



Title	Effects of fine sediment accumulation on the redd environment and the survival rate of masu salmon (<i>Oncorhynchus masou</i>) embryos
Author(s)	Yamada, Hiroyuki; Nakamura, Futoshi
Citation	Landscape and Ecological Engineering, 5(2), 169-181 https://doi.org/10.1007/s11355-009-0065-8
Issue Date	2009-07
Doc URL	http://hdl.handle.net/2115/39028
Rights	The original publication is available at www.springerlink.com
Type	article (author version)
File Information	LEE5-2_p169-181.pdf



[Instructions for use](#)

Journal title: *Landscape and Ecological Engineering*
Article ID: LEE135
Type of Paper: original paper

**Effects of fine sediment accumulation on
the redd environment and the survival rate of masu salmon
(*Oncorhynchus masou*) embryos**

Hiroyuki Yamada and Futoshi Nakamura

Graduate School of Agriculture, Hokkaido University, Sapporo, Japan

Running head: Effect of fine sediment on masu salmon embryo

Corresponding author: Hiroyuki Yamada

Address: Environmental Informatics Lab., Graduate School of Agriculture, Hokkaido University,
Sapporo, 060-8589, Japan

Phone: +81-11-706-4183 / Fax: +81-11-706-2494

E-mail: hiroyama@env.agr.hokudai.ac.jp

Grants:

- 1) Grants in Aid for Scientific Research from the Ministry of Education, Science and Culture (Nos. 13460061, 14380274, 14506039, 17780242)
- 2) Fund provided by Technology Research Centre for Riverfront Development
- 3) River Environment Fund (REF) of the Foundation of River and Watershed Environment Management (FOREM)
- 4) Workshop Fund provided by Japan Society of Erosion Control Engineering

1 **Abstract**

2 In recent years, fine sediment, produced by run-off associated with forestry activity and
3 agricultural development that accumulates on riverbeds, has exerted a deleterious influence on
4 lotic ecosystems. This study examined the Oroenukibetsu River, a tributary of the Nukibetsu
5 River, which has been affected by high loads of suspended sediments. Effects of accumulation
6 of fine sediment on the survival rate of masu salmon embryo and also on the redd environment
7 (permeability and intragravel dissolved oxygen concentration) were quantified through a field
8 experiment. Results show that the interchange of DO between intragravel and surface water was
9 not affected directly by permeability or the accumulated fine sediment, and that intragravel flow
10 rates can be an important factor controlling embryo survival. A decrease in permeability
11 associated with accumulation of fine sediment lowered the survival rate of embryos by
12 suffocation because the flux of DO that should be supplied to the embryo was severely limited.
13 This situation might be created by the combined effects of an accumulation of fine sediment on
14 the redd and a low DO concentration in the surface water because the DO concentration almost
15 coincided with the intragravel DO.

16
17 *Keywords: dissolved oxygen, eyed egg, flux, hyporheic, pool-riffle*

Introduction

Sediment pollution has become a serious issue throughout the world, and especially in East Asian countries, since the latter twentieth century. Generally, it has resulted from land use activities such as farmland development (e.g. Allan *et al.* 1997; Nakamura *et al.* 1997; Nakamura and Yamada 2005), forestry activities (e.g. Platts *et al.* 1989; Nakamura *et al.* 2004), mining (Hellowell 1986), and road construction (e.g. Barton 1977; Extence 1978; Cline *et al.* 1982). Such pollution has been defined as fine sediments, with sand, silt, and/or clay particles smaller than 2 mm. It imparts marked adverse effects on human society and aquatic ecosystems (Waters 1995). Particularly, excessive accumulations of fine sediment on riverbeds deleteriously influences habitats of fish, benthos, and periphyton (e.g. Berkman and Rabeni 1987; Wood and Armitage 1997; Watanabe *et al.* 2001; Yamada and Nakamura 2002; Nakamura *et al.* 2008).

In particular, embryos and alevins of salmonids reside in riverbeds and are therefore subject to detrimental effects of fine sediment accumulation on the riverbed. Accordingly, over the past half century, the relation between embryo survival and fine sediment accumulation has been examined (e.g. Wickett 1954; McNeil and Ahnell 1964; Tappel and Bjornn 1983; Greig *et al.* 2005). Successful incubation of salmonid embryos and emergence of fry are highly dependent upon extragravel and intragravel characteristics (chemical, geomorphological, and hydrological) of the spawning grounds (Chapman 1988; Greig *et al.* 2007). These include dissolved oxygen (DO) concentration, water temperature, substrate size, the channel gradient and configuration, water depth above the redd, surface water discharge and current velocity, permeability and porosity of the gravel deposit, and intragravel velocity in the redd. Chapman (1988) noted that salmonid embryos can be mortally affected by changes in more than one characteristic. For example, the accumulation of fine sediment engenders depletion of intragravel dissolved oxygen concentration because the fine sediment lowers the permeability sufficiently to prevent interchange between surface and subsurface water. The consequent decrease in intragravel flow rates might impair the supply and circulation of water in the redd directly. This situation occurs depending on the characteristics of each salmonid embryo, grain

1 The present study was conducted in the Oroenukibetsu River (42°35' N, 140°42' E),
2 a tributary of the Nukibetsu River. The catchment of the Oroenukibetsu River encompasses an
3 area of 22 km², with a channel length of 13 km and a riverbed slope of 1/32 (Fig. 1). Compared
4 to the Nukibetsu River, the Oroenukibetsu River has a low level of accumulated sediment
5 (Murakami *et al.* 2001); more masu salmon redds have been observed (Hokkaido Forestry
6 Research Institute *et al.* 1998).

7 A study section with numerous masu salmon redds was selected at a part of the river
8 situated 6–8 km from its confluence with the Nukibetsu River. A landslide scar exists in the
9 middle reach of the section, which is considered to be the primary source of fine sediment
10 downstream from this point. Consequently, a large amount of fine sediment accumulated in the
11 lower reaches of the study section.

13 ***Experimental period and installation of artificial redds***

14 Masu salmon spawn in the redd on the tail of a pool in early autumn, during
15 September – early October, in Hokkaido, Japan. The spawned eggs hatch when their cumulative
16 temperature reaches almost 450°C (Kato 1991). The embryo and fry inhabit the redds for almost
17 half a year until they rise into the stream currents in spring: early May (Mayama 1992). In the
18 study reach, spawning behaviour was observed in mid-September in 1999. Our experiment was
19 begun from October 1 to maintain consistency with the natural growth stage of the embryo.
20 Then, to evaluate the effect on egg survival, we used eyed eggs (collection, September 10, 1999;
21 cumulative temperature, 267.2°C), which had been sampled from pond-reared masu salmon
22 originated in the Shiribetsu River at Mori stations of the Hokkaido Fish Hatchery. Furthermore,
23 we set the experiment period for almost 3 weeks (Oct. 1–23, 1999) to reach to the cumulative
24 temperature level of 450°C, which is sufficient for embryos to hatch completely.

25 In the study river basin, the water discharge increases in spring (March – early May)
26 because of snow-melt, and occasionally in summer or in autumn because of typhoons or storms.
27 Consistently with that pattern, several floods occurred during the experiment period in autumn

1 (Fig. 2).

2 Regarding the physical spawning environment of masu salmon, it was reported that
3 the mean current velocity at the tails was 50 cm/s, and that the ranges of water depth, gravel size,
4 mound length, and width were, respectively, 9–13 cm, 0.5–2.5 cm, 141–168 cm, and 85–100 cm
5 (Sugiwaka *et al.* 1999). To satisfy these natural spawning conditions, eight tails were selected in
6 the study reach (Table 1; Fig. 1). Furthermore, the number of egg pockets in a redd was reported
7 as 1–6; the mean number of eggs was 323 (15–1080) in an egg pocket (Sugiwaka *et al.* 1999).
8 According to the structure of the natural redd, we constructed two artificial redds in each tail of
9 the pools, with one redd at a near-bank margin and another at the centre of the stream flow on
10 October 1–2 (Fig. 3). Each redd was 1.5 m long and 1 m wide. Three vibert boxes (Whitlock
11 vibert box; Whitlock 1977), each containing 400 eyed eggs, were buried in each redd; the eggs
12 were placed 15 cm below the bed surface.

13 The hydrochemical variables on redd environment were measured immediately after
14 installing the vibert boxes (October 3) and before collecting them (October 20–22). Although a
15 considerable rainfall (45 mm/day) precipitated on October 11 (Fig. 2), the measurements were
16 conducted under steady low-flow conditions to avoid flooding influences. To evaluate the fine
17 sediment accumulation for the experiment period, the riverbed materials were sampled on each
18 redd surface on October 20–22.

19

20 ***Permeability test***

21 To obtain the permeability coefficient in the redds, a field permeability measurement
22 using the packer test, an in-situ single well permeability test (Hvorslev 1951), was conducted at
23 points near the vibert box (Fig. 3, see Yamada *et al.* (2005) for detailed information). This test
24 was conducted by applying the same techniques as those used for that study. The permeability
25 coefficient (k) was then calculated from the following equation under Darcy flow conditions:

26
$$k = \frac{Q_p}{2\pi hl} \sinh^{-1} \left(\frac{l}{2r_w} \right),$$

1 where Q_p is the discharge pumped out of the well (cm^3/s), l is the strainer's sectional length (cm),
2 h is the difference between the water heads (cm), and r_w is the standpipe's inner radius (cm).

3 A standpipe made of a 4.6 cm diameter steel (100 cm long) with a strainer (0.5 mm
4 slit width) of 5 cm sectional length at the bottom of the standpipe was hammered into the
5 riverbed next to each vibert box so that the strainer was at the same depth as the vibert box (15–
6 20 cm depth). A pump with a maximum flow rate of $100 \text{ cm}^3/\text{s}$ was used to draw water out of
7 the standpipe. The flow rates pumped out of the well were measured using a flow meter with
8 accuracy of $0.001 \text{ cm}^3/\text{s}$. Each standpipe's water head was measured using a pore pressure meter
9 with a data logger of up to 0.1 cm accuracy. A water sealing mat ($20 \times 20 \text{ cm}$) was set around
10 the standpipe to prevent surface flow entering the gravel bed and the standpipe wall.

12 ***Hydraulic variables of surface water and water quality***

13 Surface water velocity and depth were measured above the redds with a portable
14 current meter (Model 3631; Yokogawa Electric Corp., Tokyo, Japan) at 60% of the water depth.
15 Two types of water surface gradients were measured for each redd; the gradient between a pit
16 and its tailspill (hereinafter designated as “the gradient of the tail”), and the other between a
17 pool head to the next pool (hereinafter designated as “the gradient of the reach”), using a tilting
18 level.

19 To investigate water quality in the redds, water samples were collected on two
20 sampling occasions (Oct. 3, and Oct. 20–22). At each sampling location, a standpipe was
21 installed immediately before sampling and fresh water was extracted using a hand pump (Hand
22 vacuum pump; Nalge Nunc International) after the water remaining in the pipe was first
23 removed. The sampling method followed the same procedure employed by Olsen and Townsend
24 (2003) and Greig *et al.* (2005). The dissolved oxygen concentration (intragravel DO), pH
25 (intragravel pH), and water temperature (intragravel temp.) were measured using a DO meter
26 (DO-14P, DKK-TOA Corp., Tokyo, Japan) that had been calibrated against the Winkler test, and
27 a pH meter (HM-14P; DKK-TOA Corp., Tokyo, Japan). The surface-water quality parameters

1 were measured above the bed surface where the vibert box was buried. Water quality was
2 allowed to vary with the diurnal temperature cycle. To eliminate the diel variation, water quality
3 data were sampled almost simultaneously on each survey day. To check chronological changes
4 of the water temperature in the redds and the cumulative temperature, intragravel water
5 temperature (IWTL) was monitored 15 cm below the bed surface at the centre of the tail sites
6 using data loggers (StowAway Tidbit Temp Logger; Onset Computer Corp., MA, USA) during
7 the experimental period (Fig. 3). Similarly, the surface water temperature was monitored using
8 the data logger at thalweg on St. 1.

10 ***Bed material sampling and grain size analysis***

11 When the vibert boxes were dug out, the upper 15 cm of bed material was collected
12 from each vibert box using a Surber sampler (25 cm quadrat, 0.25-mm mesh size). Thereafter,
13 we conducted particle size analysis in the laboratory using classified weight percentage (WP)
14 and cumulative weight percentage. The bed materials were sorted using sieves with mesh sizes
15 of 63 mm, 31.5 mm, 16 mm, 9.5 mm, 4 mm, 2 mm, 1 mm, 0.425 mm, and 0.25 mm. The
16 classified weight percentage consisted of WP 31.5–63 mm, WP 16–31.5 mm, WP 9.5–16 mm,
17 WP 4–9.5 mm, WP 2–4 mm, WP 1–2 mm, WP 0.425–1 mm, and WP 0.25–0.425 mm, and the
18 cumulative weight percentage was categorized as Fines < 4 mm, Fines < 2 mm, and Fines < 1
19 mm.

21 ***Data analyses***

22 The embryos collected from the vibert boxes were examined to identify dead embryos
23 and living alevin. The rate of embryo survival was calculated for each vibert box as follows.

$$24 \text{ Survival rate (\%)} = \frac{\text{Number of living alevins}}{\text{Total (dead embryo and living alevins)}} \times 100$$

25 To evaluate changes in water quality through subsurface flow in redds, the ratios of
26 water quality variables (DO, pH, water temperature) were calculated as follows.

1 Water quality ratio = $\frac{\text{Water quality in intragravel water}}{\text{Water quality in surface water}}$

2 The intragravel flow rates were calculated by assuming that the water surface gradient
3 reflects the hydraulic gradient because the difference in velocity heads between two points (pit
4 and tailspill) was extremely small. The rate of flow over the embryos, the intragravel flow rate,
5 Q (cm³/s), can be estimated as follows using Darcy's law:

6 $Q = kiA$,

7 where k is the permeability coefficient (cm/s), i is a hydraulic gradient (1), and A is the cross-
8 sectional area containing the embryos in a vibert box (cm²), defined as a product of the width
9 and height of the box (13 cm ×2 cm). Furthermore, the flux of intragravel dissolved oxygen, the
10 DO flux (mg/hr), reaching the embryos can be estimated by multiplying the intragravel flow
11 rate (Q) and intragravel DO concentration (mg/L).

12 The groundwater – surface water interactions (extent of groundwater upwelling) and
13 hyporheic water qualities vary with discharge fluctuations of the surface flow (Malcolm *et al.*
14 2003b; Malcolm *et al.* 2004); egg survival is mainly controlled by conditions existing during a
15 low stream flow (Soulsby *et al.* 2001). Consequently, physicochemical data (e.g., water quality,
16 water temperature, and permeability) obtained immediately before collecting the vibert boxes
17 were used to reflect the representative data under a steady low-flow condition continuing for
18 five days (Fig. 2). Regarding the intragravel water temperature, manually collected data were
19 used for this analysis. Pearson's correlation coefficient was used to evaluate the relations among
20 all variables. Stepwise multiple linear regression analysis was conducted to determine the most
21 influential variables for embryo survival. To avoid multicollinearity, those independent variables
22 that were significantly correlated mutually ($P < 0.05$) and which showed weak association with
23 survival rate were eliminated. To improve normality and equity of variance, the survival rate
24 was transformed to $x^{1/2}$, and the permeability coefficient, the DO flux, the classified weight
25 percentage (WP) and cumulative weight percentage were transformed to $\log(x + 1)$. These
26 statistical analyses were conducted using software (SPSS for Windows ver.10.1.3 J; SPSS Japan

1 Inc., Tokyo, Japan).

3 **Results**

4 Unfortunately, the vibert boxes at sites 4 (centre and bank), 7 (bank), and 8 (bank)
5 were washed away by flooding on October 11 (Fig. 2). For that reason, data at these sites were
6 missing for additional analyses.

7 Differences in physical parameters at different sites were not large (Table 1). The
8 surface water velocity and water depth respectively varied within 23–48 cm/s and from 17–26
9 cm/s. The velocity at St. 2 was slightly lower than at other sites. When collecting the vibert
10 boxes, we observed fine sediment accumulation in the interstitial spaces of the gravel bed of 3–6
11 cm in diameter. The mean grain size, survival rate, permeability, and intragravel flow rate
12 appear to decline in the sites downstream from the landslide (from St. 4 to St. 8, Appendix I).
13 Moreover, these variables tended to become lower in the near-bank sites than in the centre of the
14 pool tail.

15 Although IWTLs showed daily fluctuations synchronizing with surface water
16 temperature, the daily lowest temperature tended to be higher than that of the surface water (Fig.
17 4(a)). These daily fluctuations were observed at each site during the water sampling period (Fig.
18 4(b)). The daily variation was slightly larger at downstream sites than at upstream sites.

20 ***Relation between fine sediment deposition and environmental variables***

21 Correlation analyses showed a significant relation between permeability and some
22 other physical variables (Table 2). The permeability coefficient was positively correlated with
23 WP 16–31.5 mm and water depth, and negatively correlated with WP 2–4 mm, WP 1–2 mm,
24 WP 0.425–1 mm, Fines < 4 mm, Fines < 2 mm and Fines < 1 mm (Table 2). Furthermore, the
25 analyses of ratios of water quality and physical variables showed that the DO ratio was
26 significantly negatively correlated with the permeability coefficient, WP 0.25–0.425 mm, water
27 depth, and the gradient of the reach (Table 2). The significant influences of water depth existed

1 also on the DO ratio and permeability coefficient. Therefore, to remove the effect of water depth
2 on the correlation analyses, a partial correlation analysis was conducted using the water depth as
3 a control variable. No significant correlation between permeability coefficient and the DO ratio
4 was found ($r_p = -0.32$, $P = 0.064$, d.f. = 33). All DO ratios were lower than 1 (Fig. 5), suggesting
5 that the intragravel DO concentration was always lower than surface water DO concentration.
6 The pH ratio increased significantly with increasing permeability coefficient (Table 2, Fig. 5).
7 Although the temperature ratio was not correlated with the permeability coefficient (Table 2),
8 the variation of the temperature ratio tends to decrease concomitantly with increasing
9 permeability, reaching almost 1.0 (Fig. 5).

10 Although the intragravel DO concentration was significantly negatively correlated
11 with WP 0.25–0.425 mm, the former was not significantly correlated with permeability (Table
12 3). In particular, the intragravel DO was strongly positively correlated with surface water DO,
13 indicating that the intragravel DO concentration depends strongly on the surface water
14 concentration.

15

16 ***Relation between survival of embryos and environmental variables***

17 The correlation analysis between the survival rate and all physical and water quality
18 variables showed that the survival rate was significantly correlated with all weight percentages
19 (WP) except for WP 63–128 mm and WP 4–9.5 mm (Table 3). All variables for the cumulative
20 percentage less than 4 mm showed negative associations with the survival rate. In particular, the
21 survival rate decreased exponentially with increasing Fines < 2 mm and Fines < 1 mm (Figs.
22 6(a) and 6(b)); however, Fines < 2 mm is the much stronger predictor. The survival rate
23 decreased rapidly when Fines < 2 mm exceeded 20%; most embryos died when it exceeded
24 60% (Fig. 6(a)).

25 The survival rate was correlated significantly with the permeability coefficient,
26 surface water DO, intragravel temperature, surface water temperature, DO flux, and intragravel
27 flow rate (Table 3). The survival rate decreased concomitantly with decreasing permeability,

1 surface water DO concentration, DO flux and intragravel flow rate, being best explained by the
2 intragravel flow rate (Table 3). In addition, some observations revealed an extremely low
3 embryo survival rate when the permeability coefficient was less than 1 cm/s and the DO flux
4 was less than 1 mg/hr (Figs. 6(c) and 6(d)).

5 To determine the best combination of independent variables to explain the survival
6 rate, stepwise linear regression analysis was used. The grain size data were not used for this
7 analysis because the permeability coefficient was strongly correlated with the composition of
8 the bed material. The result showed that the survival rate was best explained by the combination
9 of the permeability coefficient, intragravel DO, and the tail gradient (Table 4). The survival rate
10 increased concomitantly with increasing permeability coefficient, intragravel DO concentration,
11 and tail gradient. The regression coefficient of the permeability coefficient was the highest
12 among these variables.

14 Discussion

15 *Effects of fine sediment on the redd environment*

16 The accumulation of fine sediment causes a decrease in intragravel flow rate (or
17 velocity) with decreasing permeability of the riverbed because of clogging of gravel bed pores.
18 Previous studies indicated that the permeability coefficient is inversely correlated with a
19 cumulative weight percentage less than 0.84 mm (McNeil and Ahnell 1964) and the weight
20 percentage of 0.125–1.0 mm (Murakami *et al.* 2001). In our study, a strong inverse correlation
21 was found with the cumulative weight percentage less than 4 mm (Fines < 4 mm). The
22 differences in specific grain size that affect the permeability coefficient between previous
23 studies and the present study suggest that permeability might depend not on a specific grain size
24 but instead on the grain size distribution.

25 Surface water enters a redd at the pit by down-welling, and is discharged at the
26 tailspill (Fig. 3) by up-welling (Vaux 1962; Cooper 1965). Generally, the discharges (intragravel
27 flow rates) depend on the hydraulic gradient and permeability in a riverbed. Although we did

1 not measure the hydraulic gradient directly, our stepwise regression analyses showed that the
2 gradient of the tail is an independent variable that is sufficiently strong to explain the survival
3 rate of embryos. The hydraulic gradient in a redd can be determined by the vertical position
4 (relative elevation) of the tailspill (Bjornn and Reiser 1991). Thereby the water surface gradient
5 (the gradient of tail) and the intragravel flow rate (or velocity) depend on local conditions
6 surrounding redd, as characterized by the water surface gradient on the redd and by the
7 permeability related to the amount of accumulated fine sediment.

8 The daily temperature variation at downstream sites was slightly greater than that at
9 upstream sites, suggesting that the subsurface water temperature was partially regulated by
10 surface water temperature warmed by insolation (Sugimoto *et al.* 1997), not by sediment
11 accumulation. We considered that our water quality data represented normal values because the
12 water temperature exhibited an ordinary pattern of daily fluctuation that was synchronized with
13 surface water temperatures.

14 The pH ratio decreased concomitantly with the decreasing permeability coefficient,
15 which is attributable to retention of intragravel water in the impermeable redds, resulting in an
16 increase in organic acids and carbon dioxide produced from the respiration of live embryos and
17 the decomposition of dead ones. The temperature ratio variation decreased concomitantly with
18 increasing permeability, which suggests that the surface water can infiltrate easily into the
19 permeable bed (Yamada *et al.* 2008). In contrast, the ratios varied under a low permeable
20 condition because the subsurface water temperature was mainly regulated by groundwater rather
21 than by surface water, as described by Malcolm *et al.* (2003b). However, partial correlation
22 analysis revealed no significant relation between permeability and the DO ratio, suggesting that
23 intragravel DO concentration was not affected directly by permeability, which varied with the
24 fine sediment accumulation.

25 In general, the intragravel DO concentration is controllable by water temperature,
26 interchange between surface and intragravel water, apparent velocity, permeability, and
27 decomposition of organic matter in the redd (Bjornn and Reiser 1991). Furthermore, intragravel

1 DO concentrations were affected by the extent of groundwater upwelling corresponding to
2 discharge fluctuation of surface water (Malcolm *et al.* 2003b). These indicated that limiting
3 factors for the intragravel DO concentration are complex locally and temporally. In particular,
4 many reports have described that intragravel DO concentration has a negative relation with
5 permeability and the percentage of fine sediment in substrates (Tagart 1976, 1984; Reiser and
6 White 1981) because interchange between surface and intragravel water is prevented by low
7 permeability (Tagart 1976, 1984). The intragravel DO concentration is high in highly permeable
8 riverbeds (Wells and McNeil 1970), although it is low in a riverbed covered by silt and such
9 materials of low permeability (Wickett 1954; Greig *et al.* 2005). In contrast, the intragravel DO
10 concentration is weakly correlated with the amount of accumulated fine sediment (Koski 1966).
11 Furthermore, the intragravel DO concentration depends on DO levels in the surface water; but is
12 consistently a little lower than that in surface water (Vining *et al.* 1985; Yamada *et al.* 2008).
13 These contrasting results are attributable to riverbed conditions. The former studies were of silty
14 riverbeds, where the permeability was extremely low, whereas the latter was on a sandy riverbed.
15 The bed situation in the present study resembled that of the latter cases. Consequently,
16 interchange of DO between intragravel and surface water was not directly affected by
17 permeability or the accumulated fine sediment; rather these influenced the intragravel flow rate,
18 which in turn affected the DO flux supplied to embryos.

19

20 ***Effects of fine sediment on embryos survival***

21 Previous reports have described that the survival rate and growth rate of embryos
22 decrease concomitantly with increasing cumulative weight percentage to 6.4 mm (Bjornn 1968),
23 4.6 mm (Platts *et al.* 1979), 3.3 mm (Koski 1966), 2 mm (Hausle and Coble 1976), 0.85 mm
24 (Koski 1966; Cederholm *et al.* 1981) and 0.84 mm (McNeil and Ahnell 1964; Tagart 1976).
25 Koski (1966) and Cederholm *et al.* (1981) reported that the survival rate of coho salmon (*O.*
26 *kisutch*) embryos decreased to 10–45% when the cumulative weight percentage to 0.85 mm
27 exceeded 20% in their field studies. In our study, the survival rate of masu salmon embryo

1 decreased to 20% when the cumulative weight percentage to 1.0 mm (Fines < 1 mm) and 2.0
2 mm (Fines < 2 mm) respectively exceeded 15% and 40% (Figs. 6(a) and 6(b)).

3 According to past studies that examined hydraulic parameters with respect to fine
4 sediment accumulation, embryo survival decreased concomitantly with decreasing permeability
5 and apparent velocity in the redd for pink salmon (*O. gorbuscha*) (Wickett 1958), chinook
6 salmon (*O. tshawytscha*) (Gangmark and Bakkala 1960), rainbow trout (*O. mykiss*) (Coble
7 1961), coho salmon (*O. kisutch*), steelhead trout (Phillips and Campbell 1961), and sockeye
8 salmon (*O. nerka*) (Cooper 1965), which agrees with our results. The correlation analyses
9 further revealed that the intragravel flow rate was a stronger explanatory variable for embryo
10 survival than permeability, as supported by its larger correlation coefficient (Table 3).

11 Many researchers have confirmed that survival rates of salmonid embryos were
12 affected by the intragravel DO concentration in the redd (e.g. Coble 1961; Phillips and
13 Campbell 1961; Sowden and Power 1985; Rubin and Glimsater 1996; Malcolm *et al.* 2003b),
14 but the critical DO concentration level was inconsistent. These differences might have
15 originated from methods applied, salmonid species, water temperature, and reductions in DO
16 associated with the embryos' respiration (Malcolm *et al.* 2004). In fact, embryo survival is
17 controlled by the DO supply to meet consumption by embryos (Wickett 1954). Supporting this,
18 our result indicates that the survival rate of masu salmon was positively correlated with the DO
19 flux. Although results of correlation analyses show that the influence of intragravel DO
20 concentration on the survival rate was insignificant, the former was selected as the independent
21 variable with the permeability coefficient based on results of regression analysis. Results
22 suggest that the combination reflects the DO flux.

23 The amount of oxygen consumed by one egg of masu salmon embryos is expected to
24 be 0.001 mg/h at about 11°C of water temperature (Kawajiri 1925). Therefore, oxygen
25 consumption by 400 embryos will reach 0.4 mg/hr. The survival rate declined to an extremely
26 low level when the DO flux became less than 1 mg/h (Fig. 6(d)), which is reasonably consistent
27 with the oxygen consumption estimated above. Consequently, the negative relation between the

1 survival rate and DO flux in our result is explainable by suffocation because of an insufficient
2 DO supply. In addition, the DO flux, required for successful incubation, increased with
3 advancement of the embryo growth-stage and increasing water temperature (Wickett 1954;
4 Bjornn and Reiser 1991). Therefore, in some cases, a high survival rate might occur even at a
5 low level of DO flux, depending on the growth stage and water temperature.

6 In conclusion, fine sediment accumulation in the riverbed enhances mortality through
7 suffocation because the reduced intragravel flow and permeability limit the DO flux that is
8 normally available to the embryos. Given the close association between DO concentration in the
9 riverbed and surface water, we expect that suffocation might become more serious under
10 conditions combining low DO concentration in the surface water and large amounts of fine
11 sediment in the riverbed.

12 Although this study did not examine the effects of large-scale valley/channel
13 morphology on exchanges between surface and subsurface flow and on quality of the spawning
14 habitat (e.g. Wondzell and Swanson 1996; Boulton *et al.* 1998; Baxter and Hauer 2000), embryo
15 survival was generally explained by changes in the riverbed permeability, DO flux and
16 hydraulic gradient in a redd associated with fine sediment deposition on a local scale (Malcolm
17 *et al.* 2003a), as indicated by the fact that the water surface gradient of the tail was a significant
18 variable in supplying DO to the redds.

19
20

Acknowledgments

21 We would like to express our gratitude to Dr Miyuki Nakajima and the staff of the
22 Hokkaido Fish Hatchery, and Dr Akiko Nagasaka in the Hokkaido Forestry Research Institute,
23 and Professor Seiji Yanai, Hokkaido Institute of Technology for providing embryos, data, and
24 other generous cooperation. We also thank Professors Tohru Araya, Koji Maekawa, Takashi
25 Yamada, and Shun-ichi Kikuchi, Faculty of Agriculture, Hokkaido University, and Professors
26 Makoto Nishigaki and Mitsuru Komatsu, Department of Environmental and Civil Engineering,
27 Okayama University, for useful advice. We are also grateful to Mrs. Tomoko Yamada, Ms.

1 Marie Murakami, and students in the Department of Forest Science, Hokkaido University, for
2 assistance. This research was supported in part by Grants in Aid for Scientific Research from the
3 Ministry of Education, Culture, Sports, Science and Technology (Nos. 13460061, 14380274,
4 14506039, and 17780242), and by funds from the Technology Research Centre for Riverfront
5 Development; the River Environment Fund (REF) of the Foundation of River and Watershed
6 Environment Management (FOREM); the workshop fund of Japan Society of Erosion Control
7 Engineering.

References

- 1
2 Allan JD, Erickson DL, Fay J (1997) The influence of catchment land use on stream integrity
3 across multiple spatial scales. *Freshwater Biology* 37: 149–161
- 4 Barton BA (1977) Short-term effects of highway construction on the limnology of a small
5 stream in southern Ontario. *Freshwater Biology* 7: 99–108
- 6 Baxter CV, Hauer FR (2000) Geomorphology, hyporheic exchange, and selection of spawning
7 habitat by bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic*
8 *Science* 57: 1470–1481
- 9 Berkman HE, Rabeni CF (1987) Effect of siltation on stream fish communities. *Environmental*
10 *Biology of Fishes* 18: 285–294
- 11 Bjornn TC (1968) Survival and emergence of trout and salmon fry in various gravel-sand
12 mixtures. *Logging and Salmon: Proceedings of a Forum*, American Institute of Fishery
13 Research Biologists. Alaska: 80–88
- 14 Bjornn TC, Reiser DW (1991) Habitat requirements of salmonids in streams. In *Influence of*
15 *Forest and Rangeland Management on Salmonid Fishes and Their Habitats*, Meehan WR
16 (ed.). American Fisheries Society Special Publication 19: 83–138
- 17 Boulton AJ, Findlay S, Marmonier P, Stanley EH, Valett HM (1998) The functional significance
18 of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics*
19 29: 59–81
- 20 Cederholm CJ, Reid LM, Salo EO (1981) Cumulative effects of logging road sediment on
21 salmonid populations in Clearwater River, Jefferson County, Washington. *Proceedings of a*
22 *conference on salmon spawning gravel: a renewable resource in the Pacific Northwest*.
23 Washington State University, Water Research Centre Report 39, Pullman: 38–74
- 24 Chapman DW (1988) Critical review of variables used to define effect of fines in redds of large
25 salmonids. *Transactions of the American Fisheries Society* 117: 1–21
- 26 Cline LD, Short RA, Ward JV (1982) The influence of highway construction on the
27 macroinvertebrates and epilithic algae of a high mountain stream. *Hydrobiologia* 96: 149–

1 159

2 Coble DW (1961) Influence of water exchange and dissolved oxygen in redd on survival of
3 steelhead trout embryos. Transactions of the American Fisheries Society 90: 469–474

4 Cooper AC (1965) The effect of transported stream sediments on survival of sockeye and pink
5 salmon eggs and alevin. International Pacific Salmon Fisheries Commission Bulletin 18

6 Extence CA (1978) The effects of motorway construction on an urban stream. Environmental
7 Pollution 17: 245–252

8 Gangmark HA, Bakkala RG (1960) A comparative study of unstable and stable (artificial
9 channel) spawning streams for incubating King salmon at Mill Creek. California Fish and
10 Game 46: 151–164

11 Greig SM, Sear DA, Carling PA (2005) The impact of fine sediment accumulation on the
12 survival of incubating salmon progeny: Implications for sediment management. Science of
13 the Total Environment 344: 241–258

14 Greig SM, Sear DA, Carling PA (2007) A review of factors influencing the availability of
15 dissolved oxygen to incubating salmonid embryos. Hydrological Processes 21: 323–334
16 DOI: 10.1002/hyp.6188

17 Hausle DA, Coble DW (1976) Influence of sand in redds on survival and emergence of brook
18 trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 105: 57–63

19 Hellawell JM (1986) Biological Indicators of Freshwater Pollution and Environmental
20 Management. Elsevier Applied Science: Barking

21 Hokkaido Forestry Research Institute, Hokkaido Fish Hatchery, Hokkaido Central Agricultural
22 Experiment Station (1998) Study of riparian environment restoration in rural areas, Bulletin
23 of Hokkaido Forestry Research Institute, Hokkaido Fish Hatchery and Hokkaido Central
24 Agricultural Experiment Station: 1–76 (in Japanese)

25 Hokkaido Forestry Research Institute, Hokkaido Fish Hatchery, Hokkaido Central Agricultural
26 Experiment Station (1999) Study of riparian environment restoration in rural areas, Bulletin
27 of Hokkaido Forestry Research Institute, Hokkaido Fish Hatchery and Hokkaido Central

- 1 Agricultural Experiment Station: 1–109 (in Japanese)
- 2 Hokkaido Forestry Research Institute, Hokkaido Fish Hatchery, Hokkaido Central Agricultural
3 Experiment Station (2000) Study of riparian environment restoration in rural areas, Bulletin
4 of Hokkaido Forestry Research Institute, Hokkaido Fish Hatchery and Hokkaido Central
5 Agricultural Experiment Station: 1–99 (in Japanese)
- 6 Hvorslev MJ (1951) Time lag and soil permeability in ground-water observations. U.S. Corps of
7 Eng. Waterways Exp. Sta. Vicksburg. Miss. Bull. 36: 50
- 8 Japan Weather Association (2000) AMeDAS annual report (CD-ROM), Japan Meteorological
9 Business Support Centre, Tokyo
- 10 Japan Weather Association (2001) Annual report of precipitation, water level and discharge
11 (uryo suii ryuuryo nenpyou), Doboku Society of Hokkaido, Sapporo
- 12 Kato F (1991) Life histories of masu and amago salmon (*Oncorhynchus masou* and
13 *Oncorhynchus rhodurus*). In Pacific Salmon Life Histories, Groot C and Margolis L (eds.).
14 UBC Press, Vancouver. 447–520
- 15 Kawajiri M (1925) On the oxygen consumption during development of the eggs and fly of the
16 masu salmon (*O. masou* land-locked). Japan Imp. Fish. 21(2): 18–20
- 17 Koski KV (1966) The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to
18 emergence in three Oregon coastal streams. Masters thesis. Oregon State University,
19 Corvallis
- 20 Malcolm IA, Soulsby C, Youngson A, Petry J (2003a) Heterogeneity in ground water – surface
21 water interactions in the hyporheic zone of a salmonid spawning stream: towards
22 integrating hydrometric and tracer approaches. Hydrological Processes 17: 601–617
- 23 Malcolm IA, Youngson A, Soulsby C (2003b) Survival of salmonid eggs in gravel bed streams:
24 effects of groundwater–surface water interactions. River Research and Applications 19(4):
25 303–316
- 26 Malcolm IA, Soulsby C, Youngson AF, Hannah DM, McLaren IS and Thorne A (2004)
27 Hydrological influences on hyporheic water quality: implications for salmon egg survival.

- 1 Hydrological Processes 18: 1543–1560. DOI: 10.1002/hyp.1405
- 2 Mayama H (1992) Studies of the freshwater life and propagation technology of masu salmon
3 (*Oncorhynchus masou* Brevoort). Scientific Reports of the Hokkaido Salmon Hatchery 46:
4 1–156 (in Japanese with English abstract)
- 5 McNeil WJ, Ahnell WH (1964) Success of pink salmon spawning relative size of spawning bed
6 materials. U.S. Fish and Wildlife Service Special Scientific Report Fisheries, 469
- 7 Murakami M, Yamada H, Nakamura F (2001) Hydraulic conductivity of substrate and
8 openwork gravel rate associated with fine sediment deposition in mountain streams,
9 southern Hokkaido. Ecology and Civil Engineering 4(2): 109–120 (in Japanese with
10 English abstract)
- 11 Nagasaka A, Nakajima M, Yanai S, Nagasaka Y (2000) Influences of substrate composition on
12 stream habitat and macroinvertebrate communities: a comparative experiment in a forested
13 and an agricultural catchment. Ecology and Civil Engineering 3: 234–254 (in Japanese
14 with English abstract)
- 15 Nakamura F, Sudo T, Kameyama S, Jitsu M (1997) Influences of channelization on discharge of
16 suspended sediment and wetland vegetation in Kushiro Marsh, northern Japan.
17 Geomorphology 18: 279–289
- 18 Nakamura F, Kameyama S, Mizugaki S (2004) Rapid shrinkage of Kushiro Mire, the largest
19 mire in Japan, due to increased sedimentation associated with land-use development in the
20 catchment. Catena 55: 213–229
- 21 Nakamura F, Yamada H (2005) Effects of pasture development on ecological functions of
22 riparian forests in Hokkaido in northern Japan. Ecological Engineering 24: 539–550
- 23 Nakamura F, Kawaguchi Y, Nakano D, Yamada H (2008) Ecological responses to anthropogenic
24 alterations of gravel-bed rivers in Japan, from floodplain river segments to the microhabitat
25 scale: a review. In Gravel-Bed Rivers VI: From Process Understanding to River
26 Restoration, Habersack H, Pie'gay H, Rinaldi M (eds.). Elsevier: 501–523
- 27 Olsen DA, Townsend CR (2003) Hyporheic community composition in a gravel-bed stream:

1 influence of vertical hydrological exchange, sediment structure and physicochemistry.
2 Freshwater Biology 48; 1363–1378

3 Phillips RW, Campbell HJ (1961) The embryonic survival of coho salmon and steelhead trout as
4 influenced by some environmental conditions in gravel beds. 14th Annual Report of the
5 Pacific Marine Fisheries Commission. Portland, Oregon; 60–73

6 Platts WS, Shirazi MA, Lewis DH (1979) Sediment particle sizes used by salmon for spawning
7 with methods for evaluation. U.S. Environmental Protection Agency EPA 600/3-79-043.
8 Corvallis, Oregon

9 Platts WS, Torquemada RJ, McHenry ML, Graham CK (1989) Changes in salmon spawning
10 and rearing habitat from increased delivery of fine sediment to the South Fork Salmon
11 River, Idaho. Transactions of the American Fisheries Society 118: 274–283

12 Reiser DW, White RG (1981) Incubation of steelhead trout and spring Chinook salmon eggs in
13 a moist environment. Progressive Fish-Culturist 43: 131–134

14 Rubin JF, Glimsater C (1996) Egg-to-fry survival of the sea trout in some streams of Gotland.
15 Journal of Fish Biology 48: 585–606

16 Sato H, Yanai S, Nagasaka Y, Nagasaka A, Sato H (2002) Influence of land use on suspended
17 sediment discharge from watersheds emptying into Funka Bay, southwestern Hokkaido,
18 northern Japan. J. Japan Soc. Hydrol. & Water Resour. 152: 117–127 (in Japanese with
19 English abstract)

20 Soulsby C, Malcolm I, Youngson A (2001) Hydrochemistry of the hyporheic zone in salmon
21 spawning gravels: a preliminary assessment in a small regulated stream. Regulated Rivers,
22 Research and Management 17: 651–665

23 Sowden TK, Power G (1985) Prediction of rainbow trout embryo survival in relation to
24 groundwater seepage and particle size of spawning substrates. Transactions of the
25 American Fisheries Society 114: 804–812

26 Sugimoto, S., Nakamura, F. and Ito, A (1997) Heat budget and statistical analysis of the
27 relationship between stream temperature and riparian forest in the Toikanbetsu Stream,

- 1 northern Japan. *Journal of Forest Research* 2: 103–107
- 2 Sugiwaka K, Takeuchi K, Suzuki K, Nagata M, Miyamoto M, Kawamura H (1999) Distribution
3 and structure of spawning redds of masu salmon in the Atsuta River. *Sci. Rep. Hokkaido*
4 *Fish Hatchery* 53: 11–28 (in Japanese with English abstract)
- 5 Tagart JV (1976) The survival from egg deposition to emergence of coho salmon in the
6 Clearwater River, Jefferson County, Washington. Master's thesis. Univ. of Washington.
7 Seattle
- 8 Tagart JV (1984) Coho salmon survival from egg deposition to emergence. Proceedings of the
9 Olympic Wild Fish Conference, Walton JM and Houston DB (eds). Peninsula College,
10 Fisheries Technology Program, Port Angeles, Washington; 173–182
- 11 Tappel PD, Bjornn TC (1983) A new method of relating size of spawning gravel to salmonid
12 embryo survival. *North American Journal of Fisheries Management* 3: 123–135
- 13 Vaux WG (1962) Interchange of stream and intergravel water in a salmon spawning riffle. U.S.
14 Fish and Wildlife Service SSR
- 15 Vining TJ, Blakely S, Freeman GM (1985) An evaluation of the incubation life-phase of chum
16 salmon in the middle Susitna River, Alaska. Alaska Department of Fish and Game Report 5.
17 Anchorage
- 18 Watanabe K, Nakamura F, Kamura K, Yamada H, Watanabe Y, Tsuchiya S (2001) Influence of
19 stream alteration on the abundance and distribution of benthic fish. *Ecology and Civil*
20 *Engineering* 42(2): 133–146 (in Japanese with English abstract)
- 21 Waters TF (1995) *Sediment in Streams – Sources, Biological Effects, and Control*. American
22 Fisheries Society Monograph, 7, Maryland
- 23 Wells RA, McNeil WJ (1970) Effect of quality of the spawning bed on the growth and
24 development of pink salmon embryos and alevins. U.S. Fish and Wildlife Service Spatial
25 Scientific Report Fisheries 616
- 26 Whitlock D (1977) *The Whitlock Vibert Box Handbook*, Federation of Fly Fisherman: West
27 Yellowstone

- 1 Wickett WP (1954) The oxygen supply to salmon eggs in spawning beds. Journal of the
2 Fisheries Research Board of Canada 11: 933–953
- 3 Wickett WP (1958) Review of certain environmental factors affection the production of pink
4 and chum salmon. Journal of the Fisheries Research Board of Canada 15: 1103–1126
- 5 Wondzell SM, Swanson FJ (1996) Seasonal and storm dynamics of the hyporheic zone of a 4th-
6 order mountain stream. I: hydrologic processes. Journal of the North American
7 Benthological Society 15: 3–19
- 8 Wood PJ, Armitage PD (1997) Biological effect of fine sediment in the lotic environment,
9 Environmental Management 21(2): 203–217
- 10 Yamada H, Nakamura F (2002) Effect of fine sediment deposition and channel works on
11 periphyton biomass in the Makomanai River, northern Japan. River Research and
12 Applications 18: 481–493
- 13 Yamada H, Nakamura F, Watanabe Y, Murakami M, Nogami T (2005) Measuring hydraulic
14 permeability in a streambed using the packer test. Hydrological Processes 19: 2507–2524
- 15 Yamada H, Kawaguchi Y, Edo K, Komiyama E (2008) Effects of fine sediment accumulation on
16 the redd environment and the survival rate of eyed embryos of Sakhalin taimen (*Hucho*
17 *perryi*) in mountain streams of northern Hokkaido. Ecol. Civil. Eng. 11(1): 29–40 (in
18 Japanese with English abstract)

Figure Captions

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

Fig. 1. Location of the Nukibetsu River Basin (a), and the study site in the Oroennukibetsu River (b). Solid circles with a number show the research sites (tail of pool).

Fig. 2. Study period and annual water discharge, air temperature, precipitation at the river mouth of Nukibetsu R. in 1999 (Japan Weather Association 2000, 2001).

Fig. 3. Installation of artificial masu salmon redd and the packer test equipment in each site.

Fig. 4. Chronological variations of intragravel and surface water (SW) temperature at each centre site for study period (a) and for water sampling period (b) in 1999 (Air temperature and precipitation data, Japan Weather Association 2000, 2001).

Fig. 5. Relation between redd permeability and water quality ratios.

Fig. 6. Relation between survival rate of masu salmon embryo and cumulative weight percentage less than 2.0 mm (Fines <2.0 mm) (a) and 1.0 mm (Fines <1.0 mm) (b), permeability (c), DO flux (d).

Table 1. Geomorphic and hydraulic description of tail and redd. "-" indicates no data.

Site	Position	Tail length (m)	Wetted width (m)		Gradient of tail (%)	Surface water velocity (cm/s)	Water depth (cm)
			Mean	SE			
1	Centre	6.10	3.07	0.11	0.29	56.57	23.67
	Bank				0.76	59.94	14.00
2	Centre	6.40	4.77	0.06	0.29	21.47	18.00
	Bank				0.18	27.11	32.00
3	Centre	10.50	3.63	0.17	0.39	41.82	22.33
	Bank				0.25	38.85	18.33
4	Centre	7.00	4.00	0.05	0.35	22.86	11.67
	Bank				0.28	20.69	14.67
5	Centre	7.00	5.50	0.15	-0.01	53.98	25.33
	Bank				0.09	34.25	22.67
6	Centre	5.00	5.55	0.04	0.26	34.74	17.00
	Bank				0.08	31.76	18.33
7	Centre	3.00	5.89	0.15	-0.01	36.95	22.67
	Bank				-	-	-
8	Centre	3.40	5.53	0.03	0.05	36.46	12.33
	Bank				0.17	37.53	16.00

Table 2. Correlation coefficients between variables. * and ** indicate significance levels at $P < 0.05$ and $P < 0.01$, respectively ($n=36$). Variables with † were transformed to $\log(x+1)$.

Variable	Permeability [†]	DO ratio	pH ratio	Temp. ratio
Permeability [†]		-0.420 *	0.379 *	0.206
WP 63-128 mm [†]	-0.123	0.279	-0.305	0.058
WP 31.5-63 mm [†]	0.293	-0.245	0.319	0.238
WP 16-31.5 mm [†]	0.565 **	0.004	0.153	0.506 **
WP 9.5-16 mm [†]	0.304	0.046	0.107	0.326
WP 4-9.5 mm [†]	-0.232	0.253	-0.130	-0.056
WP 2-4 mm [†]	-0.413 *	0.287	-0.221	-0.288
WP 1-2mm [†]	-0.453 **	0.226	-0.149	-0.234
WP 0.425-1 mm [†]	-0.457 **	0.245	-0.261	-0.188
WP 0.25-0.425 mm [†]	-0.122	-0.413 *	0.056	-0.229
Fines < 4.0 mm [†]	-0.478 **	0.236	-0.203	-0.290
Fines < 2.0 mm [†]	-0.466 **	0.190	-0.178	-0.255
Fines < 1.0 mm [†]	-0.431 **	0.094	-0.224	-0.245
Surface water velocity	0.054	-0.204	0.175	0.380 *
Water depth	0.418 *	-0.364 *	0.085	-0.051
Gradient of reach	0.209	-0.441 **	0.170	0.253
Gradient of tail	0.058	-0.318	0.293	0.335 *

Table 3. Correlation coefficients between variables. * and ** indicate significance levels at $P < 0.05$ and $P < 0.01$, respectively ($n=36$). Variables with † and †† were transformed to $x^{1/2}$ and $\log(x+1)$, respectively.

Variable	Survival rate [†]	Intragravel DO	Intragravel pH	Intragravel Temp.
Permeability ^{††}	0.434 **	-0.190	0.077	0.005
WP 63-128 mm ^{††}	0.120	0.495 **	0.230	-0.210
WP 31.5-63 mm ^{††}	0.617 **	0.095	-0.236	-0.230
WP 16-31.5 mm ^{††}	0.789 **	0.211	-0.108	-0.230
WP 9.5-16 mm ^{††}	0.677 **	0.257	-0.060	-0.291
WP 4-9.5 mm ^{††}	0.133	0.146	-0.019	-0.141
WP 2-4 mm ^{††}	-0.558 **	-0.099	0.105	0.197
WP 1-2mm ^{††}	-0.698 **	-0.115	0.003	0.114
WP 0.425-1 mm ^{††}	-0.558 **	0.061	0.027	0.059
WP 0.25-0.425 mm ^{††}	-0.471 **	-0.444 **	-0.017	0.160
Fines < 4.0 mm ^{††}	-0.679 **	-0.115	0.055	0.161
Fines < 2.0 mm ^{††}	-0.686 **	-0.102	0.024	0.124
Fines < 1.0 mm ^{††}	-0.591 **	-0.069	0.042	0.115
Surface water velocity	0.208	-0.020	-0.469 **	-0.544 **
Water depth	0.100	-0.446 **	0.177	0.379 *
Gradient of reach	0.304	-0.133	-0.434 **	-0.499 **
Gradient of tail	0.321	-0.068	-0.667 **	-0.506 **
Intragravel DO concentration	0.283		-0.116	-0.546 **
Surface water DO concentration	0.355 *	0.914 **	-0.156	-0.621 **
Intragravel pH	-0.211	-0.116		0.650 **
Surface water pH	-0.209	-0.034	0.923 **	0.614 **
Intragravel Temp.	-0.347 *	-0.546 **	0.650 **	
Surface water Temp.	-0.399 *	-0.542 **	0.666 **	0.992 **
DO flux ^{††}	0.456 **	-0.146	-0.319	-0.337 *
Intragravel flow rate ^{††}	0.549 **	-0.190	-0.326	-0.294

Table 4. Results of stepwise linear regression analysis ($n=36$).

Independent variables	Standard regression coefficient	R^2	F	P
Survival rate				
Permeability	0.43	0.19	7.88	0.008
Permeability	0.51	0.33	8.00	0.001
Intragravel DO concentration	0.38			
Permeability	0.49	0.43	7.98	< 0.001
Intragravel DO concentration	0.40			
Gradient of tail	0.32			

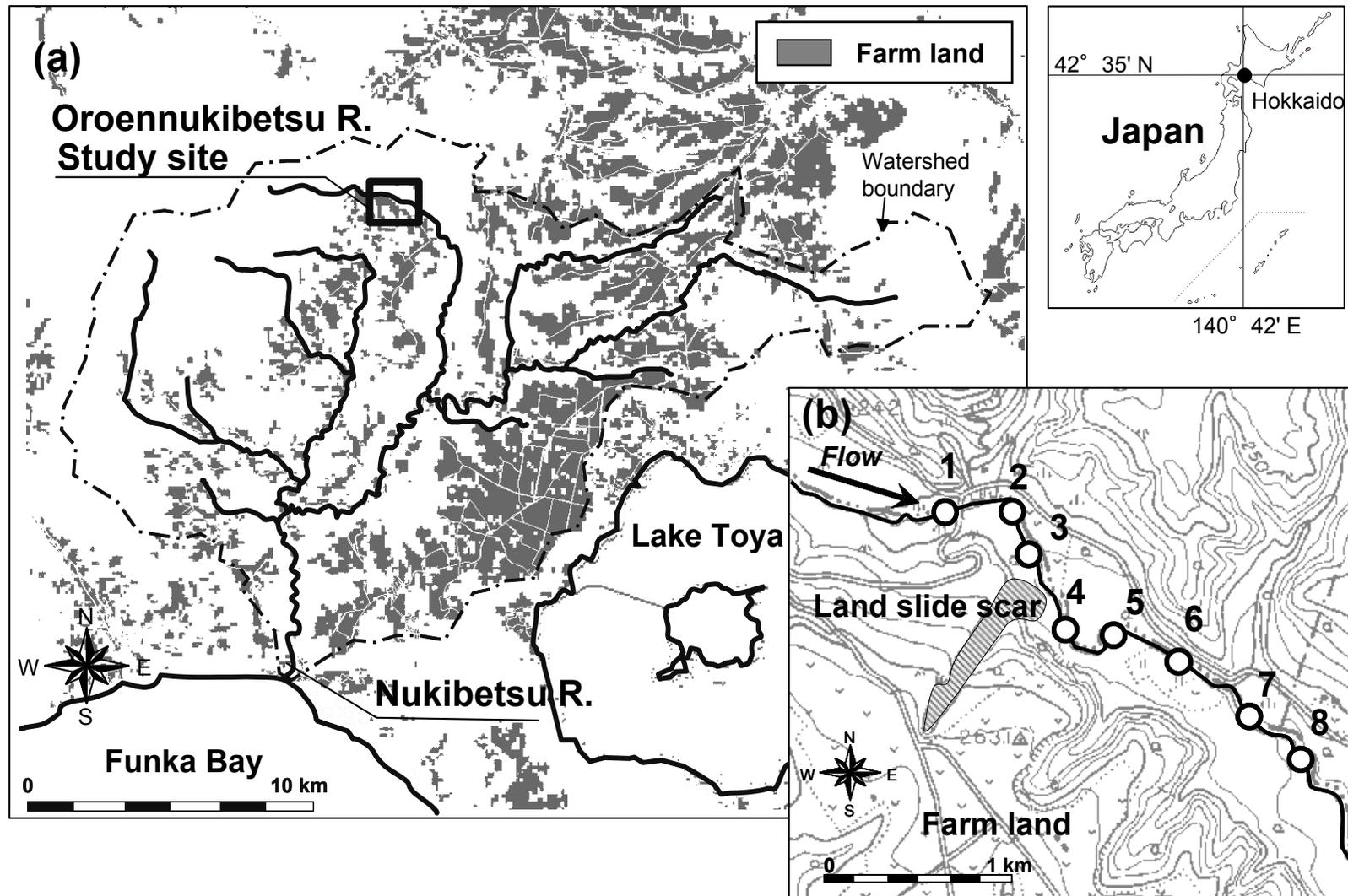


Fig. 1. Location of the Nukibetsu River Basin (a), and the study site in the Oroennukibetsu River (b). Solid circles with a number show the research sites (tail of pool).

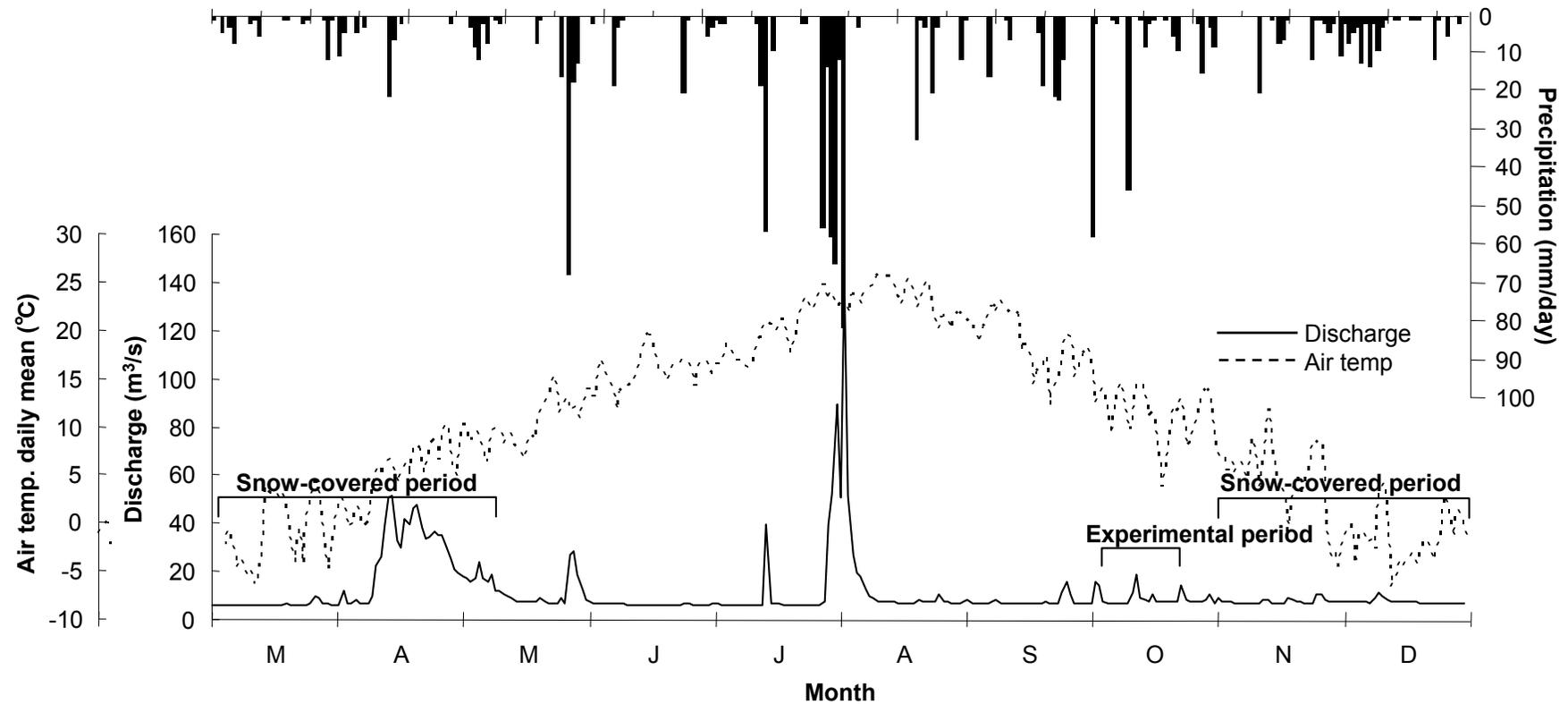


Fig. 2. Study period and annual water discharge, air temperature, precipitation at the river mouth of Nukibetsu R. in 1999 (Japan Weather Association 2000, 2001).

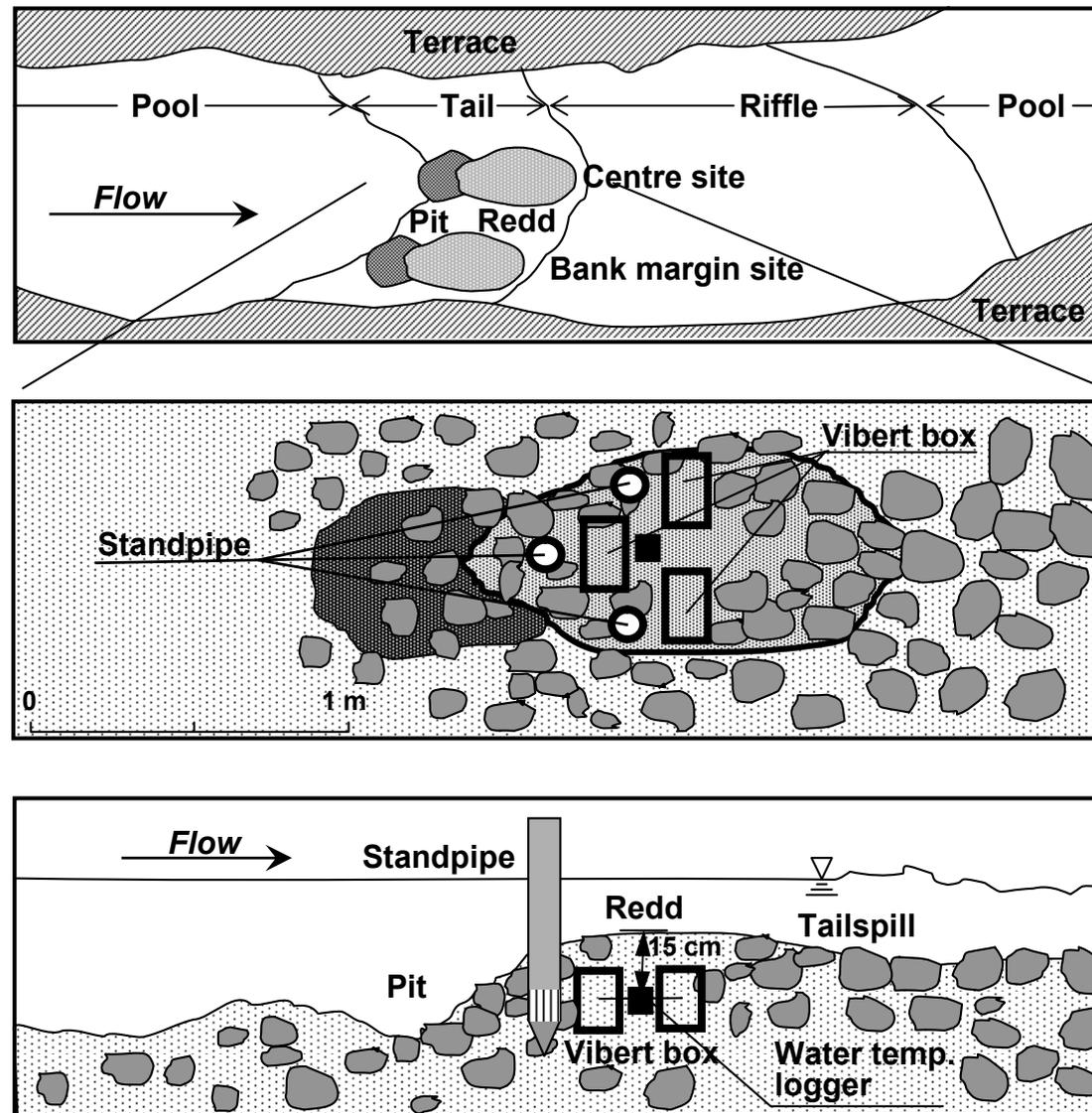


Fig. 3. Installation of artificial masu salmon redd and the packer test equipment in each site.

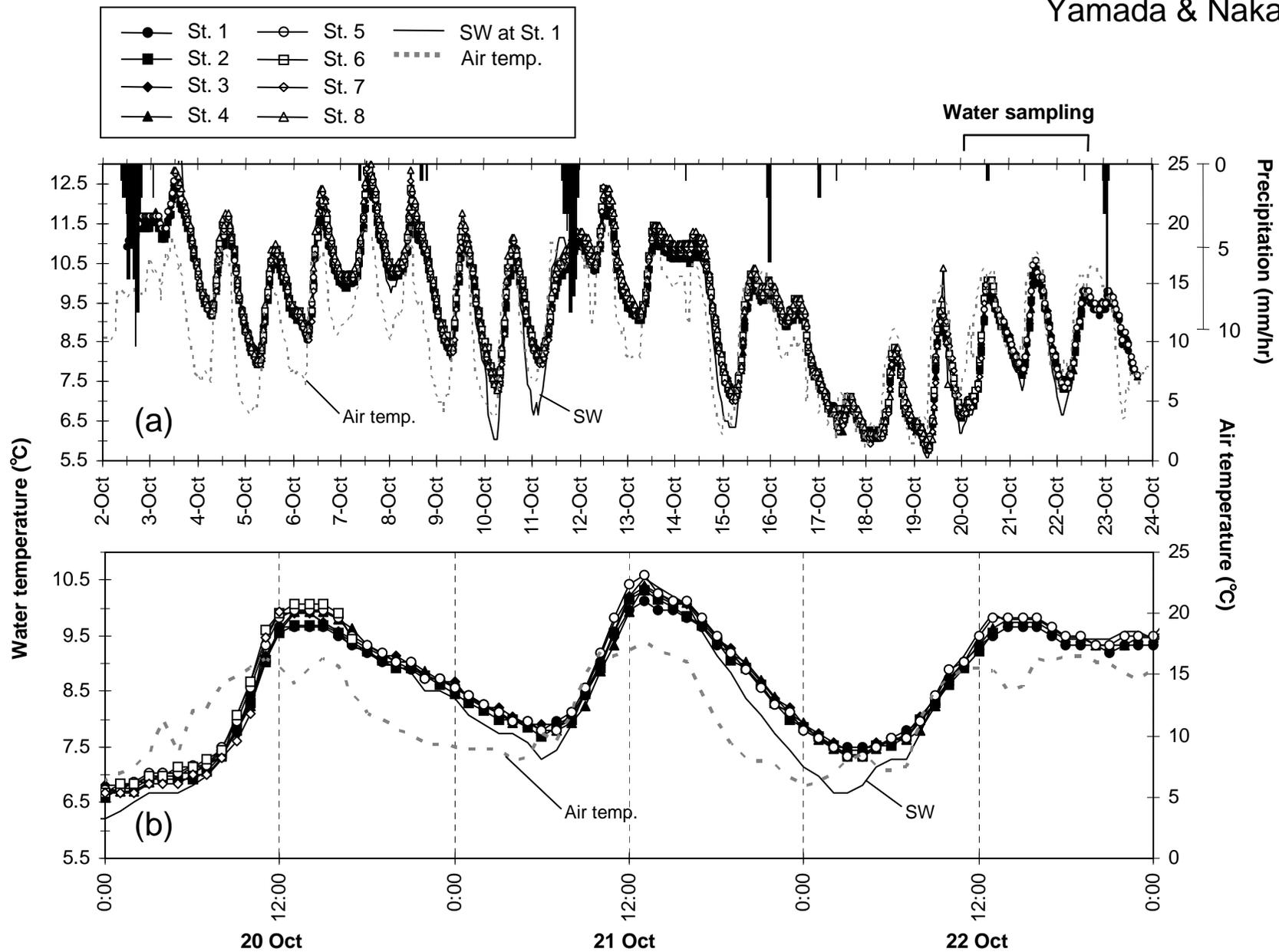


Fig. 4. Chronological variations of intragravel and surface water (SW) temperature at each centre site for study period (a) and for water sampling period (b) in 1999 (Air temperature and precipitation data, Japan Weather Association 2000, 2001).

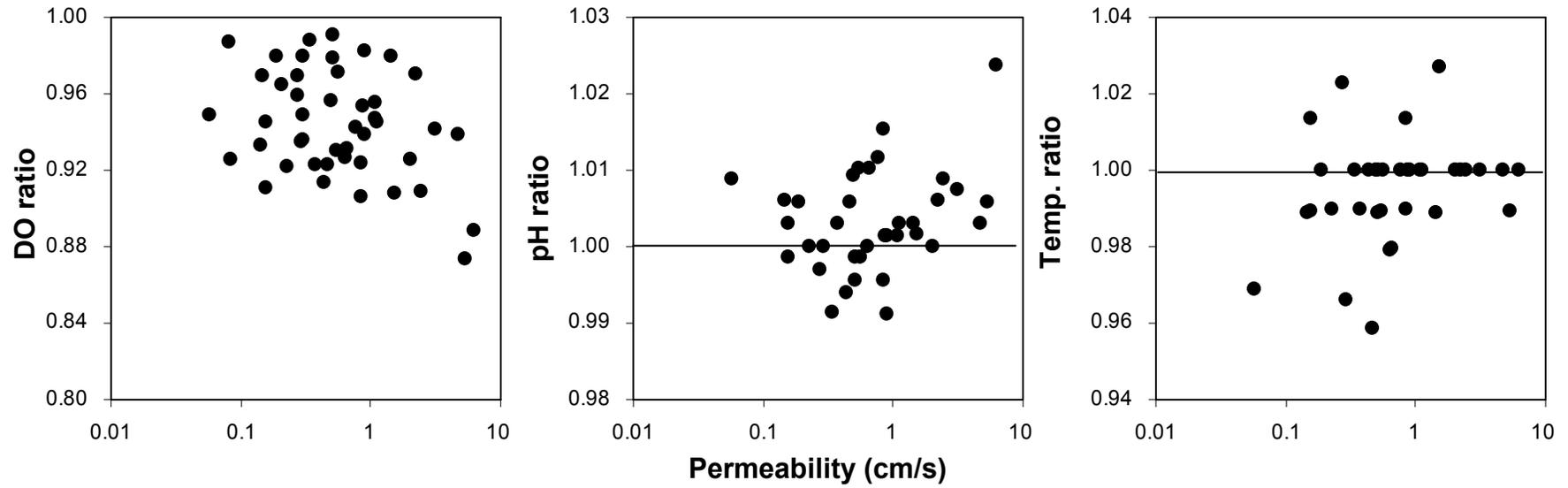


Fig. 5. Relation between redd permeability and water quality ratios.

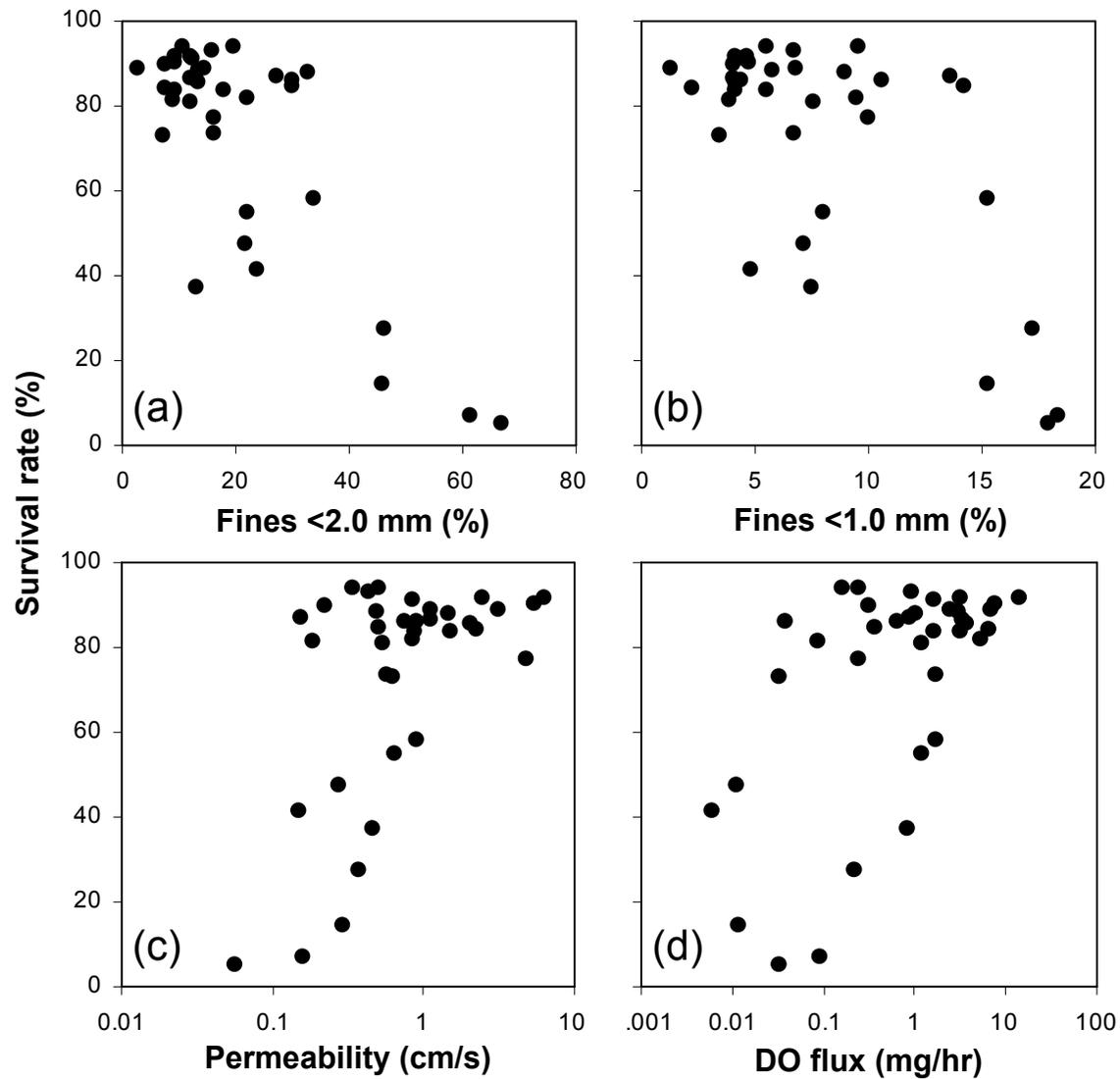


Fig. 6. Relation between survival rate of masu salmon embryo and cumulative weight percentage less than 2.0 mm (Fines <2.0 mm) (a) and 1.0 mm (Fines <1.0 mm) (b), permeability (c), DO flux (d).

