Journal of Fish Biology (2000) **56,** 890–904
doi:10.1006/jfbi.1999.1207, available online at http://www.idealibrary.com on IDEAL®

The structure and dimensions of redds and egg pockets of the endangered salmonid, Sakhalin taimen

K. Edo*‡, H. Kawamula† and S. Higashi*

**Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan and †Hokkaido Fish Hatchery, Eniwa 061-1433, Japan*

(*Received 8 July 1999, Accepted 6 December 1999*)

Each redd of the Sakhalin taimen *Hucho perryi* had a V-shaped pot that is specific to this species. The shape of each multiple-egg-pocket redd was a combination of one-egg-pocket redds, and the number of egg pockets in the redd could be estimated from the shape. False redds were small and did not have any V-shaped pots. The factors affecting redd size were examined numerically; consequently, numbers of egg pockets and eggs and female fork length were correlated significantly with tail length. Each egg pocket contained 11–920 eggs (mean: 546·7 ± 95% CL 81·9) and the egg pocket depth was correlated significantly with female fork length. Mean number of redds per female was three, and the number of females could be estimated as one third of the redds.

Key words: *Hucho perryi*; Sakhalin taimen; redd structure; egg pocket; population structure.

INTRODUCTION

In salmonid fish consisting of four genera, the genus *Hucho* shows some unique characters. They are iteroparous and reproductive up to about 16 years of age with large body size occasionally reaching *c.* 60 kg (Berg, 1962; Khatkevich, 1973; Gritsenko *et al.*, 1974). It has also been suggested that females of this genus construct multiple redds (Holčík *et al.*, 1988; Fukushima, 1994). This genus is composed of five species which are distributed in Eurasia. The Sakhalin taimen *Hucho perryi* (Brevoort) is characterized by the small number of lateral line scales (Kimura, 1966) and restrictedly distributed in far north-east Asia including the northernmost island of Japan, Hokkaido. Unlike the other four species which are strictly resident in freshwater without migrating to the sea, a few Sakhalin taimen have been collected in inshore waters (Kawamula *et al.*, 1983), suggesting that this species is mostly resident in fresh water but partly anadromous. However, even the anadromous form is often land-locked by artificial dams and obliged to spend the non-breeding period in freshwater lakes. Especially in Japan this species is now very rare, seriously endangered and close to extinction (The Environment Agency, 1991). As the Sakhalin taimen is unique ecologically and phylogenetically and very important from the viewpoint of conservation biology, more ecological study of this species is needed.

Adequate management of rare and endangered species requires knowledge of their population structure, without disturbing them. In particular, the number of spawners and subsequent recruits are the most important numerical information (Beland, 1996), and, in the stock–recruitment relationships, redds are

‡Author to whom correspondence should be addressed. Tel.: +81-11-706-2251; fax: +81-11-706-4867; email: edo@ees.hokudai.ac.jp

0022–1112/00/040890+15 $35.00/0

considered to be the core. For example, significant correlations between redd counts and number of spawners or parr have been reported in some salmonid species (Hobbs, 1937; Benson, 1953; Heggberget *et al.*, 1986; Beard & Carline, 1991; Madden *et al.*, 1993; Semple *et al.*, 1994; Beland, 1996; but see Ottaway *et al.*, 1981).

In the present study, the physical structure of the Sakhalin taimen's redd was investigated in detail and attempts were made to establish the method for estimating available parameters such as female size and numbers of females, egg pockets and eggs from the number, shape and size of redds. Those parameters will be useful for the studies of population structure of this endangered rare species.

STUDY AREA

This study was conducted in 1995 and 1996 in the Koyanosawa stream which is an upstream tributary of the Shiisorapuchi River (The Ishikari River system) draining into the Kanayama Dam Lake in central Hokkaido, northern Japan (Fig. 1). This is a second-order stream and is situated at *c.* 460 m altitude and runs through a mixed conifer and deciduous forest, with drainage area of 7·81 km^2 and gradient of *c.* 1·2% (estimated from a map). The channel bed comprises mainly gravel and stones, with small areas of sand and bedrock. The riparian zone is vegetated by willows *Salix* spp., alder *Alnus hirsuta* (Turcz.), Japanese elm *Ulmus davidiana* var. *japonica* (Nakai), etc. This creek is also inhabited by Dolly Varden *Salvelinus malma* (Walbaum), white-spotted charr *S. leucomaenis* (Pallas), freshwater sculpin *Cottus nozawae* (Snyder), brook lamprey *Lampetra reissneri* (Dybowski) and loach *Barbatula barbatula toni* (L.). In 1995, mean monthly air temperature was − 8·2° C in January and 19·4° C in July, and the annual precipitation was 1215 mm with much snow in winter.

Although this stream is >4 km long, further migration of Sakhalin taimen is interrupted by an artificial obstacle at *c.* 3 km upstream from the confluence with the Shiisorapuchi River (Fig. 1). The stream was *c.* 3–5 m wide and 1 m deep at maximum.

A population of Sakhalin taimen is sustained in the Kanayama Dam Lake, and, in the mating season, the adult males and females migrate to the upstream tributaries. Although this migration season depends somewhat on the process of snow thawing, it usually occurs in May when the tributaries are deep and the water temperature is 6–7° C. After the adults finish spawning, they return to the Kanayama Dam Lake.

METHODS

From 4 to 15 May 1995, observers walked daily along the riverside and, whenever a redd was discovered, described its position and shape. Redds were readily discerned by a change in the texture and patina of the bed surface, and composed of a depression in the gravel, termed ' pot ' lying at the head of a slightly raised area of gravel, the ' tail ' (Ottaway *et al.*, 1981). Within 2 days after the spawning season had finished on 15 May, the size of redds was recorded by measuring total length, pot length, tail length and tail width (Fig. 2). According to Ottaway *et al.* (1981), tail area was also calculated as 0·25 $\pi L W$ where L and W were length and width of a tail, respectively. Overall, totals of 42

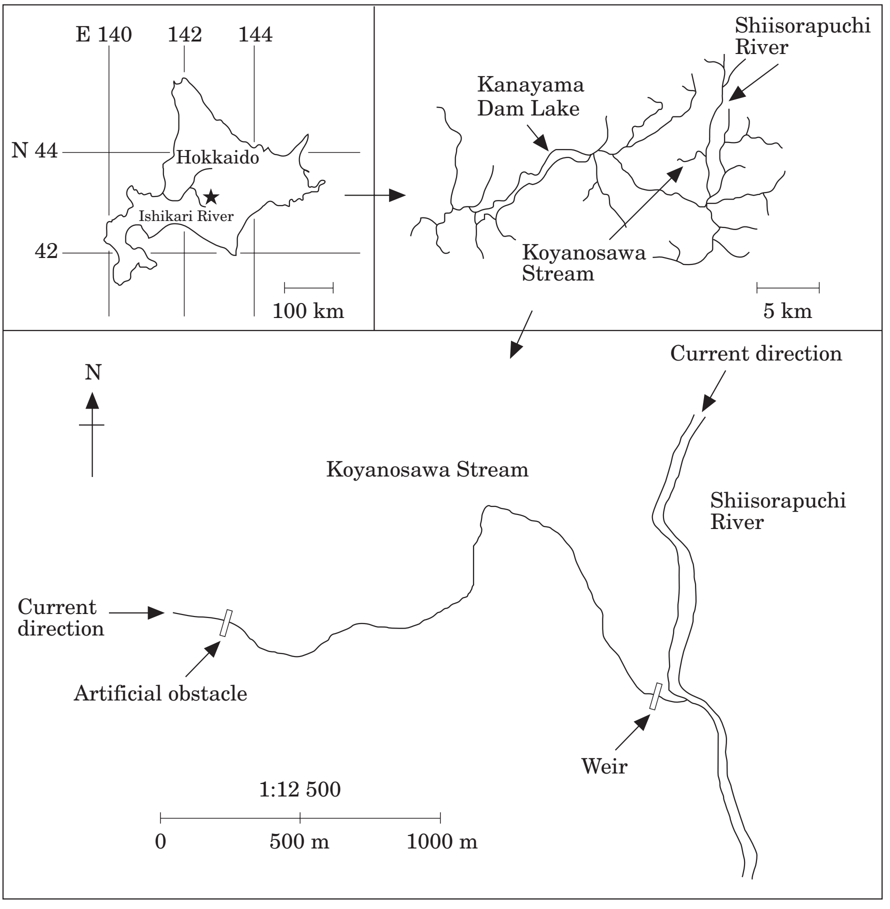

FIG. 1. Location of Koyanosawa Stream.

redds and 22 false redds were described in 1995 (see results about the discrimination between redds and false redds). Of these, three redds were superimposed on others (superimposition rate 7·14%), and therefore the size of three previously made redds could not be recorded.

In 1996, a weir was set up on 9 May at the lower end of Koyanosawa stream to capture all the Sakhalin taimen which had migrated to this stream for spawning. When a female was caught, her individual characteristics such as scars, body size and nuptial coloration were described visually. After release to the creek by opening the front part of the weir without touching her body, each female was followed daily carefully to identify her redd site. Since Sakhalin taimen spawned on glides or riffles where the water depth was only *c.* 20–30 cm (unpubl. data) and spent at least 2 h to finish spawning on each redd site, the observation of spawning behaviour and identification with each female could be conducted with no difficulties. Whenever a female constructed her redd, the venue was marked and the shape of the redd was described. Since females moved downstream after they finished spawning, they were captured and anaesthetized to measure their fork length.

Within 2 days after the spawning season had finished on 26 May, the size of redds and false redds were recorded in the manner of 1995, and at the same time, current velocity and substratum were also recorded at each redd. The current velocity was measured at *m* point [Fig. 2(a)] 5 cm above the substratum using a portable current metre (Tanida *et al.*, 1985). For the description of the substratum, a quadrat of 50 × 50 cm was chosen

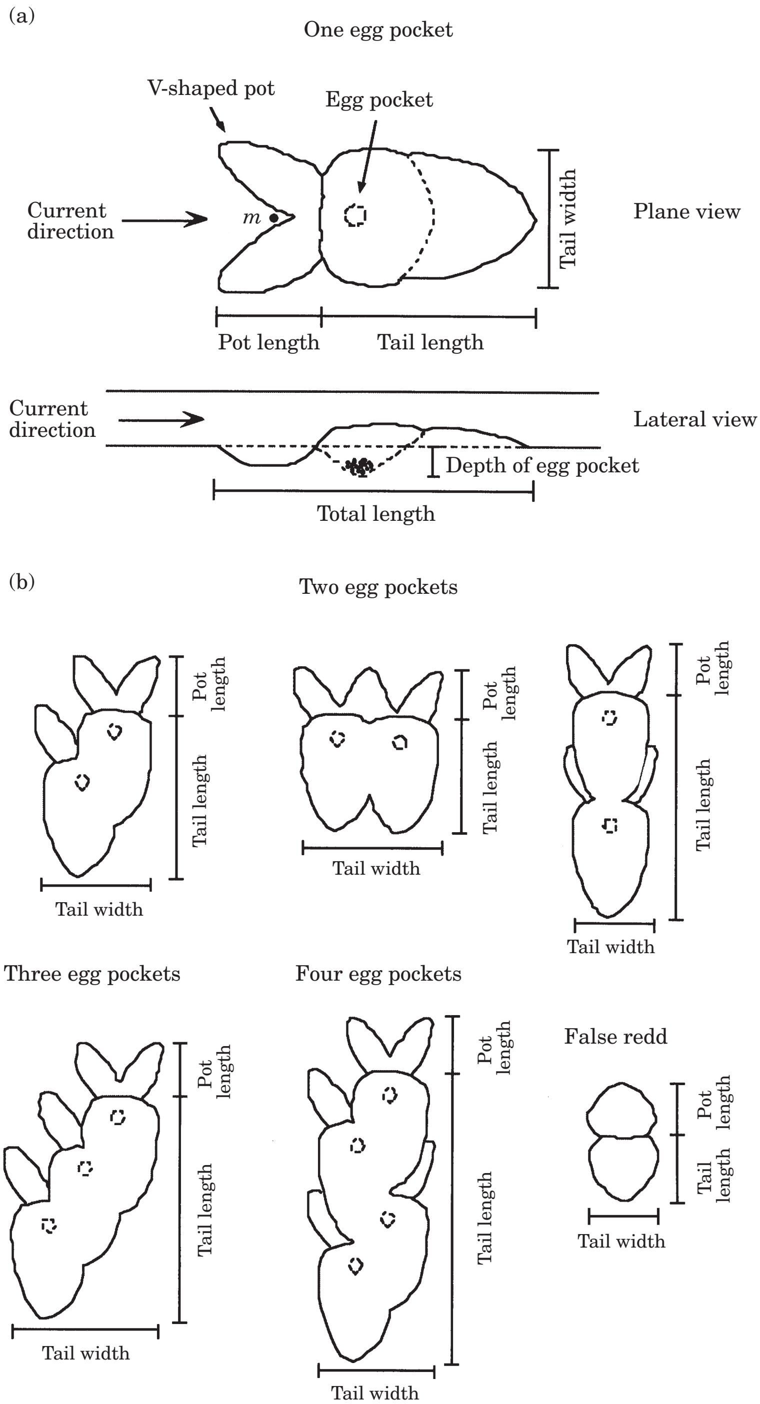

FIG. 2. Shape variation of redds with various numbers of egg pockets. The current velocity was measured at point *m* of V-shaped pot.

on the undisturbed bed surface adjacent to the upstream part of each redd tail. The gravel within the quadrat was classified into the following four grades: I, dominated by *c.* 3 cm diameter gravel particles with many sand grains: II, diameter *c.* 3 cm with few sand grains; III, diameter *c.* 3–5 cm; IV, diameter *c.* 5 cm or more. The number of each grade was used as a score for the substratum in the statistical analysis.

In mid- to late June when the eggs were eyed and therefore tolerant to physical shocks, all the redds were excavated to determine the location of egg pockets within the redd, number of egg pockets per redd, egg pocket depth and number of eggs per pocket. Since the eggs of Sakhalin taimen are eyed when the accumulated water temperature reaches *c.* 200° C-days (Kawamula *et al.*, 1996), the eyeing time was determined by scanning daily water temperatures in mid-water using the thermistor connected to a data logger (Optic StowAway and Optic Shuttle, Onset Inc.) at 10-min intervals. The redd was excavated manually (Fukushima, 1994; Elliott, 1995; Knapp & Vredenburg, 1996) upstream from the end of tail gently while watching the stream bed through a glass box. In this excavation, the eggs were drifted carefully little by little and collected in a downstream net of mesh size 3 mm. Since in this season the water depth of each redd site was *c.* <20 cm and the current velocity was so gentle (<one-half of that of the breeding period), the excavation of redds could be conducted with no difficulties and almost all eggs were removed. If some eggs floated out of the net, the number of them could be counted because of the small number of drifting eggs and gentle current velocity. The egg pocket was located at a point where an aggregation of eggs was discovered. The depth of the egg pocket was represented by the distance between the bed level and the deepest point of the pocket. Because the excavation process was always monitored, eggs that fell to a lower position during excavation could be distinguished from eggs that stayed where they had been deposited. After the number of eggs per pocket was counted in the laboratory, all the eggs were returned to their natal redds for the conservation of this rare fish species. The emergence of many juvenile taimens was observed in this creek in late July to August. Overall, totals of 18 redds and five false redds were constructed in 1996. Of these, two redds were superimposed on others (superimposition rate 11·2%), and therefore the size of the two earlier redds could not be recorded.

RESULTS

SHAPE, SIZE AND NUMBER OF REDDS

In 1996, each female made two to four redds with an average of three redds, and a total of five false redds and 16 true redds was recorded: seven with one egg pocket, six with two egg pockets, two with three egg pockets and one with four egg pockets. The fundamental shape of a redd was given by a redd with only one egg pocket [Fig. 2(a)]. Each redd could be divided into two parts, tail and V-shaped pot that is specific to this species. The egg pocket was 14–27 cm deep (mean 19·1 ± 95% CL 1·2, n=32) and always located at a forward point of the tail, containing 11–920 eggs (mean 546·7 ± 95% CL 81·9, n=32). This point was also an intersection of the two arms of the V-shaped pot excavated to supply the gravel for covering the egg pockets. The shape of other redds was a variation or combination of this fundamental shape [Fig. 2(b)]. A false redd with no egg pocket did not have the V-shaped pot. True redds with multiple egg pockets were a combination of the fundamental shape, indicating that the number of egg pockets per redd could be estimated from the redd shape, especially from the number of arms of V-shaped pots. On the basis of observation in 1996, the number of egg pockets was estimated for each of 61 redds recorded in 1995: 22 false redds with no egg pocket, 19 with one egg pocket, 13 with two egg pockets and seven with three egg pockets.

TABLE I. Correlations among five dimensions of redds; the correlations above and below the diagonal are the values of 1995 and 1996, respectively

	Total length	Pot length	Tail length	Tail width	Tail area
				1995 (n=39)	
Total length		0·57**	0·94***	0·47**	0·70***
Pot length	0·44		0·26	0·19	0·23
Tail length	0·98***	0·24		0·47**	0·72***
Tail width	0·49	0·22	0·48		0·95***
Tail area	0·79**	0·26	0·79***	0·90***	
		1996 (n=16)			

*P<0·05; **P<0·001; ***P<0·0001.

In both 1995 and 1996, pot length was almost independent of redd size dimensions, i.e. total length, tail length, tail width and tail area; while tail area was significantly correlated with the size dimensions other than pot length (Table I). In 1995 when the sample size was larger than in 1996, the correlation (0·47) between tail length and tail width was significant and total length was significantly correlated with all size dimensions.

In both years, the differences among redds with one, two and three egg pockets (Table II) were not significant in pot length but significant in total length, tail length, tail width and tail area, and multiple comparison tests (Scheffe's method) detected that tail area was significantly different among the three groups of redds (Table II). In 1995, the tail width was also significantly different among the three types of redds. False redds were small in all of the five dimensions. Discriminant analysis (jackknife classification) detected that they were discriminated from redds at a level of 96·15% in 1995 and 90·65% in 1996 by using pot length, tail length and tail width (Table III).

FACTORS AFFECTING REDD SIZE DIMENSIONS

For 16 redds excavated in 1996, current velocity (mean 51·1 ± 95% CL 6·2 cm s^{-1}), substratum (2·3 ± 0·3), number of egg pockets (1·8 ± 0·4), number of eggs (1013·3 ± 360·8) and female fork length (75·8 ± 7·4 cm) were chosen to reveal the environmental or biological factors affecting each redd size dimension. Pot length was not significantly correlated with any factors (Table IV). Other dimensions showed a significant correlation with numbers of egg pockets and eggs. The redd tail length showed the highest correlation with number of eggs (r=0·78, P<0·001) and seemed useful for estimating number of eggs using a simple regression line $y=11{\cdot}372\,x-955{\cdot}498$ [Fig. 3(a)]. In addition to number of eggs, tail length was also significantly correlated with female fork length (r=0·86, P<0·05). This suggests that redd tail length is useful for estimating not only number of eggs but also female size. The simple regression line was $y=0{\cdot}217\,x+37{\cdot}048$ between redd tail length (x) and female fork length (y) [Fig. 3(b)].

FACTORS AFFECTING THE DEPTH OF EGG POCKETS

For each egg pocket excavated in 1996, its depth, female fork length, current velocity and substratum were described. The depth of egg pocket did not show

TABLE II. Size of redds and false redds

Dimensions	Redd (1995)					ANOVA results		False redd (1995)
	One egg pocket (n=19)	Two egg pockets (n=13)	Three egg pockets (n=7)	Four egg pockets (n=0)	Total (n=39)	F	P	(n=22)
Total length (cm)	185·3 ± 10·3a (140 ~ 240)	244·2 ± 27·4b (180 ~ 345)	255·0 ± 23·2b (200 ~ 285)	—	217·4 ± 14·8 (140 ~ 345)	15·26	<0·0001	110·2 ± 5·8 (90 ~ 155)
Pot length (cm)	52·4 ± 6·8 (20 ~ 85)	58·1 ± 6·6 (40 ~ 80)	61·4 ± 17·9 (30 ~ 95)	—	55·9 ± 5·1 (20 ~ 95)	0·98	NS	43·4 ± 2·8 (35 ~ 55)
Tail length (cm)	132·9 ± 7·6a (105 ~ 180)	186·2 ± 24·5b (120 ~ 285)	193·6 ± 12·0b (170 ~ 215)	—	161·5 ± 12·7 (105 ~ 285)	17·70	<0·0001	66·8 ± 5·1 (50 ~ 110)
Tail width (cm)	72·6 ± 5·5a (50 ~ 90)	98·8 ± 13·7b (65 ~ 140)	166·4 ± 17·7c (130 ~ 195)	—	98·2 ± 12·3 (50 ~ 195)	58·66	<0·0001	41·8 ± 2·9 (35 ~ 55)
Tail area (cm^2)	7622·5 ± 761·7a (4123·3 ~ 9896·0)	14 341·1 ± 2423·9b (7912·9 ~ 20 891·6)	25 298·2 ± 3065·6c (19 399·3 ~ 28 706·3)	—	13 034·6 ± 2290·8 (4123·3 ~ 28 706·3)	74·73	<0·0001	2225·0 ± 309·5 (1511·9 ~ 4751·7)
	Redd (1996)					ANOVA results		False redd (1996)
	(n=7)	(n=6)	(n=2)	(n=1)	(n=16)	F	P	(n=5)
Total length (cm)	190·7 ± 14·3a (175 ~ 225)	240·8 ± 36·1ab (180 ~ 310)	272·5 ± 24·5b (260 ~ 285)	360	230·3 ± 26·8 (175 ~ 360)	6·65	<0·05	115·0 ± 17·5 (85 ~ 140)
Pot length (cm)	54·3 ± 9·4 (35 ~ 70)	57·5 ± 10·7 (40 ~ 75)	65·0 ± 19·6 (55 ~ 75)	60	57·2 ± 6·0 (35 ~ 75)	0·53	NS	45·0 ± 5·4 (35 ~ 50)
Tail length (cm)	136·4 ± 12·0a (115 ~ 165)	183·3 ± 32·0b (130 ~ 250)	207·5 ± 4·9b (205 ~ 210)	300	173·1 ± 24·7 (115 ~ 300)	7·10	<0·01	70·0 ± 12·8 (50 ~ 90)
Tail width (cm)	75·0 ± 7·4a (65 ~ 90)	100·0 ± 17·7a (75 ~ 130)	180·0 ± 29·4b (165 ~ 195)	130	100·9 ± 18·6 (65 ~ 195)	29·42	<0·0001	45·0 ± 6·2 (35 ~ 50)
Tail area (cm^2)	8103·6 ± 1332·3a (5870·9 ~ 10 367·3)	14 052·1 ± 2125·0b (10 720·7 ~ 17 357·3)	29 305·2 ± 4098·5c (27 214·0 ~ 31 396·3)	30 630·5	14 392·4 ± 4098·4 (5870·9 ~ 31 396·3)	66·68	<0·0001	2529·0 ± 733·7 (1374·4 ~ 3534·3)

Data are mean ± 95% CL and range (in parentheses). Results of one-way ANOVA and multiple comparison test (Scheffe's method) testing for differences among redds with one, two and three egg pockets are also shown. Significant differences by multiple comparison test are denoted by the letters a, b and c; data denoted by the same letter are not significantly different (P>0·05).

TABLE III. Results of discriminant analysis (jackknife classification) on the size difference between redds and false redds; three dimensions (pot length, tail length and tail width) were used as independent variables

Year	Groups	No. of cases	Classification results	
			Correct	False
1995	False redds	22	22 100%	0 0%
	Redds	39	36 92·3%	3 7·7%
	Pooled	61	96·15%	3·85%
1996	False redds	5	5 100%	0 0%
	Redds	16	13 81·3%	3 18·8%
	Pooled	21	90·65%	9·35%

TABLE IV. Correlation between redd dimensions and environmental or biological factors

Dimensions of redd (n=16)	Environmental or biological factors				Female fork length† (n=6)
	Current velocity†	Substratum‡	No. of egg pockets‡	No. of eggs†	
Total length	−0·07	0·21	0·77*	0·73**	0·78
Pot length	−0·39	−0·03	0·23	0·04	0·25
Tail length	0·02	0·38	0·79*	0·78**	0·86*
Tail width	0·1	0·74	0·79*	0·54*	0·48
Tail area	0·01	0·21	0·93*	0·77**	0·65

In the correlation between redd dimensions and female fork length, the mean size of each redd dimension was calculated for each female to avoid pseudo-replication.
†Pearson's correlation coefficient (r); ‡Spearman's rank correlation coefficient (ρ).
*$P<0·05$; **$P<0·001$.

any significant correlations with current velocity ($r=-0·09$, $P>0·05$) and substratum ($\rho=0·025$, $P>0·05$), but show significant correlation with female fork length ($r=0·85$, $P<0·05$) with the simple regression line $y=2·809\,x+23·473$ where y and x are female fork length and egg pocket depth, respectively (Fig. 4).

DISCUSSION

Female semelparous salmonids spawn in a single redd which contains multiple egg pockets (Foerster, 1968; Hawke, 1978; van den Berghe & Gross, 1984). She protects her redd from other females who attempt to superimpose their own redds on her redd (Burner, 1951; Briggs, 1953; McNeil, 1962; Hanson & Smith, 1967; Schroder, 1973; Keenleyside & Dupuis, 1988; Noltie, 1990). Even in some

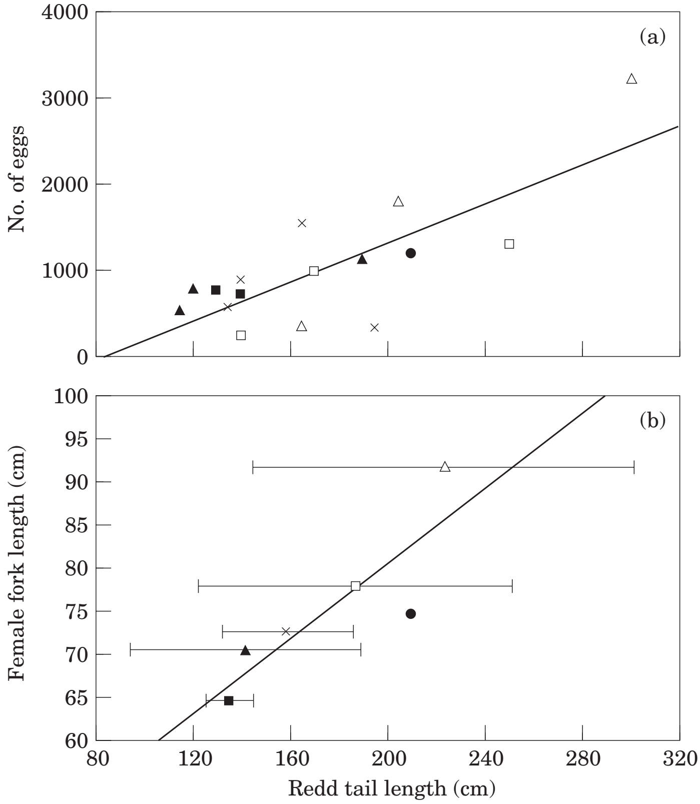

FIG. 3. Regression lines to estimate number of eggs and female fork length from the redd tail length. Six females were followed in 1996 and each point with 95% CL shows values from the same individual. (a) $y=11{\cdot}372x-955{\cdot}498$; $r=0{\cdot}78$; $n=16$; $P<0{\cdot}001$. (b) $y=0{\cdot}217x+37{\cdot}048$; $r=0{\cdot}86$; $n=6$; $P<0{\cdot}05$.

iteroparous species such as brown trout *Salmo trutta* L., Atlantic salmon *Salmo salar* L., Miyabe charr *Salvelinus malma miyabei* (Walbaum) and Dolly Varden, most females construct a single redd containing multiple egg pockets (Elliott, 1984; Crisp & Carling, 1989; Maekawa & Hino, 1990; Kitano, 1995). In those single-redd species it has been almost impossible to locate the position of egg pockets or to estimate the number of egg pockets from the shape and size of redd without excavating it (Chapman, 1988; Young *et al.*, 1989; Grost *et al.*, 1991). Unlike those species which cover the egg pockets by supplying gravel and sand from various upstream directions in the same manner of digging behaviour (McCart, 1967; Foerster, 1968; Tautz & Groot, 1975; van den Berghe & Gross, 1984), the Sakhalin taimen covers its egg pockets by supplying gravel and sand from only two upstream directions, consequently forming a V-shaped pot which is useful for estimating the location and number of egg pockets.

The ratio of false redds is 54% in coho salmon *Oncorhynchus kisutch* (Walbaum), 68% in chinook salmon *O. tshawytscha* (Walbaum) (Briggs, 1953), 18% in brown trout (Hardy, 1963), 42% in Atlantic salmon and 63% in brown trout (Barlaup *et al.*, 1994), and the high occurrence of false redds can lead to a substantial overestimation of the spawning stock (Briggs, 1953; Barlaup *et al.*, 1994). In contrast, Knapp & Vredenburg (1996) have mentioned that any bias

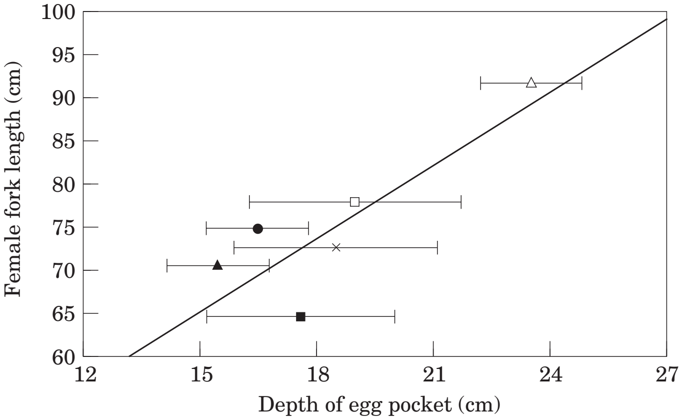

FIG. 4. Regression line to estimate female fork length from the depth of the egg pocket. Mean egg pocket depth with 95% CL is given for each of six females. $y=2{\cdot}809x+23{\cdot}473$; $r=0{\cdot}85$; $n=6$; $P<0{\cdot}05$.

associated with including false redds should be small in the study of California golden trout *Oncorhynchus mykiss aguabonita* (Jodan), because >90% of excavated redds contained eggs. In Sakhalin taimen, the false redds constitute 20–30% and are not negligible, probably because the female density is much lower than in other species and the sites suitable for the construction of their redds are abundant in their habitat stream. They can choose new redd sites readily by abandoning the ongoing construction of the redd which was found unsuitable. Nonetheless, the false redds are discriminated easily from true redds by their size and shape and can be excluded from the numerical analysis of true redds. It is reasonable that false redds of Sakhalin taimen are small and do not have any V-shaped pots, because females need not cover the pocket when they do not spawn in it.

Correlations among redd size dimensions have been analysed in brown trout, Atlantic salmon and rainbow trout *Oncorhynchus mykiss* (Walbaum) and detected to be highly significant between tail length and tail width (Crisp & Carling, 1989). Whereas Fukushima (1994) has reported the length–width correlation as high as $r=0{\cdot}722$ in the tail of Sakhalin taimen redd, the present study shows the value of $r=0{\cdot}47$ ($P<0{\cdot}001$) in 1995 and 0·48 (NS) in 1996. This difference is mostly because Fukushima has treated only one- or two-egg-pocket redds. Especially in the redds with three or four egg pockets, the variation of redd shape is larger and the length–width correlation should be smaller than in redds with one or two egg pockets.

Unlike in brown trout, Atlantic salmon and rainbow trout which show significant correlation between tail length and pot size (Crisp & Carling, 1989), the pot length is almost independent of tail dimensions in Sakhalin taimen. This is mostly because pot length was represented by the entirely undisturbed V-shaped pot which was made last in the construction of a redd with multiple egg pockets; in those redds, the size proportion was eventually distorted at the tail.

It has been reported in other species that redd size is affected by current velocity and substratum (Burner, 1951), although Ottaway *et al.* (1981) and Crisp & Carling (1989) have suggested that those physical factors seem less effective than female fork length. In Sakhalin taimen, Fukushima (1994) has suggested that the redd size is affected by the number of egg pockets. The present study has confirmed that the redd size is affected more considerably by the numbers of egg pockets and eggs than by current velocity or substratum. Simple regression analysis suggests a significant effect of female size on redd size as so far reported in brown trout (Ottaway *et al.*, 1981), Atlantic salmon and rainbow trout (Crisp & Carling, 1989).

The deeper egg pockets have been considered more tolerant to wash-out, stranding, predation, mechanical damage, agitation and superimposition (Smirnov, 1955; McNeil, 1962; Reed, 1967; Schroder, 1973; van den Berghe & Gross, 1984; Kitano, 1995). Although the eggs may be at a respiratory disadvantage when buried in a bed with much fine sediment (Coble, 1961; Tappel & Bjornn, 1983; Chapman, 1988; Crisp & Carling, 1989; Lisle & Lewis, 1992), Dill & Northcote (1970) have revealed experimentally that the eggs do not suffer in respiration at a depth shallower than *c.* 30 cm. Therefore, the egg pocket depth has been regarded as an indicator for egg vulnerability (van den Berghe & Gross, 1984; Crisp & Carling, 1989; Kitano, 1995). In a study of coho salmon which covers the egg pockets in the same manner of digging behaviour, van den Berghe & Gross (1984) have found that the egg pocket depth is significantly correlated with pot depth. However, Crisp & Carling (1989) have reported that such a significant correlation is not detected in brown trout, Atlantic salmon and rainbow trout. The effects of current velocity and substratum on the depth of egg pockets are also controversial in many species of salmonid fish (Burner, 1951; Arnold, 1974; Fraser, 1975; Crisp & Carling, 1989). In Sakhalin taimen, the deeper egg pockets appear more effective in avoiding disturbance by superimposition. However, the superimposition rate (about 10%) in this species is much lower than in coho salmon (van den Berghe & Gross, 1989), sockeye salmon *Oncorhynchus nerka* (Walbaum) (Foerster, 1968; Hoopes, 1972) and pink salmon *O. gorbuscha* (Walbaum) (Keenleyside & Dupuis, 1988; Noltie, 1990). Moreover, the wash-out and stranding of eggs occur rarely because this species spawns at the end of the snow-melt period and the water level is relatively stable in their hatching season. Egg predation has been observed rarely and the incubating period in the redd (<*c.* 3 months) is shorter than in other salmonid species which usually take 4–6 months. These facts suggest that the egg pocket depth is less critical to egg mortality in Sakhalin taimen than in other salmonid species. However, it is possible that the information about egg pocket depth of many species reflects real differences between geographical locations and sites or local population conditions (e.g. flow regime, sediment loads, spawner density, etc) (Ottaway *et al.*, 1981). To avoid these effects, more close study of egg pocket depth is needed in various sites, populations and species.

Significant correlation between egg pocket depth and female size has been reported in brown trout (Ottaway *et al.*, 1981; Crisp & Carling, 1989), Atlantic salmon and rainbow trout (Crisp & Carling, 1989). Therefore, Crisp & Carling (1989) have used female size for estimating the egg pocket depth. In the rare Sakhalin taimen, however, it is hard to capture females and measure their body size. Hence, the female fork length (F) should be estimated from the formula $F=2{\cdot}809\ D+23{\cdot}473$ or $F=0{\cdot}217\ L+37{\cdot}048$ where D and L are egg pocket depth and tail length, respectively.

In addition to female size, the number of females is important for estimating the population structure of this species. Significant correlation between the number of females and the redd count has been reported in Atlantic salmon (Heggberget *et al.*, 1986; Madden *et al.*, 1993; Semple *et al.*, 1994), brown trout and brook trout *Salvelinus fontinalis* (Mitchill) (Hobbs, 1937; Benson, 1953; Beard & Carline, 1991). In redd counting, not only the occurrence of false redds but also redd superimposition can lead to substantial over- or underestimation, respectively, of the spawning stock. In the present study, the number of redds per female were obtained from the daily counts of newly made redds throughout the spawning season and so the underestimation from superimposition could be avoided. Since each female Sakhalin taimen constructed an average of three redds in 1996, the number of females can be estimated as one third of the number of redds. For instance in 1995 when 42 redds were constructed at the Koyanosawa creek, the number of females spawned could be estimated to be 14. Barlaup *et al.* (1994) have predicted the number of redds per female in brown trout and Atlantic salmon by using the relationship between the observed mean fecundity and mean number of eggs per redd. However, Elliott (1995) mentioned that fecundity was usually higher than estimated number of eggs per redd and these egg losses could be due to some egg retention by the female or to egg losses from the redd during spawning. In Sakhalin taimen, remarkable egg retention has been reported and the number of retained eggs ranged from several hundreds to 4500 (Gritsenko *et al.*, 1974), and retention has been confirmed in the study (unpubl. data). Hence, especially in iteroparous species like Sakhalin taimen, egg retention should be considered when the number of redds per female is predicted from the relationship between the fecundity and number of eggs per redd.

The parameter such as number of eggs is also important for estimating the population structure. This parameter is the most important limiting factor for subsequent parr abundance. In Sakhalin taimen, the number of eggs per redd (N_e) is estimated from tail length (T_l) by using $N_e = 0{\cdot}068\ T_l + 35{\cdot}710$. The estimation of eggs may enable fisheries managers to transplant artificially hatched eggs to reaches where the density of eggs is lower than in other reaches. Anyhow, some parameters important in the study of the population structure of Sakhalin taimen can be estimated from the number, shape and size of redds at a low cost and without disturbing the behaviour of this rare and endangered species.

We thank S. Nakano for valuable advice and revision of the manuscript; K. Hieda, Y. Namisaka, H. Takeichi, H. Shibao, M. Sawamura, T. Yamamoto, K. Akiba, Y. Koseki, M. Namiki, K. Ookawa, T. Murai, H. Hirosawa, T. Shimamura and M. Sato for assistance in fieldwork; and F. Miura for helpful advice and encouragement.

References

Arnold, G. P. (1974). Rheotropism in fish. *Biological Reviews* **49,** 515–576.

Barlaup, B. T., Lura, H., Saegrov, H. & Sundt, R. C. (1994). Inter- and intra-specific variability in female salmonid spawning behaviour. *Canadian Journal of Zoology* **72,** 636–642.

Beard, T. D. & Carline, R. F. (1991). Influence of spawning and other stream habitat features on spatial variability of wild brown trout. *Transactions of the American Fisheries Society* **120,** 711–722.

Beland, K. F. (1996). The relation between redd counts and Atlantic salmon (*Salmo salar*) parr populations in the Dennys River, Maine. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 513–519.

Benson, N. G. (1953). The importance of groundwater to trout populations in the Pigeon River, Michigan. *Transactions of the North American Wildlife Conference* **18,** 268–281.

Berg, L. S. (1962). *Freshwater Fishes of the U.S.S.R. and Adjacent Countries*, Vol. 1. Jerusalem: The Israel Program for Scientific Translations.

van den Berghe, E. P. & Gross, M. R. (1984). Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **41,** 204–206.

van den Berghe, E. P. & Gross, M. R. (1989). Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* **43,** 125–140.

Briggs, J. C. (1953). The behavior and reproduction of salmonid fishes in a small coastal stream. *California Fish Game, Fisheries Bulletin* **94**.

Burner, C. J. (1951). Characteristics of spawning nests of Columbia River salmon. *U.S. Fish and Wildlife Service Fishery Bulletin* **52,** 97–110.

Coble, D. W. (1961). Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. *Transactions of the American Fisheries Society* **90,** 469–474.

Chapman, D. W. (1988). Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* **117,** 1–21.

Crisp, D. T. & Carling, P. A. (1989). Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* **34,** 119–134.

Dill, L. M. & Northcote, T. G. (1970). The effects of gravel size, egg depth, and egg density on intra-gravel movement and emergence of coho salmon (*Oncorhynchus kisutch*) alevins. *Journal of the Fisheries Research Board of Canada* **27,** 1191–1199.

Elliott, J. M. (1984). Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–1983. *Journal of Animal Ecology* **53,** 327–350.

Elliott, J. M. (1995). Fecundity and egg density in the redd for sea trout. *Journal of Fish Biology* **47,** 893–901.

Foerster, R. E. (1968). The sockeye salmon, *Oncorhynchus nerka. Bulletin of the Fisheries Research Board of Canada* **162,** 1–966.

Fraser, J. C. (1975). Determining discharges of fluvial resources. *F.A.O. Fisheries Technical Paper* **43,** 1–102.

Fukushima, M. (1994). Spawning migration and redd construction of Sakhalin taimen, *Hucho perryi* (Salmonidae) on northern Hokkaido Island, Japan. *Journal of Fish Biology* **44,** 877–888.

Gritsenko, O. F., Malkin, E. M. & Churikov, A. A. (1974). Sakhalinskii taimen' *Hucho perryi* (Brevoort) reki Bogatoni (vostochnoe poberezh'e Sakhalin). *Izvestiya TINRO* **93,** 91–100. (Japanese translation; in *Sakana to Ran* **143,** 25–34, 1976.)

Grost, R. T., Hubert, W. A. & Wesche, T. A. (1991). Description of brown trout redds in a mountain stream. *Transactions of the American Fisheries Society* **120,** 582–588.

Hanson, A. J. & Smith, H. D. (1967). Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*) of mixed age-groups. *Journal of the Fisheries Research Board of Canada* **24,** 1955–1977.

Hardy, C. J. (1963). An examination of eleven stranded redds of brown trout (*Salmo trutta*), excavated in the Selwyn River during July and August, 1960. *New Zealand Journal of Sciences* **6,** 107–119.

Hawke, S. P. (1978). Stranded redds of quinnat salmon in the Mathias River, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **12,** 167–171.

Heggberget, T. G., Haukebø, T. & Veie-Rosvoll, B. (1986). An aerial method of assessing spawning activity of Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in Norwegian streams. *Journal of Fish Biology* **28,** 335–342.

Hobbs, D. F. (1937). Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. *Fisheries Bulletin of New Zealand* **6,** 1–104.

Holčík, J., Hensel, K., Nieslanik, J. & Skácel, L. (1988). *The Eurasian Huchen,* Hucho hucho*: Largest Salmon of the World.* Dordrecht: Dr W. Junk.

Hoopes, D. T. (1972). Selection of spawning site by sockeye salmon in small streams. *U.S. National Marine Fisheries Service Fishery Bulletin* **70,** 447–458.

Kawamula, H., Mabuchi, M. & Yonekawa, T. (1983). The Japanese huchen, *Hucho perryi* (Brevoort), collected in brackish water Lake Akkeshi, eastern Hokkaido, Japan. *Scientific Reports of the Hokkaido Fish Hatchery* **38,** 47–55 (in Japanese with English abstract).

Kawamula, H., Hara, A., Teranishi, T. & Matsuzaka, H. (1996). *Breeding techniques of Sakhalin taimen (Hucho perryi).* Tokyo: Exploitative Association of New Fish Species.

Keenleyside, M. H. A. & Dupuis, H. M. C. (1988). Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Zoology* **66,** 262–265.

Khatkevich, V. (1973). Chevitsa-perspektivnyi ob'ekt lososevodstva. *Rybovodstvo i Rybolovstvo* **1,** 19.

Kimura, S. (1966). On the life history of the salmonid fish, *Hucho perryi* (Brevoort), found in Nemuro, Hokkaido. *Japanese Journal of Ichthyology* **14,** 17–25 (in Japanese with English summary).

Kitano, S. (1995). Intra-population variation of growth and reproduction in fluvial Dolly Varden (*Salvelinus malma*). Ph.D. Thesis, Hokkaido University, Sapporo, Japan.

Knapp, R. A. & Vredenburg, V. T. (1996). Spawning by California golden trout: characteristics of spawning fish, seasonal and daily timing, redd characteristics, and microhabitat preferences. *Transactions of the American Fisheries Society* **125,** 519–531.

Lisle, T. E. & Lewis, J. (1992). Effects of sediment transport on survival of salminid embryos in a natural stream: a simulation approach. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 2337–2344.

Madden, G. A., Cronin, P. J., Dubee, B. L. & Seymour, P. D. (1993). Using artificial barriers to protect and enhance Atlantic salmon. *Technical Report of the New Brunswick Department of Natural Resources and Energy, Frederiction, N.B.*

Maekawa, K. & Hino, T. (1990). Spawning tactics of female Miyabe charr (*Salvelinus malma miyabei*) against egg cannibalism. *Canadian Journal of Zoology* **68,** 889–894.

McCart, P. (1967). Digging behaviour of *Oncorhynchus nerka* spawning in streams at Babine Lake, British Columbia. In *Symposium on Salmon and Trout in Streams* (Northcote, T. G., ed.), pp. 39–51. Vancouver: H. R. MacMillan Lectures in Fisheries, University of British Columbia.

McNeil, W. J. (1962). Mortality of pink and chum salmon eggs and larvae in SE Alaska streams. Ph.D. Thesis, University of Washington, Seattle.

Noltie, D. B. (1990). Intrapopulation variation in the breeding of male pink salmon (*Oncorhynchus gorbuscha*) from a Lake Superior tributary. *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 174–179.

Ottaway, E. M., Carling, P. A., Clarke, A. & Reader, N. A. (1981). Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. *Journal of Fish Biology* **19,** 593–607.

Reed, R. J. (1967). Observations of the fishes associated with spawning salmon. *Transactions of the American Fisheries Society* **9,** 62–67.

Semple, J. R., Zamora, P. J. & Rutheford, R. (1994). Effects of dredging on egg to fry emergence, survival, and juvenile Atlantic salmon abundance, Debert River, Nova Scotia. *Canadian Technical Reports of Fisheries and Aquatic Sciences* No. 2023.

Schroder, S. L. (1973). Effect of density on spawning success of chum salmon *Oncorhynchus keta* in an artificial channel. M.Sc. Thesis, University of Washington, Seattle.

Smirnov, A. I. (1955). The effects of mechanical agitation at different periods of development on the eggs of autumn chum salmon. *Akademiya Nauk SSSR* **105,** 873–876. (Translation Fisheries Research Board of Canadian Biological Standards Nanaimo, B.C., *Translation Series* **230**.)

Tanida, K., Yamashita, K. & Rossiter, A. (1985). A portable current meter for field use. *Japanese Journal of Limnology* **46,** 219–221.

Tappel, P. D. & Bjornn, T. C. (1983). A new method of relating size of spawning gravel to salmonid embryo survival. *North American Journal of Fisheries Management* **3,** 123–135.

Tautz, A. F. & Groot, C. (1975). Spawning behavior of chum salmon *Oncorhynchus keta* and rainbow trout *Salmo gairdneri. Journal of the Fisheries Research Board of Canada* **32,** 633–642.

The Environment Agency (1991). *Japan Red Data Book, Vertebrates Edition*. Tokyo: Japan Wildlife Research Center.

Young, M. K., Hubert, W. A. & Wesche, T. A. (1989). Substrate alteration by spawning brook trout. *Transactions of the American Fisheries Society* **118,** 379–385.