival ($4.7\ mg\ L^{-1}$; Deans Bank). Both hyporheic water temperature ($F_{2,11} = 1.331$, $P = 0.304$, observed power$_{\alpha=0.05} = 0.229$) and oxygen concentration ($F_{2,11} = 0.634$, $P = 0.549$, observed power$_{\alpha=0.05} = 0.130$) were similar in control redds (no didymo cover), redds located within didymo (Maori Point and Fraser River) and random didymo-covered locations (Fig. 3*a*, *b*). Hyporheic water temperature was significantly cooler (9.7 + 0.1°C (mean + s.e.)) than the river surface water temperature (11.5 + 0.5°C; $F_{2,25} = 9.301$, $P = 0.001$, observed power$_{\alpha=0.05} = 0.961$); river surface water showed considerably more variability (larger s.e.) than the hyporheic water.

Discussion

The present study aimed to encourage more detailed investigations of the effects of didymo on salmonid egg development and redd selection, and the environmental impacts of didymo in general. The degree of didymo cover did not show any significant effects on VHG or K_v, although there was a significant difference in the vertical exchange potential between the sites, with the Fraser River samples having a significantly lower exchange potential. However, the limited sample size has to be considered in the evaluation of the results and the findings

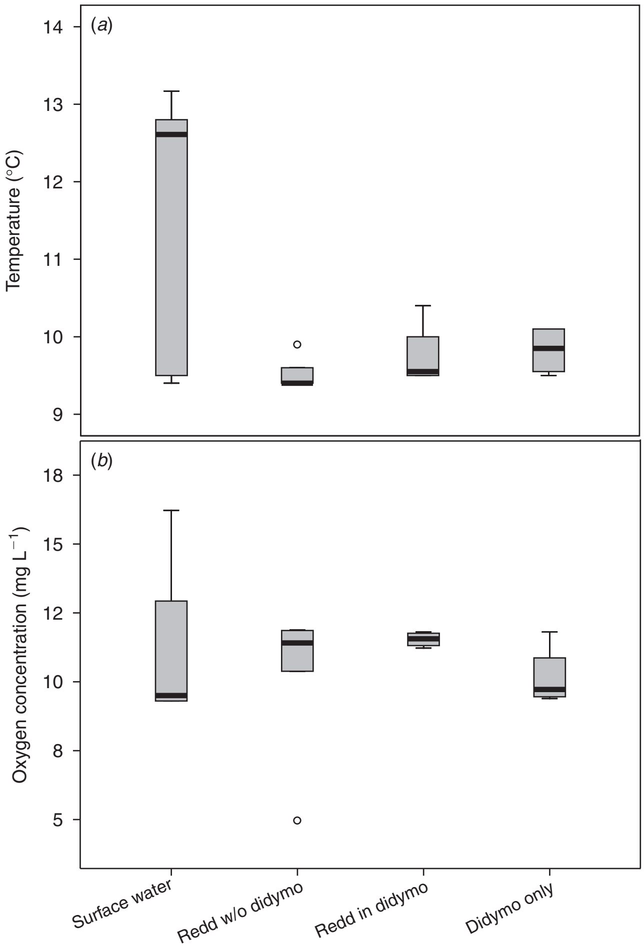

Fig. 3. Boxplot of (*a*) water temperature and (*b*) oxygen concentration in surface river water and in redds (hyporheic water) not affected by didymo, redds affected by didymo and non-redd locations with didymo cover (didymo only).

might not be directly transferable to other river systems. Surface water–groundwater interactions can fluctuate significantly on a temporal scale (Malcolm *et al*. 2003*a*), directly affecting hydraulic parameters. In the present study, hydraulic parameters were measured during periods of normal flow in all sites, that is, in discharge conditions that were prevalent during the time of egg incubation. Therefore, we feel that the sampling design, with one measurement in time, does not affect the general interpretation of the study.

The VHG was highly variable between sites and treatments, and the range of measured VHG values (−0.009 to −0.012) was similar to the range of values reported in other studies. Fall chinook salmon selected areas with a negative VHG of approximately −0.05 (Geist *et al*. 2002) and bull trout spawned predominantly in areas with VHG values averaging between −0.099 and −0.042 (Baxter and Hauer 2000). Similarly, the majority of redds in the present study were located in downwelling hyporheic exchange zones. We did not find a significant effect of the degree of didymo cover on the exchange potential. Therefore, didymo appeared to have no measurable effect on the exchange potential between the surface water and groundwater. However, there was a significant difference in the surface water–groundwater exchange potential between the sites, with the Fraser River samples having the least negative, or even positive, VHG values in the non-redd locations. This might indicate a possible effect of didymo on the surface water–groundwater exchange potential in this heavily affected area (100% cover). In contrast, the difference in VHG could also result from the difference in substrate (finer substrate in the Fraser River), lower hydraulic pressure owing to the much smaller discharge in the Fraser River ($<5\,m^3\,s^{-1}$ at the time of sampling) compared with the Clutha River ($\sim 250\,m^3\,s^{-1}$), differences in general bed morphology or a combination of all these factors.

Hydraulic conductivity values varied little between sites or with the degree of didymo cover and were high compared with other studies (Geist 2000). There was considerable variation in the hydraulic conductivity measured in redds and at non-redd sites in the sites affected by didymo (Maori Point and Fraser River); however, this difference was not significant. We can only speculate that this might partly be a result of the low sample size, and that didymo potentially has an effect on hydraulic conductivity at non-redd sites, either by increasing sedimentation or acting as a barrier on the streambed surface. Either way, the spawning activity of trout appears to counter any potential negative effects because the hydraulic conductivity in the redds was similar at sites with and without didymo.

The degree of didymo cover did not show any negative effect on hyporheic oxygen concentration. The hyporheic oxygen concentration in redds was similar to river water and adequate for salmonid egg development (Sowden and Power 1985; Malcolm *et al*. 2003*b*). Therefore, the measurable surface water–riverbed exchange potential (downwelling water) seems sufficient to prevent a decrease in oxygen levels in trout redds. As we could not measure hyporheic oxygen concentration in the most affected area (Fraser River) because of instrument malfunction, we do not know if the average lower exchange potential would have negatively affected oxygen concentrations in redds at this site. The temperature of the river water was more variable (larger range of measured values) than that of hyporheic water and significantly warmer. This probably reflects the time of sampling and lags in temperature between river and hyporheic water as a result of advected heat.

Given the limited number of samples collected in the present study, we have to be cautious in concluding that didymo has no measurable effects on hydraulic conditions in trout redds. There was a decrease in the potential surface water–groundwater exchange at the most affected site and affected non-redd locations had lower hydraulic conductivity, although this difference was not significant. In light of these findings, it would be desirable to conduct further studies to increase the number of replicates and to test for possible negative impacts of didymo in other systems.

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