Ecology, 82(5), 2001, pp. 1238–1246
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SALMONID HABITAT–GEOMORPHOLOGY RELATIONSHIPS IN LOW-GRADIENT STREAMS

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Abstract. A link between stream geomorphology and lotic ecosystems was demonstrated by quantitatively examining the precise locations of salmonid redds with respect to the planform geometry of streams using a differential global positioning system. A total stream distance of 59 km was surveyed in 17 streams, in which a total of 309 redds of Sakhalin taimen (*Hucho perryi*) were recorded. The average size ($\pm$SD) of these redds was 227 $\pm$ 60 cm in length and 122 $\pm$ 42 cm in width. A meta-analysis of these data showed that channel sinuosity was significantly greater at sites where Sakhalin taimen redds were constructed than the average stream sinuosity. This salmonid preference for highly sinuous reaches was detected when the sinuosity index was calculated at 50-m increments and became insignificant at greater distance increments. This habitat–sinuosity relationship will be more pronounced in streams with only moderately sinuous channels, less abundant large woody debris, and higher spawner densities.

Key words: channel sinuosity; differential global positioning system; Hucho perryi; *lotic ecosystems; meta-analysis; redds; Sakhalin taimen; salmonid spawning habitat; stream geomorphology.*

INTRODUCTION

Stream geomorphology, including the shape, profile, plan view, and structural elements, strongly influences the hydraulic characteristics of streams (Rosgen 1994, Ziemer and Lisle 1998); which in turn determine the distribution, abundance, and habitat for fish in streams (Beschta and Platts 1986, Bisson et al. 1987, Lanka et al. 1987, Sullivan et al. 1987, Naiman 1998). The majority of the previous research on the physical aspects of fish habitat have focused on small scale habitat features such as channel unit or microhabitat in relation to fish populations (Bustard and Narver 1975, Shirvell and Dungey 1983, Moyle and Baltz 1985, Bowlby and Roff 1986, Winkle et al. 1990, Baltz et al. 1991). The effect of larger scale habitat features like stream size and planform on fish populations has been increasingly recognized, but few systematic, quantitative assessments have been undertaken (see Benda et al. 1992, Payne and Lapointe 1997). Because a general association exists across the different scales of the geomorphic characteristics of natural rivers and streams (Hubert and Kozel 1993, Montgomery and Buffington 1998), the habitat–geomorphology relationship at the channel unit or microhabitat scale can be extrapolated to much larger spatial scales.

For salmonids, relative position in a pool–riffle sequence plays an important role in determining sites for redd construction. For instance, Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and chinook salmon (*Oncorhynchus tshawytscha*) spawn exclusively at the tails of pools or, equivalently, the crests of riffles where stream water downwells into the gravel (White 1942, Crisp and Carling 1989, Vronskii and Leman 1991). Conversely, other salmonids like chum salmon (*O. keta*) and sockeye salmon (*O. nerka*) spawn slightly upstream or in the middle of pool reaches where intragravel water upwells (Lorenz and Eiler 1989, Salo 1991, Fukushima and Smoker 1998). Regardless of exactly where salmonids construct their redds, their spawning habitat depends in large part on the pool–riffle microhabitat sequence. Because the pool–riffle sequence is commonly formed at a channel bend in low-gradient alluvial streams (Beschta and Platts 1986, Lisle 1986), it can be hypothesized that the density of redds in such streams is higher in reaches with abundant bends or high sinuosity. Ono (1995) supported this hypothesis when he reported a significant correlation between the sinuosity of eight 150-m reaches and the number of salmonid redds in these reaches.

In this paper, I will test the hypothesis that salmonid redd placement is positively correlated with stream reach sinuosity in low-gradient streams. This will be done by quantitatively examining the precise locations of Sakhalin taimen (*Hucho perryi*) redds in multiple streams relative to the planform geometry of the stream using a differential global positioning system (DGPS) that provides accurate and reliable spatial data of latitude, longitude, and altitude.

Although the effects of channel sinuosity on stream hydraulics have been well described (Williams 1986, Ebisemiju 1994, Rosgen 1994, Lajczak 1995, Rinaldi and Johnson 1997), the ecological importance of stream sinuosity has been neglected by the stream managers, engineers, and ecologists responsible for designing stream recovery and restoration programs (Brookes 1988, Newbury and Gaboury 1993, Koebel 1995). As

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a result, loss of sinuous or meandering rivers and streams due to channelization and channel incision has impaired the capacity and threatened the persistence of viable lotic ecosystems (Brookes 1988, Wilcock and Essery 1991, Hupp 1992, Mattingly et al. 1993, Newbury and Gaboury 1993, Shields et al. 1994, Jurajda 1995).

Sakhalin taimen construct redds exclusively at pool tails where the streamflow breaks over the lip of the pool into the riffle below (Fukushima 1994). Because of this strong connection between spawning site preference and stream geomorphology at a microhabitat scale, this species can serve as an ideal organism for testing the habitat–sinuosity hypothesis. In Hokkaido, the northernmost large island of Japan, Sakhalin taimen spawn from late April to early May after the stream discharge subsides after the snowmelt freshets (Fukushima 1994). The Sakhalin taimen spawners typically vary in length from ~50 to 70 cm (Kimura 1966, Kawamura et al. 1983; M. Fukushima, *personal observation*), but they can grow to over one meter in some river systems (Yamashiro 1965). Aside from Hokkaido, they inhabit Sakhalin Island, the southern Kurile Islands, and the Primorye region of Siberia, Russia (Kimura 1966). Sakhalin taimen are currently classed as endangered in Japanese river systems primarily because of severe habitat degradation including stream channelization (Japanese Environment Agency 1999).

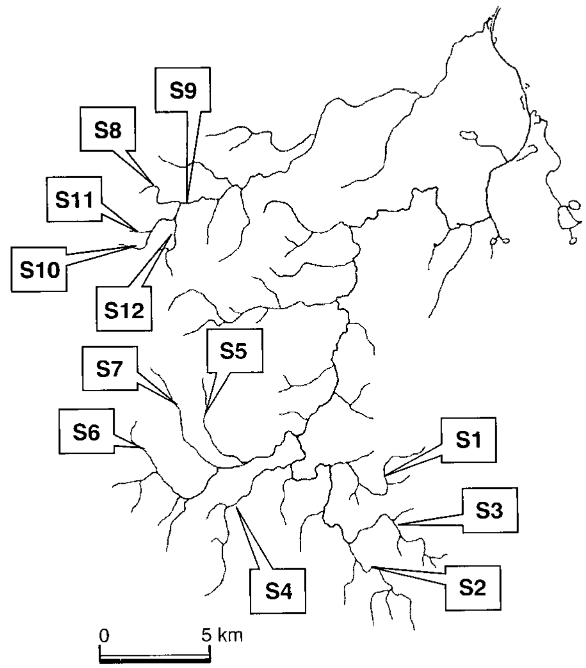

FIG. 1. Map of study streams, showing tributaries where channel geometry was surveyed and the Sakhalin taimen redds were counted.

METHODS

Study streams

The Sarufutsu River arises from low elevation mountains (<500 m) in northern Hokkaido and flows ~53 km into the Sea of Okhotsk, draining a watershed area of 370 km^2 (Fig. 1). A total of 17 first- or second-order headwater tributaries (Strahler 1957) were selected from the drainage basin for the field survey of stream morphology and Sakhalin taimen redd position. The study streams flow on unconsolidated, erodible material (predominantly Tertiary shale), and the substratum is composed primarily of well-sorted gravel (i.e., smaller than 64 mm in diameter). The study streams are highly sinuous, have gradients typically <1%, and have well preserved riparian zones dominated by coniferous and deciduous trees. Other salmonids inhabiting the study streams include whitespotted charr (*Salvelinus leucomaenis*), masu salmon (*Oncorhynchus masou*), chum salmon (*O. keta*), and pink salmon (*O. gorbuscha*).

Field surveys using DGPS

The planform geometry of the study streams and precise locations of Sakhalin taimen redds were recorded using a differential global positioning system (DGPS) during late April through early May 1998. The DGPS consisted of a remote receiver (Trimble Pathfinder Pro XR, Trimble Navigator, Sunnyvale, California, USA) and a base station receiver (Trimble Series 4000); the latter was installed at a known stationary location in an adjacent town (latitude = 45°07′44″ N, longitude = 142°21′75″ E). The two receivers were never farther apart than 30 km during field reconnaissance, which is within the range where negligible DGPS data degradation should occur (Trimble 1995).

A field observer logged position data with the remote receiver at an interval of either eight seconds for smaller streams (channel width <5 m) or 10 s for larger streams (channel width >5 m) as the observer traveled mid-channel upstream. This delineated each stream planform with a series of ~100–1500 positions (hereafter referred to as ''survey positions''). Two adjacent survey positions were normally separated by 5–10 m, depending on the speed of the observer wading in the stream. For the first-order streams, the field survey started at a downstream confluence with a second-order stream. For the second-order streams, the field survey started from a downstream boundary of Sakhalin taimen spawning grounds and covered a reach of up to several kilometers depending on the extent of the spawning grounds. When the observer came across Sakhalin taimen redds in the stream, he recorded their positions (''redd positions'') with the remote receiver. The survey positions and redd positions recorded in the field were later differentially corrected based on the base station data that had been constantly logged throughout the field survey. The differentially corrected data were displayed on the Universal Transverse Mercator coordinate system using Pathfinder Office

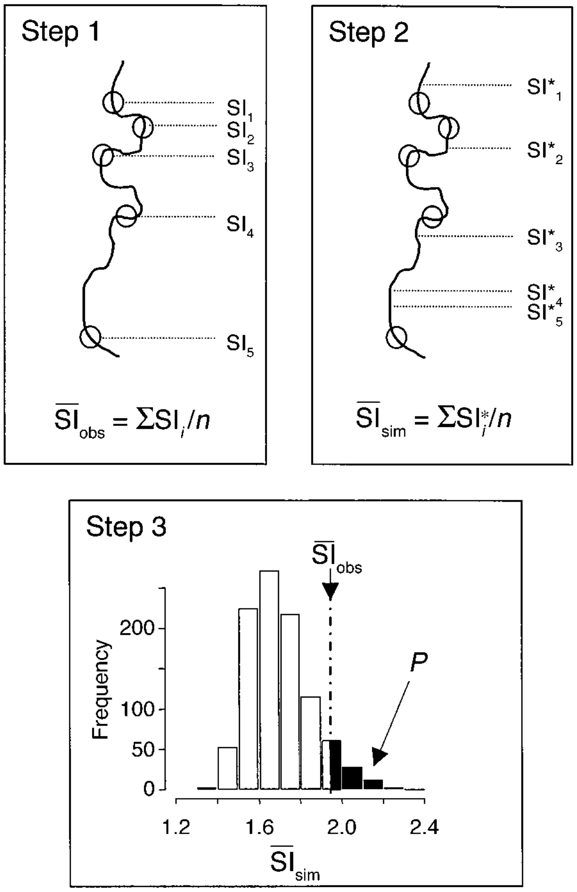

FIG. 2. Schematic diagram showing the procedure of the Monte Carlo test (see *Methods: Analyses of the relationship between channel sinuosity and redd locations* for the detailed explanation). $\overline{SI}$ = average channel sinuosity observed (obs) or simulated (sim). P = the proportion of $\overline{SI}_{sim}$ larger than $\overline{SI}_{obs}$ to the total number of replications (1000).

(Trimble 1995) for the analysis of channel geometry and spawning habitat selection by Sakhalin taimen.

Analyses of the relationship between channel sinuosity and redd locations

In the strict sense, the survey positions were distributed along the streams quasi systematically because of a fixed time interval for data logging, but I assumed these positions were randomly distributed because the number of the positions in each stream was sufficiently large. The redd positions, on the other hand, can be considered to be survey positions selected by spawning Sakhalin taimen either arbitrarily or preferentially.

A series of Monte Carlo tests were applied to the streams in cases where >10 redds were observed to test the habitat–sinuosity hypothesis. Data from streams where <10 redds were observed were not used for these analyses. The Monte Carlo test begins with calculating average channel sinuosity ($\overline{SI}_{obs}$) over all n redd positions observed in a given stream (Step 1, Fig. 2). Subsequently, another n positions were randomly chosen using a computer from all survey positions in the stream irrespective of the presence or absence of redds, and average channel sinuosity was again calculated ($\overline{SI}_{sim}$, Step 2). This procedure of random sampling was repeated 1000 times to produce a population distribution of $\overline{SI}_{sim}$ for that stream (Step 3). Then, the proportion of $\overline{SI}_{sim}$ larger than $\overline{SI}_{obs}$ to the total number of $\overline{SI}_{sim}$(i.e., 1000) was obtained, which ranges from 0 to 1. This proportion approaches to 0 as $\overline{SI}_{obs}$ becomes greater with respect to the simulated distribution of $\overline{SI}_{sim}$, thus representing the significance of the test.

Channel sinuosity was expressed with a sinuosity index, that is the length of a reach as measured along the midpoint of the channel divided by the straight-line distance between the two end points of the reach (Müller 1968). However, since this index varies depending on how far the two end points are separated along a channel (Ebisemiju 1994), the above Monte Carlo test was conducted independently by redefining the sinuosity index at three along-channel distances or distance increments. When calculating the sinuosity index, an upstream distance immediately above the selected position was measured (i.e., that position served as a downstream end point). Pools are typically located upstream from redds and whether these pools are formed through the process of channel bending or meandering is of the greatest interest.

To combine the Monte Carlo test results across all study streams, and to reach a general conclusion regarding the effect of channel sinuosity on fish spawning habitat, a meta-analysis was conducted. In this analysis, the log response ratio of $\overline{SI}_{obs}$ to the mean of 1000 $\overline{SI}_{sim}$ (hereafter denoted as $\overline{\overline{SI}}_{sim}$) was used as a measure of the effect (Hedges et al. 1999). The 95% confidence interval (CI) of the log response ratio was then calculated to see whether it overlapped with 0.

To examine the effect of the size and sinuosity of study streams on the morphology of redds, the following variables were measured to the nearest 10 cm for each redd and redd site: (1) the length of redd including a pit on its upstream perimeter and a mounded tailspill downstream; (2) the maximum width of redd; and (3) active channel width (Church 1992) at the redd site. Pearson product–moment correlation coefficients were calculated between each of these variables and the sinuosity index measured at 50-m increments above the redds.

RESULTS

Characteristics of study streams and Sakhalin taimen redds

A total stream distance of 59 km was surveyed in 17 first and second order tributaries of the Sarufutsu River. These surveys located a total of 309 Sakhalin taimen redds, giving an average redd density of 5.24/km. Individual redds were easily identified in the field because stream discharge was sufficiently low and no

TABLE 1. Summary of the study streams and the Sakhalin taimen redds observed in the Sarufutsu River system, 1998.

Stream	Distance surveyed (km)	Channel width (m)	Channel slope (%)	Redds (no.)	Redd density (*n*/km)
S1	2.38	2.6	0.75	16	6.7
S2	5.77	5.4	0.56	36	6.3
S3	2.31	4.2	0.64	31	13.4
S4	4.15	5.8	0.69	13	3.1
S5	4.06	3.9	0.62	18	4.4
S6	2.85	6.7	0.64	14	4.9
S7	4.41	5.9	0.75	31	7.0
S8	5.63	5.7	0.79	37	6.6
S9	5.31	8.3	0.38	30	5.7
S10	4.98	4.7	1.03	22	4.4
S11	2.86	3.6	0.81	16	5.6
S12	2.27	6.3	0.71	17	7.5

Note: Distance surveyed and channel slope were calculated from the DGPS data, while channel width is average active channel width measured at redd sites.

significant rain fell during the survey. Twelve streams contained >10 redds and, therefore, were subjected to further statistical analysis. These streams ranged in active channel width from 2.6 to 8.3 m, channel gradient from 0.38% to 1.03%, and Sakhalin taimen redd density from 3.1 to 13.4 per km (Table 1). The streams with steeper gradients and narrower channels were usually first order headwater streams, while those with gentler, wider channels were usually second order (Fig. 1). The DGPS data were fairly accurate with the 95% confidence interval for estimate error for the individual streams ranging from 0.9 to 1.4 m horizontally and from 1.1 to 1.5 m vertically.

Before evaluating the sinuosity–habitat relationship within streams, $\overline{\overline{SI}}_{sim}$ and the coefficient of variation of $\overline{SI}_{sim}$ were calculated at distance increments of 40, 60, 80, 100, 150, 200, and 250 m, by performing 1000 random samplings of *n* survey positions at each incremental distance, in order to characterize the planform geometry of each study stream (Fig. 3). In most streams, $\overline{\overline{SI}}_{sim}$ first increased rapidly, peaked at an incremental distance between 100 and 200 m, and then remained relatively constant. Larger streams such as S7, S8, S9, and S12, however, tended to have the peak of $\overline{\overline{SI}}_{sim}$ at longer incremental distance (>250 m). The coefficient of variation of $\overline{SI}_{sim}$, on the other hand, normally peaked at a slightly shorter distance (<100 m), and then decreased with an increasing distance increment.

The average size (±SD) of Sakhalin taimen redds was 227 ± 60 cm in length and 122 ± 42 cm in width. The redds tended to be longer and, to a lesser extent, wider in larger streams; i.e., redd length, redd width, and active channel width were positively correlated ($P < 0.001$, Table 2). However, neither the redd size nor channel width were correlated with the sinuosity index ($P > 0.05$).

Within-stream spawning habitat selection by Sakhalin taimen

The Monte Carlo test was conducted at the three incremental distances of 50, 100, and 200 m. $\overline{\overline{SI}}_{sim}$ was positively correlated with $\overline{SI}_{obs}$ regardless of the incremental distances ($r = 0.814$, $P < 0.01$ at 50 m; $r = 0.707$, $P < 0.05$ at 100 m; $r = 0.803$, $P < 0.01$ at 200 m). At 50-m increments $\overline{SI}_{obs}$ was slightly greater than the corresponding value of $\overline{\overline{SI}}_{sim}$ in all streams (Fig. 4A). At greater distance increments the values of $\overline{\overline{SI}}_{sim}$ and $\overline{SI}_{obs}$ became comparable, plotting around the replacement line of $\overline{SI}_{obs} = \overline{\overline{SI}}_{sim}$ (Fig. 4B, C). As a result, P values of the Monte Carlo test were <0.5 in all streams at 50-m increments, and tended to be smaller than the corresponding values at greater distance increments (Table 3). However, $\overline{SI}_{obs}$ was significantly larger than $\overline{\overline{SI}}_{sim}$ in only two streams (S2 and S5) for the 50-m increment ($P < 0.05$). The difference was significant only in one stream (S5) for the 100-m increment, and there were no significant differences for the 200-m increment ($P > 0.05$).

Meta-analysis concluded collectively that channel sinuosity above Sakhalin taimen redds was indeed significantly greater than the average sinuosity of streams at the 50-m increments but not significant at the 100- and 200-m increments (Fig. 5). The 95 % CI was farther apart from zero at the 50-m increment than at the 100- and 200-m increments. Reaches of 50 m upstream from redds probably needed to be particularly more sinuous or needed to have habitat associated with higher channel sinuosity for a female Sakhalin taimen when deciding spawning sites. The DGPS data of S5, for which the *P*-value at the 50-m increment was the smallest, illustrate that Sakhalin taimen redds tended to be constructed in highly sinuous reaches (Fig. 6).

DISCUSSION

This study showed Sakhalin taimen preferred to spawn at sites above which stream reaches have higher than average sinuosity for that stream. This connection between channel planform and salmonid spawning habitat selection accounts for previous observations that salmonids typically construct redds at similar locations along streams from year to year (Hoopes 1972, Fukushima 1994, Fukushima and Smoker 1998). If spawning habitat selection were based on or strongly influenced by other factors such as weather, water temperature, or species interactions, the spatial distribution of redds would be more variable between years.

The Sakhalin taimen preference for spawning sites located below highly sinuous reaches was detected when the sinuosity index was calculated at a 50-m increment but was not statistically significant at 100- and 200-m increments. The small low-gradient streams included in this study usually contained at least one or two pools within a 50-m reach; whereas, a 100- to 200-m reach usually contained more than several pools and

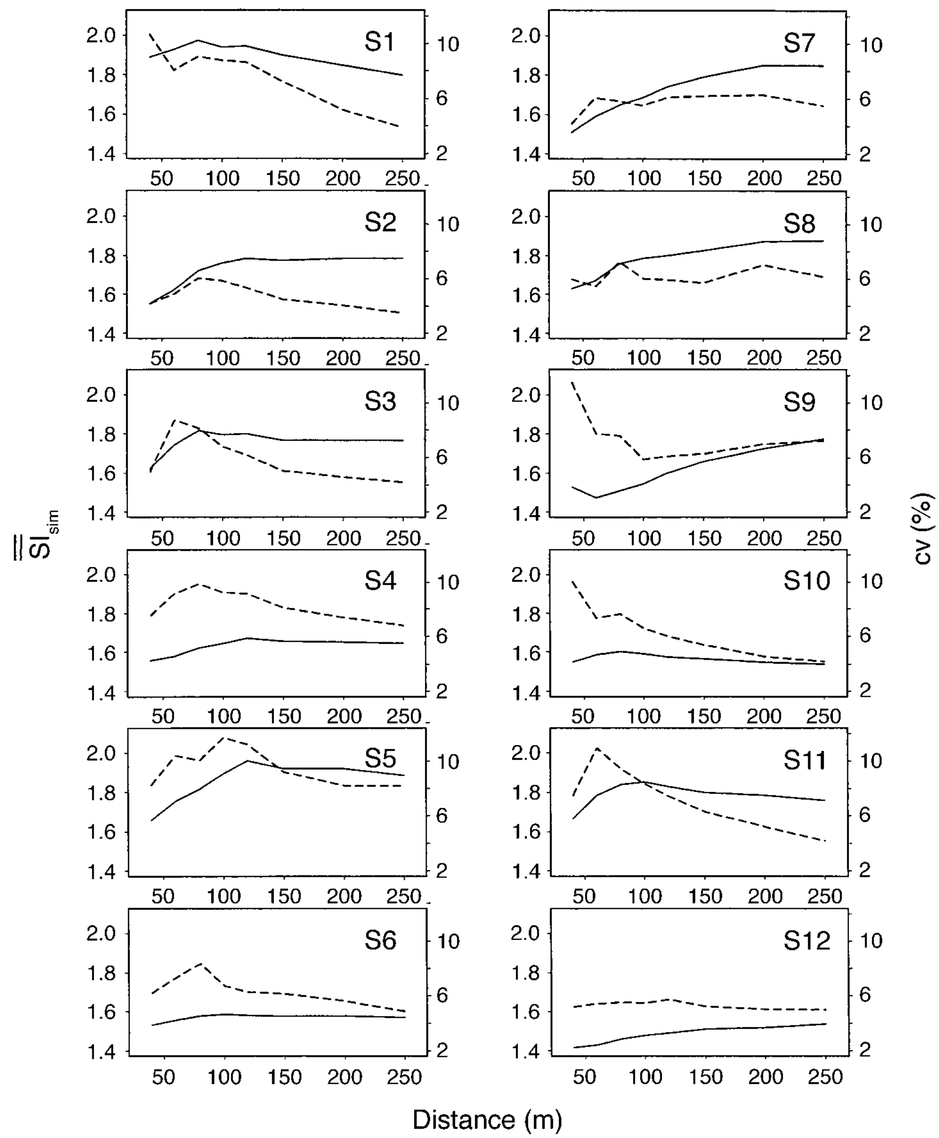

FIG. 3. The mean of 1000 $\overline{SI}_{sim}$ ($\overline{\overline{SI}}_{sim}$, solid line) and the coefficient of variation (CV) of $\overline{SI}_{sim}$ (broken line) calculated at the incremental distances of 40, 60, 80, 100, 150, 200, and 250 m.

riffles (Beschta and Platts 1986, Lisle 1986, Heede and Rinne 1990). At short distance increments, which may only contain one or two stream bends, the value of the sinuosity index rapidly increases as the distance between two end points increases (Fig. 3). However, when the distance increment exceeds 100 or 200 m and includes several bends, this index asymptotically approaches its maximum for that stream. At the same time, the index becomes less sensitive to where it is calculated along a stream, as indicated by the declining

TABLE 2. Pearson product-moment correlation coefficients (sample sizes in parentheses) between redd length, redd width, active channel width, and 50-m sinuosity index.

Variable	Redd length	Redd width	Channel width
Redd width	0.580 (313)***		
Channel width	0.356 (315)***	0.222 (323)***	
Sinuosity index	−0.017 (235)	−0.037 (238)	−0.102 (243)

Note: Redds were measured in a total of 17 tributaries including the 12 streams listed in Table 1.
*** $P < 0.001$.

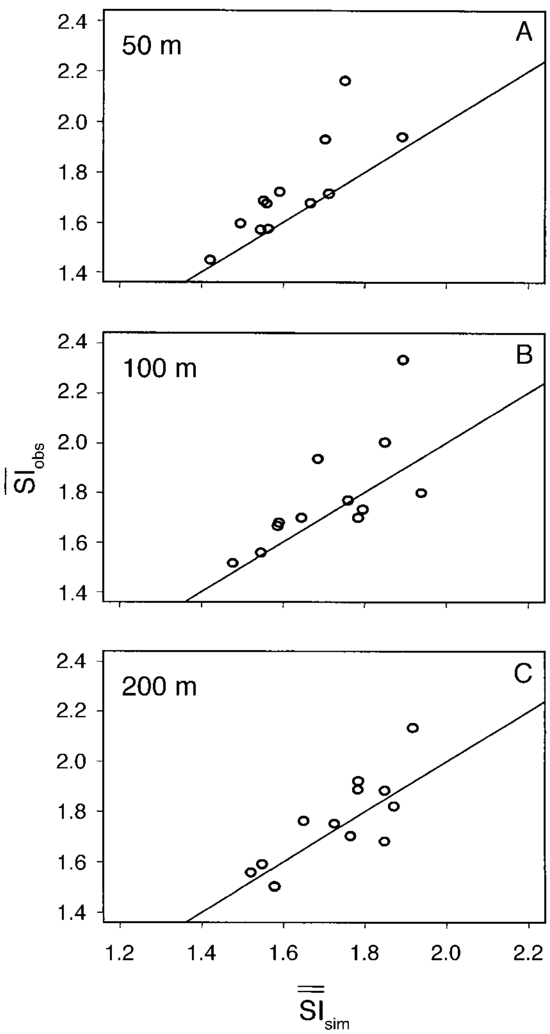

FIG. 4. The relationship between the mean of 1000 $\overline{SI}_{sim}$ ($\overline{\overline{SI}}_{sim}$) and the mean channel sinuosity measured at redd positions ($\overline{SI}_{obs}$) at the incremental distances of 50, 100, and 200 m. A replacement line of $\overline{SI}_{obs}$ = $\overline{\overline{SI}}_{sim}$ is also shown in each panel.

TABLE 3. *P* values of the Monte Carlo test for the equality of sinuosity index calculated at redd positions and that calculated at randomly chosen survey positions. The sinuosity index was defined at three incremental distances.

	Incremental distances		
Stream	50 m	100 m	200 m
S1	0.350	0.802	0.968
S2	0.047	0.434	0.068
S3	0.442	0.677	0.780
S4	0.149	0.320	0.177
S5	0.016	0.037	0.081
S6	0.349	0.209	0.811
S7	0.400	0.009	0.356
S8	0.412	0.790	0.605
S9	0.146	0.414	0.359
S10	0.144	0.182	0.262
S11	0.082	0.154	0.079
S12	0.337	0.294	0.288

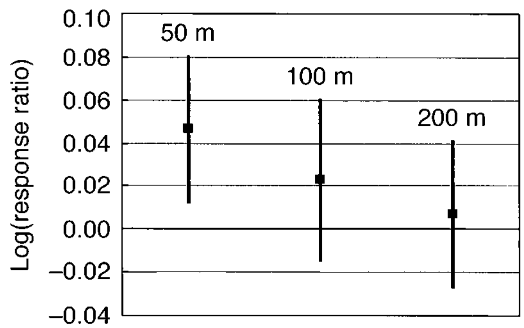

FIG. 5. Meta-analyses on the selectivity of highly sinuous stream reaches by spawning Sakhalin taimen. The 95% confidence intervals of the log response ratio, $\ln(\overline{SI}_{obs}:\overline{\overline{SI}}_{sim})$, are shown for the incremental distances of 50, 100, and 200 m.

coefficients of variation of $\overline{SI}_{sim}$. As a result, important local variations in sinuosity to spawning Sakhalin taimen were likely to be masked and evened out at spatial scales >100 m.

It is important to realize that the actual mechanism underlying the relationship between channel sinuosity and spawning habitat is the formation of a pool–riffle sequence that creates the hydraulic and substrate conditions suitable for egg deposition by salmonids (Adams and Beschta 1980, Vronskii and Leman 1991, Wilcock and Essery 1991). In the pool to riffle transitional

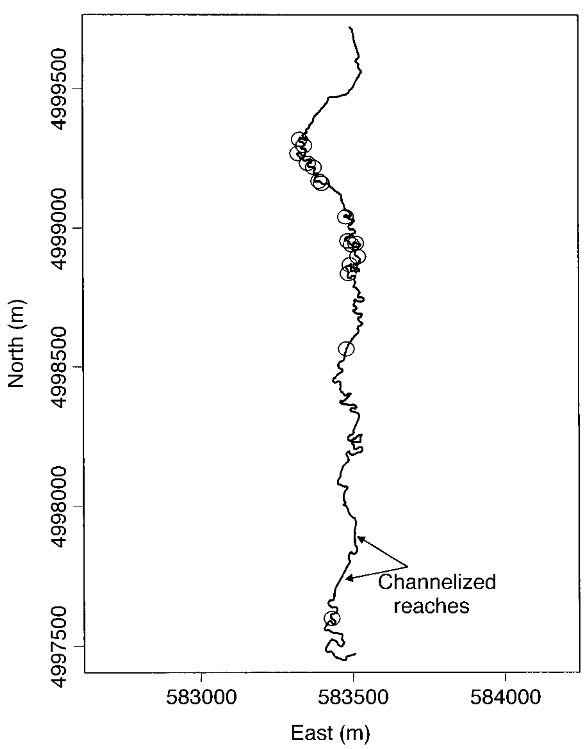

FIG. 6. DGPS data for S5 showing its channel planform and the locations of Sakhalin taimen redds indicated by circles. The data are displayed on the Universal Transverse Mercator coordinate system.

zone, stream water generally permeates into the gravel with its flow rate maximized at the riffle crest exactly where salmonids, including Sakhalin taimen, commonly deposit their eggs (Vaux 1968, Vronskii and Leman 1991). Seepage water through the interstices of gravel provides oxygen to developing embryos and removes waste materials from the vicinity of eggs and alevins in the gravel (McNeil 1969). Therefore, it is a pool–riffle sequence and not simply a sinuous or meandering channel that is the true measure of salmonid spawning habitat quality. Although this study showed that Sakhalin taimen redds tended to be longer and larger in larger streams, areas available to their spawning are dependent more importantly on the frequency of pools and riffles in a stream.

The DGPS data of redd and survey positions from all study streams cannot be pooled and analyzed by a single Monte Carlo test by assuming random habitat selection among the streams. This is because different streams might have subpopulations of Sakhalin taimen that were destined to migrate into specific streams where they had been imprinted, as is the case in many salmonid populations (Armstrong 1974, Quinn and Fresh 1984, Burger et al. 1985, Heggberget et al. 1988, Halvorsen and Stabell 1990). In fact, there were no significant correlations between the Sakhalin taimen redd densities and average stream sinuosity indices in the 17 study streams at any distance increments between 10 and 250 m ($P > 0.05$).

Although the overall effect of 50-m channel sinuosity on spawning habitat selection was found to be significant by meta-analysis, the number of streams where this effect was detected by individual Monte Carlo tests was rather small. I believe the following three characteristics of the study streams can account for this inconsistency. Firstly, the study streams flow through pristine environments, and no human activities have altered original channel geomorphology except in S5 where two reaches of ~100- and 200-m in length were channelized (Fig. 6). The average sinuosity of the study streams was typically >1.5 (Fig. 4), above which streams are classified as meandering (Schumm 1963). Sinuous channels with highly repetitive pool–riffle sequences were apparently not in short supply for spawning Sakhalin taimen. As a result, the *P*-values of Monte Carlo tests were raised higher than they would otherwise be if the streams were moderately channelized or contained more straight reaches. In fact, the *P*-value at the 50-m incremental was most significant in S5, a tributary with a moderate number of straight reaches (Table 3). Secondly, the numbers of redds observed in the study streams were very small, resulting in more variable $\overline{SI}_{sim}$, longer tails for its simulated population distribution, and thus larger *P*-values.

Thirdly and most importantly, another factor besides channel sinuosity played a significant role in creating pool–riffle sequences in the study streams; that is large woody debris (LWD). LWD is often the most important pool-forming agent in small systems and performs a variety of functions essential to stream fish communities (Bisson et al. 1987, Beechie and Sibley 1997, Cederholm et al. 1997, Bilby and Bisson 1998). Although no quantitative data on the abundance of LWD were obtained in the Sarufutsu River system, a considerable proportion of the pools in this system appeared to be formed by LWD. This may have lowered $\overline{SI}_{obs}$ and again increased the *P*-values of Monte Carlo tests because LWD creates pools even in straight reaches and allows fish to spawn in these reaches (Bisson et al. 1987). However, considering the fact that in low gradient meandering streams, bank failure caused by channel bending is the most common process delivering LWD to streams (Keller and Swanson 1979), high channel sinuosity and abundant LWD are probably not independent phenomena. In summary, preference for highly sinuous reaches by spawning salmonids will be better manifested in streams with moderately and not greatly sinuous channels with less abundant LWD, and will be detected more clearly when spawner density is high.

Acknowledgments

I would like to thank Seiichi Nohara, Goichiro Takahashi, and Mike Brett for their comments on earlier drafts of the manuscript. I also thank Kenichi Suzuki and students of Hokkaido University for the assistance in the field. This research benefited from the advice and counsel of Yugo Ono who first pointed out the hypothesis tested in this paper.

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