WATER RESOURCES RESEARCH, VOL 29, NO. 7, PAGES 2275–2285, JULY 1993

The Sizes of Salmonid Spawning Gravels

G. MATHIAS KONDOLF

Department of Landscape Architecture, College of Environmental Design, University of California, Berkeley

M. GORDON WOLMAN

Department of Geography and Environmental Engineering, Johns Hopkins University, Baltimore, Maryland

The availability of suitably sized spawning gravels limits salmonid (salmon and trout) populations in many streams. We compiled published and original size distribution data to determine distinguishing characteristics of spawning gravels and how gravel size varies with size of the spawning fish. Median diameters of 135 size distributions ranged from 5.4 to 78 mm, with 50% falling between 14.5 and 35 mm. All but three spawning gravel size distributions were negatively skewed (on a log-transformed basis), with 50% of the skewness coefficients falling between −0.24 and −0.39. Fewer than 20% of the distributions were bimodal. Although tending to be coarser, spawning gravels had sorting and skewness values similar to other fluvial gravels reported in the literature. The range of gravel sizes used by fish of a given species or length is great, but the relation between fish size and size of gravel can be described by an envelope curve. In general, fish can spawn in gravels with a median diameter up to about 10% of their body length.

INTRODUCTION

Availability of suitably sized gravels can limit the spawning success of salmonids (salmon and trout) [*Allen*, 1969]. Fisheries publications since the 1950s have attempted to describe spawning gravel sizes but have failed to employ a consistent approach to measurement. Biologists commonly identify suitable spawning gravels based on their appearance alone. Authors have explored the use of a single gravel size statistic as an index of gravel quality [*Shirazi and Seim*, 1981; *Lotspeich and Everest*, 1981]. However, since gravel size requirements vary with a fish's life stage, no single statistic can serve as an effective indicator of gravel quality. Emphasis on a simple index has often precluded reporting of complete size distributions, rendering comparisons between studies difficult.

Field biologists maintain that since larger fish can excavate heavier particles and can hold in stronger currents they can therefore construct redds and spawn in larger gravels. Because larger gravels tend to be associated with higher velocities, these variables are not independent. Behavioral patterns also affect the relation between fish size and gravel size. For example, pink salmon (*Oncorhynchus gorbuscha*) spawn in tidal reaches of coastal rivers, where gravels are small and contain abundant fine-grained sediment, while silver (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) ascend rivers to headwater reaches, where gradients are high and bed material is coarser.

This study augmented size distributions reported for spawning and other gravels in the literature with data collected in original field work. The combined data set was analyzed to characterize spawning gravels in general, compare them with other fluvial gravels, and see how they relate to fish size.

Paper number 93WR00402.
0043-1397/93/93WR-00402$05.00

METHODS: COMPILATION OF SIZE DISTRIBUTIONS AND REDD CHARACTERISTICS

Size distributions were compiled from 22 sources, of which only four were in the open literature, 18 were agency and consultant reports or theses, so-called "grey" literature [*Wilbur*, 1990], or unpublished. Data from some reports were not included because too few sieves were used to adequately characterize the size distribution or because insufficient supporting data were available. Size distributions often represented averages or composites of many samples collected in one study area. For purposes of comparison among studies, average values were computed for studies reporting individual size distributions. Many studies refer to "spawning gravels" without stating whether the samples were obtained from redds or from potential spawning gravels. This distinction is important, since the process of spawning tends to modify gravel size by reducing fine sediment content [*Kondolf et al.*, this issue].

We plotted cumulative size distributions, read percentile values from the curves, and calculated the following size descriptors: median, geometric mean, *dg*, sorting index, *sg*, skewness, *sk* [*Inman*, 1952; *Vanoni*, 1975], and graphic mean, *mg* [*Folk*, 1980]:

$$dg = [(D84)(D16)]^{0.5}$$

$$mg = [(D84)(D50)(D16)]^{0.333}$$

$$sg = [(D84)/(D16)]^{0.5}$$

$$sk = \log (dg/D50)/\log (sg)$$

where *D50* is the median diameter, *D84* is the grain size at which 84% of the sample is finer, *D16* is the size at which 16% of the sample is finer. Data on length of spawning fish were obtained by consulting published sources, by recording field observations, and by contacting experts familiar with regional species.

Sorting and skewness for averaged and individual gravel samples were plotted against median and mean size. *D50* and other redd characteristics (redd area, water velocity, and depth over redds) were plotted against length of the spawning fish. The degree to which gravels were bimodal was assessed by inspection of cumulative size distribution curves. The degree to which gravels followed a lognormal distribution was also examined by *Kondolf* [1988].

LIMITATIONS OF THE DATA

Definition of Coarse and Fine Tails of Size Distributions

Data from many studies could not be used because too few sieves were used to adequately define size distribution curves at the tails (e.g., *McNeil and Ahnell* [1964], *Burns* [1970], *Peterson* [1978], and many samples of *Platts et al.* [1979]). Many studies did not define the upper limit of the largest size class; this creates a problem in plotting the cumulative curve because no total sample limit can be defined. In compiling data we often needed to use our judgement to extrapolate the progression of sieve sizes which may influence the value of the largest fractions, *D95* and *D90*. Inadequate definition of the fine tails of distributions was less common [*Chambers et al.*, 1954, 1955], probably because assessment of fine sediment has been an objective of most recent studies.

Often it is impossible to obtain an adequately large sample of coarse gravel due to a redd's limited dimensions. The resultant small size of coarse gravel samples may lead to substantial errors, especially in calculation of the *D95, D90,* and *D84* [*Church et al.*, 1987]. Discarding large rocks from samples may be a source of variability among studies. *Chambers et al.* [1954, 1955] excluded rocks larger than 152 mm, *Helle* [1970] those larger than 100 mm, and *Hobbs* [1937] those larger than 76 mm. Other studies may have employed similar unreported practices. Exclusion of large rocks increases the percentages computed for other size classes, resulting in smaller grain sizes at percentile values of *D16*, *D50,* etc.

Spatial and Temporal Variability

Most data entries represent averages or composites of multiple samples (up to 310) collected in one river or stream. While these averages may reflect typical site conditions, they may mask variability among individual samples in one reach. Similarly, temporal variability in gravel size at one site may not be reflected in a one-time sampling. Temporal variations in fine sediment content documented by *Cederholm and Salo* [1979], *Adams and Beschta* [1980], and *Scrivener and Brownlee* [1982] may result from infiltration into stable gravel beds or scour and fill [*Lisle*, 1989]. The gravel deposits themselves may be subject to complete washout and replacement in some years [*Kondolf et al.*, 1991].

Influence of Study Site Selection

The choice of "representative" sampling sites may influence observed gravel size and hydraulic conditions. Atypical sites, which could illustrate the adaptability of the fish, may be less often studied. For example, the use of radiotagging revealed that the large (>100 cm in length) chinook salmon of the Kenai River, Alaska utilize depths and velocities far greater than recorded elsewhere [*Burger et al.*, 1983]. Chum salmon (*Oncorhynchus keta*) of the Susitna River select sites with upwelling currents to spawn because the upwelling prevents freezing of the eggs. These fish commonly excavate 30 cm of silt before locating gravel in which to deposit their eggs [*Vining et al.*, 1985]. Standards based on representative sites would have indicated these to be unsuitable for spawning.

Sampling site selection also may be influenced by working conditions. Often, the maximum depth recorded at redds coincides with the maximum depth penetrable with chest waders. Redds in deeper parts of the channel may be difficult to see, to reach, and to sample.

RESULTS AND DISCUSSION

Presentation of Data

Background information, size descriptors, and redd characteristics for gravels presented in Table 1 are grouped by species of spawning fish. Size distributions for representative entries of trout redds are presented in Figure 1 in standard cumulative curves. We also used box-and-whisker plots modified after *Tukey* [1977] (Figure 2): the box encompasses the middle 50% of the distribution (limited by the "hinges" of the *D25* and *D75* values) with a horizontal line marking the median size (*D50*). Conventionally, the "whiskers" extending above and below the box represent the upper and lower extremes of the data [*Tukey*, 1977]. However, due to limitations in measuring individual grains of fine sediments, we chose the *D90* and *D10* as limits to the whiskers. Also, we chose to plot the ordinate on a logarithmic scale to better encompass the wide range of grain sizes present.

The box-and-whisker plots provide a clear picture of the range and central tendency of sediment size distributions and permit comparison of multiple samples. Although less complete, these plots avoid the confusion created by overlapping conventional cumulative distribution curves (Figure 1).

General Properties of Spawning Gravel Size Distributions

The median value of *D50*s of the 135 spawning gravel entries was 22 mm (Table 2). The range is quite large, from 5.4 mm for coho salmon (*Oncorhynchus kisutch*) redds in Flynn Creek, Oregon [*Koski*, 1966], to 78 mm for potential chinook salmon redds in the Columbia River near Vantage, Washington [*Chambers et al.*, 1954]. The range would be even greater if we included spawning sites of chum salmon in side channels of the Susitna River, Alaska (*D50* = 0.1 mm). Of the *D50*s from our data set, 50% occurred between 14.5 and 35 mm. Half the entries for graphic mean occurred between 10 and 27 mm, for geometric mean, between 8.7 and 24 mm.

The sorting index ranged from 1.6 in chinook salmon redds in the Yuba River, California, to 21.1 in chum salmon spawning beds in the Susitna River side channels. Half of the values for sorting index lie between 3.3 and 5.2, with a median value of 4.0 (Table 2). The vertical spread of the box-and-whisker plots (Figures 1 and 2) provides an indication of sorting. (The spread of the box-and-whisker plots is from the tenth to ninetieth percentiles, while the sorting

TABLE 1. Tabulation of Fish Species and Length, River Location, Gravel Site Descriptors, and Data Sources for Data Set Complied for This Study

Entry	Reference	Species	Location	Fish Length, cm	*n*	Size Descriptors*				
						D50	*dg*	*mg*	*sg*	*sk*
1	*Witzel* [1980]	brook trout	Sheldon Ck, Ontario	18	32	8.9	4.6	5.7	5.5	−0.39
2	*Witzel* [1980]	brook trout	Skunk Ck, Ontario	18	6	8.2	3.8	4.9	5.7	−0.44
3	*Witzel* [1980]	brook trout	Galt Ck, Ontario	18	3	7.2	3.9	4.8	4.7	−0.40
4	*Witzel* [1980]	brook trout	Congers Ck, Ontario	18	16	10.7	4.8	6.3	5.5	−0.47
5	*Warner* [1963]	Atlantic salmon	Cross Lake Thoroughfare, Maine	49	23	16.5	7.2	9.5	4.8	−0.52
6	*Warner* [1963]	Atlantic salmon	Long Lake Thoroughfare, Maine	53	10	15.0	7.0	9.0	4.7	−0.49
7	*Hobbs* [1937]	brown trout	Various rivers, New Zealand	43	5	18.5	14.8	15.9	3.5	−0.17
8	*Reiser and Wesche* [1977]	brown trout	Douglas Ck ab Cheyenne Div, Wyoming	31	20	24.0	15.5	17.9	4.4	−0.29
9	*Reiser and Wesche* [1977]	brown trout	Douglas Ck be Cheyenne Div, Wyoming	31	53	28.0	19.7	22.1	2.7	−0.36
10	*Reiser and Wesche* [1977]	brown trout	Lake Ck, Wyoming	31	16	11.0	8.1	9.0	5.8	−0.17
11	*Reiser and Wesche* [1977]	brown trout	Pioneer Canal, Wyoming	31	6	17.0	9.6	11.6	3.5	−0.45
12	*Reiser and Wesche* [1977]	brown trout	Laramie R at "EP" site, Wyoming	31	60	32.0	11.1	15.8	7.9	−0.51
13	*Reiser and Wesche* [1977]	brown trout	Laramie R be Pioneer Canal, Wyoming	31	7	18.0	10.2	12.3	4.1	−0.40
14	*Reiser and Wesche* [1977]	brown trout	Hog Park Ck, Wyoming	31	8	17.0	9.3	11.3	5.2	−0.37
15	*Witzel* [1980]	brown trout	Shunk Ck, Ontario	32	4	9.2	4.8	6.0	5.0	−0.40
16	*Witzel* [1980]	brown trout	Galt Ck, Ontario	32	2	5.8	4.4	4.8	5.6	−0.16
17	*Witzel* [1980]	brown trout	Beatty Saugeen R, Ontario	32	5	14.5	8.7	10.3	4.2	−0.36
18	*Witzel* [1980]	brown trout	Syndenham R, Ontario: site 1	32	6	8.4	5.2	6.1	5.2	−0.29
19	*Witzel* [1980]	brown trout	Syndenham R, Ontario: site 2	32	30	9.9	5.4	6.6	5.0	−0.38
20	P. Carling (unpublished data, 1987)	brown trout	Carl Beck, England	29	22	50.0	21.0	27.9	5.2	−0.52
21	P. Carling (unpublished data, 1987)	brown trout	Eggleshope Beck, England	29	35	19.0	10.3	12.6	8.6	−0.29
22	*Maddux et al.* [1987]	rainbow trout	Colorado R, Arizona	45	2	10.5	5.7	7.0	5.2	−0.36
23	this study	rainbow trout	Colorado R Tributaries, Arizona	40	10	32.0	24.3	26.6	2.9	−0.26
24	*Orcutt et al.* [1968]	steelhead trout	N Fork Clearwater R tributaries, Idaho	76	60	42.0	25.7	30.2	4.3	−0.34
25	*Orcutt et al.* [1968]	steelhead trout	Salmon R tributaries, Idaho	76	8	46.0	19.1	25.5	5.8	−0.50
26	*Chambers et al.* [1954, 1955]	steelhead trout	Kalama R, Washington	75	3	31.0	23.5	25.7	3.9	−0.20
27	*Hobbs* [1937]	chinook salmon	Winding R, New Zealand	81	2	16.5	15.2	15.6	3.3	−0.07
28	*Burger et al.* [1983]	chinook salmon	Kenai R, Arkansas	101	4	31.8	27.8	28.9	2.7	−0.14
29	*Burger et al.* [1983]	chinook salmon	Benjamin CK, Alaska	94	4	22.0	23.2	22.7	2.7	0.06
30	*Vronskiy* [1972]	chinook salmon	Kamchatka R, Siberia; main stem	90	2	47.0	30.0	34.7	3.7	−0.34
31	*Vronskiy* [1972]	chinook salmon	Kamchatka R, Siberia: arm 1	90	2	26.0	22.0	23.2	3.9	−0.12
32	*Vronskiy* [1972]	chinook salmon	Kamchatka R, Siberia: arm 2	90	2	16.0	12.7	13.6	3.8	−0.17
33	this study	chinook salmon	Crooked Ck, Alaska	90	4	36.0	27.0	29.6	2.3	−0.34
34	this study	chinook salmon	Yuba R, California	81	1	34.0	25.8	28.2	2.2	−0.34
35	*Chambers et al.* [1954, 1955]	chinook salmon	Kalama R, Washington	86	13	54.0	39.5	43.7	3.0	−0.28
36	*Chambers et al.* [1954, 1955]	chinook salmon	Snake R, Idaho	86	8	21.0	17.2	18.3	3.4	−0.16
37	*Chambers et al.* [1954, 1955]	chinook salmon	Cispus R, Washington	82	7	50.0	35.1	39.3	3.2	−0.30
38	*Chambers et al.* [1954, 1955]	chinook salmon	Imnaha R, Oregon	82	4	41.0	34.8	36.6	2.9	−0.15
39	*Chambers et al.* [1954, 1955]	chinook salmon	American R, Washington	82	5	35.0	25.6	28.3	3.0	−0.28
40	*Chambers et al.* [1954, 1955]	chinook salmon	Cowlitz R, Washington	82	8	51.0	29.0	34.9	3.9	−0.42
41	*Chambers et al.* [1954, 1955]	coho salmon	Spring Ck, Washington	65	4	35.0	20.3	24.3	3.4	−0.44
42	*Chambers et al.* [1954, 1955]	coho salmon	Toutle R, Washington	65	4	16.5	15.2	15.6	3.2	−0.07
43	*Chambers et al.* [1954, 1955]	coho salmon	Burns Ck, Washington 1953	65	7	29.0	21.0	23.3	3.3	−0.27

TABLE 1. (continued)

Entry	Reference	Species	Location	Fish Length, cm	n	Size Descriptors* D50	dg	mg	sg	sk
44	*Chambers et al.* [1954, 1955]	coho salmon	Burns Ck, Washington 1954	65	4	33.0	22.1	25.2	3.1	−0.36
45	*Koski* [1966]	coho salmon	Deek Ck, Oregon	67	nr	12.0	3.6	5.4	10.6	−0.51
46	*Koski* [1966]	coho salmon	Needle Branch, Oregon	67	nr	6.3	2.7	3.6	9.6	−0.37
47	*Koski* [1966]	coho salmon	Flynn Ck, Oregon	67	nr	5.4	2.7	3.4	9.1	−0.31
48	*Helle* [1970]	pink salmon	Olsen Ck, Alaska: upper intertidal	43	12	8.8	7.6	8.0	4.2	−0.10
49	*Helle* [1970]	pink salmon	Olsen Ck, Alaska: low gradient	43	10	11.0	6.8	8.0	5.1	−0.29
50	*Helle* [1970]	pink salmon	Olsen Ck, Alaska: midintertidal	43	43	10.0	7.5	8.2	4.7	−0.19
51	*Helle* [1970]	pink salmon	Olsen Ck, Alaska: lower intertidal	43	29	8.0	5.6	6.3	5.3	−0.21
52	*Chambers et al.* [1954, 1955]	sockeye salmon	Okanagan R, British Columbia	65	12	25.0	18.0	20.0	3.3	−0.27
53	*Chambers et al.* [1954, 1955]	sockeye salmon	Little Wenatchee R, Washington	50	4	17.8	13.4	14.7	2.7	−0.29
54	this study	sockeye salmon	Quartz Ck, Alaska	35	3	19.0	18.4	18.5	3.5	−0.03
55	*Spoon* [1985]	brown trout	Missouri R, Montana	50	11	22.5	17.4	18.9	3.0	−0.24
56	*Spoon* [1985]	brown trout	Beaver Ck, Montana	29	15	13.0	7.4	8.9	6.2	−0.31
57	this study	brown trout	Owens R tributaries, California	23	12	18.0	13.3	14.7	3.2	−0.26
58	*Hartman and Galbraith* [1970]	rainbow trout	Lardeau R, British Columbia	75	6	23.5	14.7	17.1	3.6	−0.37
59	*Platts et al.* [1979]	rainbow trout	N. Fork Boise R, Idaho	30	45	20.0	12.4	14.5	6.5	−0.25
60	*Spoon* [1985]	rainbow trout	Missouri R, Montana	44	27	12.5	8.3	9.5	4.6	−0.27
61	*Spoon* [1985]	rainbow trout	Beaver Ck, Montana	44	19	15.0	9.3	10.9	4.9	−0.30
62	*Maddux et al.* [1987]	rainbow trout	Colorado R, Arizona	45	1	16.0	5.2	7.6	10.5	−0.47
63	this study	rainbow trout	Colorado R tributaries, Arizona	40	8	21.9	15.5	17.4	3.8	−0.26
64	this study	rainbow trout	Nantahala R, North Carolina (gravel < 90 mm)	21	14	24.5	16.5	18.7	3.8	−0.30
65	this study	rainbow trout	Natahala R, North Carolina (all rocks)	21	14	46.3	26.6	31.9	4.0	−0.40
66	*Chambers et al.* [1954, 1955]	steelhead trout	Kalama R, Washington	75	2	40.0	28.1	31.5	4.3	−0.24
67	T. Bjornn (unpublished data, 1987)	steelhead trout	Tucannon R, Oregon: mouth	66	2	12.4	8.2	9.4	2.9	−0.38
68	T. Bjornn (unpublished data, 1987)	steelhead trout	Tucannon R, Oregon: upstream	66	4	25.4	16.2	18.8	3.7	−0.34
69	*Cederholm and Salo* [1979]	steelhead trout	Stequaleho Ck, Washington: site 1	65	34	19.5	10.9	13.2	5.4	−0.35
70	*Cederholm and Salo* [1979]	steelhead trout	Stequaleho Ck, Washington: site 2	65	43	22.0	11.7	14.4	5.1	−0.38
71	*Cederholm and Salo* [1979]	steelhead trout	Stequaleho Ck, Washington: site 3	65	38	22.0	12.0	14.7	4.8	−0.38
72	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington: site 1	70	27	10.4	9.3	9.6	4.8	−0.07
73	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington site 2	70	22	13.5	9.3	10.5	4.8	−0.24
74	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington: site 3	70	25	18.0	9.6	11.8	5.6	−0.36
75	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington: site 4	70	39	19.0	9.8	12.2	6.5	−0.35
76	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington: site 5	70	73	23.0	11.2	14.2	5.3	−0.43
77	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington: site 6	70	61	15.0	10.8	12.0	4.0	−0.24
78	*Cederholm and Salo* [1979]	steelhead trout	Clearwater R, Washington: site 7	70	17	22.0	6.9	10.2	8.4	−0.54
79	*Shirazi et al.* [1981]	steelhead trout	Beaver Ck, Oregon	68	3	26.5	17.9	20.3	3.3	−0.33
80	*Shirazi et al.* [1981]	steelhead trout	Three Rivers, Oregon	68	3	32.4	19.6	23.1	3.8	−0.38
81	*Shirazi et al.* [1981]	steelhead trout	Gopher Ck, Oregon	68	3	33.7	23.8	26.6	2.7	−0.35
82	*Shirazi et al.* [1981]	steelhead trout	Rock Ck, Oregon	68	3	36.7	31.1	32.7	2.7	−0.17
83	*Chambers et al.* [1954, 1955]	chinook salmon	Columbia R, Washington	86	4	78.0	41.4	51.0	3.2	−0.55
84	*Chambers et al.* [1954, 1955]	chinook salmon	Snake R, Idaho	86	10	21.0	14.5	16.4	4.1	−0.26

TABLE 1. (continued)

Entry	Reference	Species	Location	Fish Length, cm	n	Size Descriptors*				
						D50	dg	mg	sg	sk
85	*Chambers et al.* [1954, 1955]	chinook salmon	Kalama R, Washington	86	7	49.0	30.6	35.7	4.0	−0.34
86	*Chambers et al.* [1954, 1955]	chinook salmon	Cowlitz R, Washington	82	14	42.0	25.5	30.0	4.9	−0.31
87	*Chambers et al.* [1954, 1955]	chinook salmon	Imnaha R, Oregon	82	3	52.0	31.7	37.3	3.8	−0.37
88	*Chambers et al.* [1954, 1955]	chinook salmon	Cispus R, Washington	82	10	37.0	23.2	27.0	4.7	−0.30
89	*Chambers et al.* [1954, 1955]	chinook salmon	American R, Washington	82	8	34.0	24.3	27.1	3.2	−0.28
90	W. F. Van Woert and E. J. Smith, Jr. (unpublished data, 1962)	chinook salmon	Sacramento R, California	84	3	44.0	24.7	29.8	4.7	−0.38
91	W. F. Van Woert and E. J. Smith, Jr. (unpublished data, 1962)	chinook salmon	Cottonwood Ck, California	84	12	31.0	18.6	22.0	4.8	−0.33
92	W. F. Van Woert and E. J. Smith, Jr. (unpublished data, 1962)	chinook salmon	Cow Ck, California	84	3	52.0	32.1	37.6	3.2	−0.41
93	W. F. Van Woert and E. J. Smith, Jr. (unpublished data, 1962)	chinook salmon	Battle Ck, California	84	3	66.0	36.9	44.7	3.5	−0.46
94	*Platts et al.* [1979]	chinook salmon	S. Fork Salmon R, Idaho: Stolle Meadow	86	145	22.0	8.5	11.6	7.1	−0.49
95	*Platts et al.* [1979]	chinook salmon	S. Fork Salmon R, Idaho: Poverty Area	86	310	11.2	6.8	8.0	7.5	−0.25
96	*Platts et al.* [1979]	chinook salmon	S. Fork Salmon R, Idaho: Glory Area	86	80	16.5	8.7	10.7	6.4	−0.34
97	*Platts et al.* [1979]	chinook salmon	Johnson Ck, Idaho	86	100	24.5	11.6	14.8	5.8	−0.43
98	*Platts et al.* [1979]	chinook salmon	Bear Valley Ck, Idaho	86	20	10.8	6.9	8.0	5.9	−0.25
99	*Platts et al.* [1979]	chinook salmon	Elk Ck, Idaho	86	20	15.2	9.0	10.7	3.9	−0.39
100	*Platts et al.* [1979]	chinook salmon	Loon Ck, Idaho	86	20	21.5	11.7	14.3	5.1	−0.37
101	*Platts et al.* [1979]	chinook salmon	Salmon R, Idaho: lower Decker site	86	5	27.0	15.3	18.4	5.1	−0.35
102	*Platts et al.* [1979]	chinook salmon	Salmon R, Idaho: upper Decker site	86	5	13.2	10.6	11.4	4.6	−0.14
103	*Platts et al.* [1979]	chinook salmon	Alturas Ck, Idaho	86	20	14.5	10.7	11.8	4.3	−0.21
104	*Shirazi et al.* [1981]	chinook salmon	Grant Ck, Oregon	82	4	30.0	19.9	22.7	3.6	−0.32
105	*Shirazi et al.* [1981]	chinook salmon	Rogue R, Oregon: Old Bridge	82	4	37.8	35.9	36.4	1.9	−0.08
106	*Shirazi et al.* [1981]	chinook salmon	Rogue R, Oregon: Hatchery	82	3	39.7	30.4	33.1	4.0	−0.19
107	*Shirazi et al.* [1981]	chinook salmon	Rogue R, Oregon: Sand Hole	82	3	69.3	62.7	64.6	1.6	−0.21
108	*Shirazi et al.* [1981]	chinook salmon	Rogue R, Oregon: Dam Site	82	1	59.0	35.5	41.9	2.4	−0.59
109	*Shirazi et al.* [1981]	chinook salmon	Rogue R, Oregon: Big Butte Ck	82	3	35.0	21.8	25.4	3.3	−0.40
110	*Chapman et al.* [1984]	chinook salmon	Columbia R (Vernita), Washington	86	2	43.0	35.1	37.4	2.9	−0.19
111	this study	chinook salmon	Crooked Ck, Alaska	90	4	41.3	25.9	30.2	2.3	−0.58
112	this study	chinook salmon	Yuba R, California	81	1	35.0	25.1	28.0	2.2	−0.42
113	*Chambers et al.* [1954, 1955]	coho salmon	Spring Ck, Washington	65	2	13.0	10.4	11.2	3.5	−0.18
114	*Chambers et al.* [1954, 1955]	coho salmon	Toutle R, Washington	65	2	10.0	8.8	9.1	3.7	−0.10
115	*Chambers et al.* [1954, 1955]	coho salmon	Burns Ck, Washington (1953)	65	1	29.0	24.0	25.5	2.9	−0.18
116	*Chambers et al.* [1954, 1955]	coho salmon	Burns Ck, Washington (1954)	65	4	33.0	25.3	27.6	2.5	−0.29
117	*Helle* [1970]	pink salmon	Olsen Ck, Alaska: upper intertidal	43	22	9.2	6.8	7.5	5.4	−0.18
118	*Helle* [1970]	pink salmon	Olsen Ck, Alaska: Middle Slough	43	25	6.5	4.6	5.2	5.0	−0.21
119	*Helle* [1970]	pink salmon	Little Ck, Alaska	43	25	9.6	9.6	9.6	3.3	0.00
120	*Shirazi et al.* [1981]	chum salmon	Porcupine Ck, Alaska: main stem	65	2	9.6	6.6	7.5	1.9	−0.57
121	*Shirazi et al.* [1981]	chum salmon	Porcupine Ck, Alaska: intertidal	65	3	11.2	7.8	8.8	3.7	−0.28
122	*Shirazi et al.* [1981]	chum salmon	Porcupine Ck, Alaska: E. Fork	65	3	38.1	23.6	27.6	3.3	−0.40

TABLE 1. (continued)

Entry	Reference	Species	Location	Fish Length, cm	n	Size Descriptors*				
						D50	dg	mg	sg	sk
123	*Shirazi et al.* [1981]	chum salmon	Porcupine Ck, Alaska: W. Fork	65	3	13.1	10.9	11.6	2.4	−0.21
124	*Shirazi et al.* [1981]	chum salmon	Kari Ck, Alaska	65	3	41.2	30.1	33.3	3.8	−0.24
125	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: main stem	65	2	62.0	28.1	36.4	5.5	−0.46
126	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: side channel 10	65	4	21.8	7.6	10.7	9.5	−0.47
127	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: side channel 21	65	5	36.4	18.0	22.7	6.7	−0.37
128	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: slough 10	65	3	42.3	4.6	9.6	22.9	−0.71
129	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: slough 11	65	6	20.5	15.4	16.9	4.8	−0.18
130	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: slough 21	65	3	42.7	19.7	25.4	6.4	−0.42
131	*Vining et al.* [1985]	chum salmon	Susitna R, Alaska: silt	65	4	0.1	0.1	0.1	2.3	0.06
132	*Vining et al.* [1985]	chum salmon	Fourth of July Ck, Alaska	65	4	25.7	20.0	21.6	4.2	−0.18
133	*Chambers et al.* [1954, 1955]	sockeye salmon	Okanagan R, British Columbia	65	5	48.0	32.7	37.0	2.7	−0.38
134	*Chambers et al.* [1954, 1955]	sockeye salmon	Little Wenatchee R, Washington	50	4	14.5	9.9	11.2	3.5	−0.30
135	this study	sockeye salmon	Quartz Ck, Alaska	35	3	22.9	16.7	18.5	3.3	−0.27
136	*Conkling* [1934]	na	Alluvial fans, California	na	33	26.1	17.0	19.5	3.9	−0.31
137	*Krumbein* [1940]	na	San Gabriel Canyon, California	na	15	9.4	5.3	6.4	6.4	−0.31
138	*Krumbein* [1942]	na	Arroyo Seco, California	na	20	5.0	3.8	4.2	6.8	−0.14
139	*Plumley* [1948]	na	Rapid Ck terraces, South Dakota	na	10	23.0	12.2	15.0	5.1	−0.39
140	*Plumley* [1948]	na	Bear Butte Ck terraces, South Dakota	na	7	29.6	19.4	22.2	3.9	−0.31
141	*Plumley* [1948]	na	Battle Ck terraces, South Dakota	na	6	21.3	10.0	12.8	7.1	−0.39
142	*Schlee* [1957]	na	Upland gravels, Maryland	na	72	5.2	2.2	3.0	11.2	−0.35
143	*Morris and Johnson* [1967]	na	Arapahoe County, Colorado	na	1	2.7	2.7	2.7	1.5	−0.02
144	*Morris and Johnson* [1967]	na	Douglas County, Colorado	na	1	4.1	4.3	4.2	1.6	0.08
145	*Morris and Johnson* [1967]	na	Arkansas R Valley, Kansas	na	1	8.3	8.4	8.3	1.5	0.02
146	*Knott and Lipscomb* [1983]	na	Chulitna R, Alaska	na	10	20.2	19.7	19.8	2.0	−0.03

Most entries are averages of more than one sample, as indicated by *n*. Abbreviations: Ck, creek; R, river; ab, above; be, below; nr, not reported; and na, not available.

*Values are in millimeters, except for *sg* and *sk*, which are dimensionless. For definitions, see the text.

index is computed using the sixteenth and eighty-fourth percentiles.)

All but three of the 135 spawning gravel size distributions were negatively skewed, with half of the skewness coefficients falling between −0.24 and −0.39. Negative skewness appears as extended whiskers below the box reflecting extended fine sediment tails. This negative skewness is characteristic of these log-transformed distributions: without transformation, these distributions would be positively skewed.

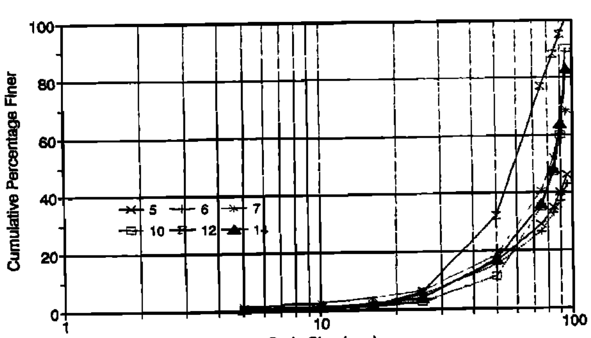

Fig. 1. Illustrative cumulative size distribution curves of six representative redd gravels of Atlantic salmon and brown trout. Each plot is labeled with the number corresponding to its entry in Table 1. Note the difficulty reading individual curves when more than one similar distribution is plotted on the same diagram.

Spawning gravels tend to be coarser than many gravels reported by sedimentary geologists but not different in sorting and skewness. The "typical" values for "water-laid gravels" reported by *Morris and Johnson* [1967] are smaller and less negatively skewed than for most spawning gravels (Table 1). This may represent a past tendency not to report the full range of sizes and a lack of very large gravel sizes represented in most continental depositional sequences.

Modality of Gravels

Pettijohn [1975] concluded from a review of data presented by *Conkling et al.* [1934], *Krumbein* [1940, 1942], and *Plumley* [1948] that most gravels are bimodal, in contrast to sands, which tend to be unimodal. Bimodal distributions are characterized by two distinct modes in frequency curves,

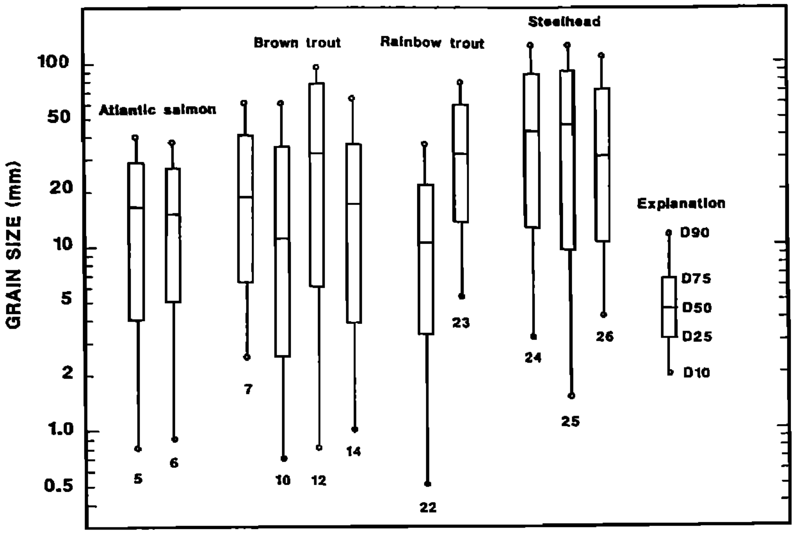

Fig. 2. Box-and-whisker plots [modified from *Tukey*, 1977] of 11 representative redd gravels of trout, including the six plotted on conventional cumulative size distribution curves in Figure 1. Each plot is labeled with the number corresponding to its entry in Table 1. Box encompasses the middle 50% of the distribution, with the median indicated by the horizontal line. Whiskers extend to *D90* and *D10*.

one typically in the sand range, the other in the gravel range. In cumulative frequency curves these are reflected in a steep fine tail, a flatter middle portion, and a steeper leg in the gravel range. However, *Ibbeken* [1992] examined 76 river and beach gravels in Calabria, found that bimodality was not characteristic of individual rivers, years, or specific source-area conditions.

Kondolf [1988] inspected cumulative frequency curves of 76 gravels and found less than 20 could be considered bimodal at all, and only 10 displayed bimodality well. Most spawning gravel curves had an extended fine tail (negatively skewed) but lacked a distinct secondary mode in the sand range.

Mean Size and Its Relationship to Other Properties

Church et al. [1987, pp. 51–52] noted that "mixtures of clastic material frequently display variance proportional to the mean size, which is not surprising since all sizes may be present up to some cutoff point." To determine if sorting and skewness were related to grain size in our data set, the values of these descriptors were plotted as functions of graphic mean diameter. Skewness was unrelated to size, but sorting was less variable and somewhat better for coarser gravels (Figures 3 and 4), inconsistent with the findings of *Church et al.* [1987].

Our data set represents a wide range of sampling environments, while *Church et al.* [1987] based their work on 78 samples from one river. If the size of framework grains (the larger particles supporting the gravel deposit) were the only independent variable, then we could expect higher standard deviation in coarser gravels due to a wider range of sizes present. Our opposite results may reflect the influence of fine sediment content on both mean size and sorting.

If framework size is held constant, larger amounts of matrix fine sediment should decrease mean size and increase standard deviation. Such a relation is suggested in Figures 5 and 6, which show standard deviation clearly related to *D16* but with only a possible weak relation to *D84*. Thus in our data set, sorting may be controlled more by the presence of fine sediment than large particles. (Exclusion of large particles during sampling noted earlier would contribute to this effect.)

Influence of Fish Size on Redd Characteristics

Redd characteristics such as gravel size, water depth and velocity, redd dimensions, and depth of egg burial have been argued to vary with the size of spawning fish [*Crisp and*

TABLE 2. Spread of Size Descriptors for Entries in Data Set

	Spawning Gravels					Other Gravels		
Size Descriptor	Extremes	*P25*	*P50*	*P75*	Extremes	Extremes	*P50*	Extremes
Median, *D50*	78	35	22	14.5	0.13	30	9.4	2.7
Graphic mean, *mg*	65	27	16	10.2	0.1	22	8.3	2.7
Geometric mean, *dg*	62	24	15	8.7	0.1	19	8.4	2.2
Geometric sorting coefficient, *sg*	21	5.2	4.0	3.3	1.6	11	3.9	1.5
Skewness, *sk*	0.1	−0.24	−0.31	−0.39	−0.7	0.1	−0.3	−0.4

All 135 entries for redd and potential spawning gravels combined under "spawning gravels." *P75*, *P50*, and *P25* designate the first quartile, median, and third quartile, respectively. All units in millimeters except *sg* and *sk*, which are dimensionless.

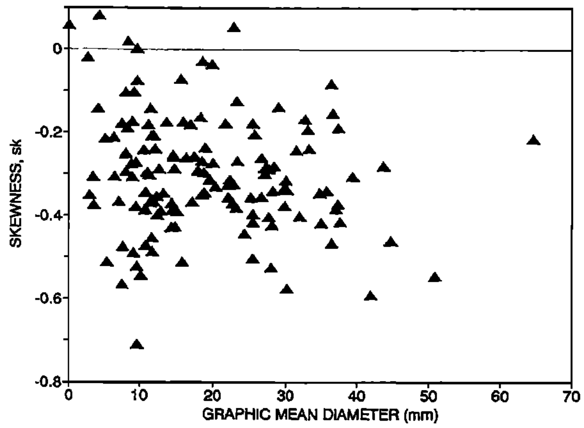

Fig. 3. Skewness plotted against mean diameter (graphic mean diameter) for spawning gravel entries in data set (Table 1).

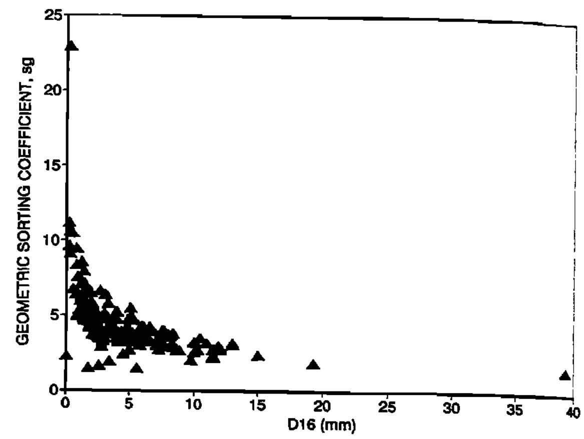

Fig. 5. Sorting coefficient plotted against *D16* for spawning gravel entries in data set (Table 1).

Carling, 1989]. However, few published data, including spawning preference studies, describe these relations. Differences in spawning gravel size have been attributed to size of fish species [e.g., *Burner*, 1951; *Chambers et al.*, 1954, 1955; J. W. Hunter, unpublished manuscript, 1973). *Van den Berghe and Gross* [1984] and *Crisp and Carling* [1989] found depth of egg burial was related to size of the spawning female. By contrast, other authors have found no relation between fish size and redd characteristics [e.g., *Vronskiy*, 1972].

Two attributes related to fish size and spawning gravel size are evident in our data set. First, the range of sizes used by each species is very large, as is illustrated by box-and-whisker plots of median diameters (Figure 7). Second, these plots suggest that different species use different ranges of gravel sizes, differences confirmed to be significant by a one-way ANOVA analysis of variance, which showed that variation in gravel size between species exceeded variation within species (F ratio = 6.15, $p < 0.0001$). The relation between fish size and gravel size can be compared directly by plotting median gravel size against fish length (Figure 8). The gravel size range for a given fish length is large, but it is possible to draw an envelope curve through the maximum sizes used. The envelope curve shown in Figure 8 excludes two outlying points: redd gravels (*D50* = 50 mm) from Carl Beck in England, which likely include lag gravels too large for the fish to move, and gravels in the Nantahala River (*D50* = 46 mm), which were identified by biologists as potential spawning gravels but for which we have no direct evidence of spawning use. Not surprisingly, larger fish can use larger gravels, with the envelope curve indicating that the fish can use gravels with median diameters up to about 10% of their body length.

Larger fish can construct redds in larger gravels because (1) they can lift more weight by virtue of the greater suction their tails can exert on the streambed and (2) they can hold in more powerful currents, which help to dislodge gravels. However, while a large chinook salmon may be capable of spawning in steep, coarse-bedded channels, she may choose to utilize smaller gravels in lower-gradient reaches instead. Thus the relation between fish size and spawning gravel size is best viewed as defining an envelope curve, with the gravel sizes actually used by fish determined largely by availability. Other redd characteristics, such as water depth and velocity, may display similar relations. *Crisp and Carling* [1989] developed an envelope curve relating mean velocity to fish size for brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) in Britain. *Kondolf* [1988] compiled available data on redd area, velocity, and depth at redd sites, and found 30-cm fish could spawn in velocities of up to 0.5 m

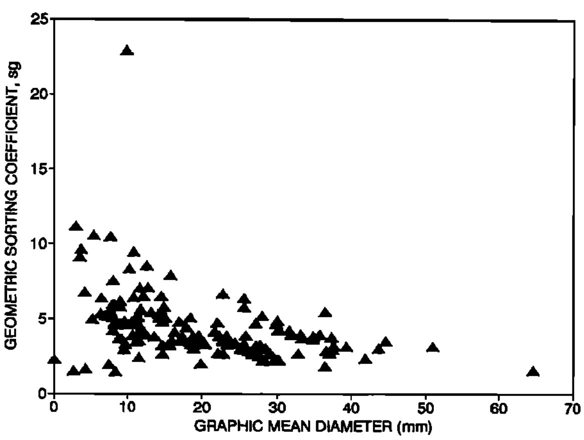

Fig. 4. Sorting coefficient plotted against mean diameter (graphic mean diameter) for spawning gravel entries in data set (Table 1).

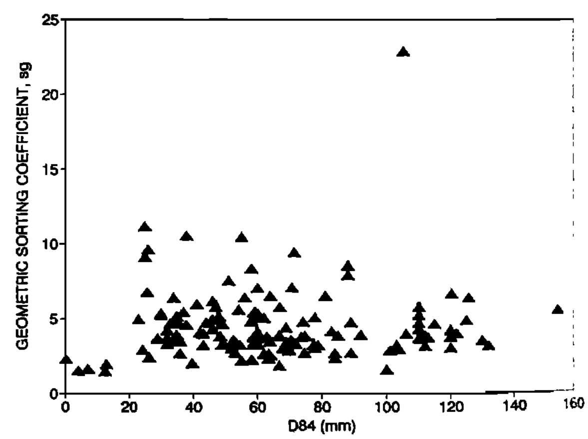

Fig. 6. Sorting coefficient plotted against *D84* for spawning gravel entries in data set (Table 1).

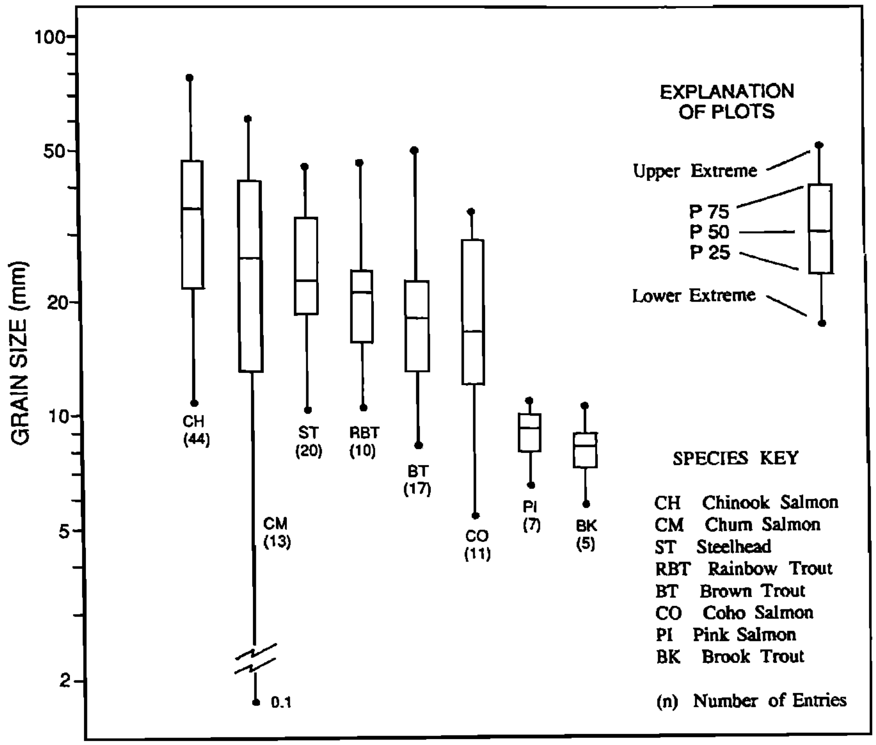

Fig. 7. Box-and-whisker plots showing spread of median sizes reported by species for entries in data set (Table 1). These box-and-whisker plots follow the format of *Tukey* [1977], with the whiskers extending to upper and lower extremes.

s^{-1}, quite similar to the 0.6 m s^{-1} found by *Crisp and Carling* [1989] for the same size fish.

The relation between fish size and redd characteristics is confounded by a spawning run's size variability, local gravel size availability, and the presence of upwelling or downwelling currents. Fish size varies widely within a given population, as illustrated in tributaries to the Owens River in eastern California where a single stream may have spawning brown trout ranging in size from 20 to 45 cm (D. Wong, California Department of Fish and Game, personal communication, 1987). If a narrow range of gravel sizes were available in such a stream, different sized fish would use similar gravels.

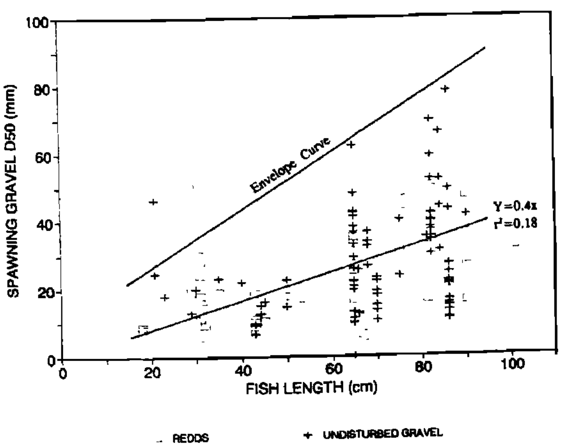

Fig. 8. Relation between median size of spawning gravel and length of spawning fish for entries in data set (Table 1). The envelope curve defines the upper limit of acceptable gravel sizes but excludes two outlying points (entries 65 and 20) to better constrain most data.

The age structure (and thus average size) of fish spawning in a given reach may fluctuate yearly or over the long term. For example, when W. F. Van Woert and E. J. Smith, Jr. (unpublished manuscript, 1962) sampled spawning gravels of the Upper Sacramento River, California in the early 1960s, the spawning run of chinook salmon had a 50 : 50 ratio between fish of ocean ages 3 and 4 (average size 73 versus 95 cm). Due to increased commercial harvests offshore, the ratio has shifted to 65 : 35, and the average size of spawning chinook salmon in the Upper Sacramento River has decreased accordingly (F. Meyer and J. Hayes, California Department of Fish and Game, personal communication, 1987).

The size of available spawning gravels may vary substantially from site to site because of factors such as climate, drainage area, basin lithology, structure, local channel slope, and anthropogenic land use factors. Since utilization of habitat components is influenced by availability [*Baldrige and Amos*, 1981], the gravel sizes used may vary with the sizes available. Individual samples of rainbow trout (*Oncorhynchus mykiss*) spawning gravels in the Colorado River and tributaries ranged from 9.5 to 64 mm in median size and did not increase with fish size. In fact, gravel sizes appeared to decrease with increasing fish size because the smallest fish used steep tributary streams with coarse gravels while the larger fish used the smaller gravels of the mainstem [*Kondolf et al.*, 1989].

Salmonids have evolved to make use of extreme habitats. Larger fish possess an increased range of available options due to their ability to spawn in coarse gravels. However, fish select spawning gravels based not only on particle size but also on factors such as water depth and velocity, cover, and the presence of upwelling or downwelling currents (e.g., chum salmon of the Susitna River). The influence of these and other factors could further confound the relation between fish size and spawning gravel size.

Acknowledgments. The authors are indebted to the many colleagues who shared insights and techniques, especially Mike Sale, Glenn Cada, Steve Railsback, Yetta Jager, and Craig Brandt (Oak Ridge National Laboratory), Christopher Estes (Alaska Department of Fish and Game), Tom Lisle (U.S. Department of Agriculture (USDA) Redwood Science Laboratory), and Carl McLemore (USDA Forest Service, Corvallis, Oregon). We are likewise indebted to the many colleagues who shared data, as detailed in the work by *Kondolf* [1988]. This manuscript has been immeasurably improved by the editorial suggestions of Lisa Micheli and anonymous reviewers. This publication is based in part on work performed in the laboratory graduate participation program under contract DE-AC05-760R00033 between the U.S. Department of Energy and Oak Ridge Associated Universities. Manuscript preparation was partially supported by the University of California White Mountain Research Station and a grant from the University of California Water Resources Center administered by the Center for Environmental Design Research.

REFERENCES

Adams, J. N., and R. L. Beschta, Gravel bed composition in Oregon coastal streams, *Can. J. Fish. Aquatic Sci.*, *37*, 1514–1521, 1980.

Allen, K. R., Limitations on production in salmonid populations in streams, *Symposium on Salmon and Trout in Streams*, edited by T. G. Northcote, pp. 3–18, University of British Columbia, Vancouver, 1969.

Baldrige, J. E., and D. Amos, A technique for determining fish habitat suitability criteria: A comparison between habitat utilization and availability, in *Proceedings of the Symposium on Acquisition and Utilization of Aquatic Habitat Inventory Information*, pp. 251–258, American Fisheries Society, Portland, Oreg., 1981.

Burger, C. V., D. B. Wangaard, R. L. Wilmont, and A. N. Palmisano, Salmon investigations in the Kenai River, Alaska, 1979–1981, report, 139 pp., U.S. Fish and Wildlife Serv., Nat. Fish. Res. Cent., Alaska Field Sta., Anchorage, 1983.

Burner, C. J., Characteristics of spawning nests of Columbia River salmon, *U.S. Fish Wildlife Serv. Bull.*, *61*, 97–110, 1951.

Burns, J. W., Spawning bed sedimentation studies in northern California streams, *Calif. Fish Game*, *56*, 253–270, 1970.

Cederholm, C. J., and E. O. Salo, The effects of logging road landslide siltation on the salmon and trout spawning gravels of Stequaleho Creek and the Clearwater River Basin, Jefferson County, Washington, 1972–1978, *Rep. FRI-UW-7915*, Fish. Res. Inst., Univ. of Wash., Seattle, 1979.

Chambers, J. S., R. T. Pressey, J. R. Donaldson, and W. R. McKinley, Research relating to study of spawning grounds in natural areas, annual report, contract DA 35026-Eng-20572, Dept. of Fish., State of Wash., Olympia, 1954.

Chambers, J. S., G. H. Allen, and R. T. Pressey, Research relating to study of spawning grounds in natural areas, annual report, contract DA.35026-Eng-20572, Wash. State Dep. of Fish., Olympia, 1955.

Chapman, D. W., D. E. Weitkamp, T. L. Welsh, and T. H. Schadt, Effects of minimum flow regimes on fall chinook spawning at Vernita Bar, 1978–82, report, Don Chapman Consultants and Parametrix, Boise, Idaho, 1984.

Church, M. A., D. G. McLean, and J. F. Wolcott, River bed gravels: Sampling and analysis, in *Sediment Transport in Gravelbed Rivers*, edited by C. R. Thorne, J. C. Bathurst, and R. D. Hey, pp. 43–79, John Wiley, New York, 1987.

Conkling, H., R. Eckis, and P. L. K. Gross. Groundwater storage capacity of valley fill, *Calif. Div. Water Resour. Bull.*, *45*, 279 pp., 1934.

Crisp, D. T., and P. A. Carling. Observations on siting, dimensions, and structure of salmonid redds, *J. Fish. Biol.*, *34*, 119–134, 1989.

Folk, R. L., *Petrology of Sedimentary Rocks*, 182 pp., Hemphill, Austin, Tex., 1980.

Hartman, G. F., and D. M. Galbraith, The reproductive environment of the Gerrard stock rainbow trout, *Fish. Manage. Publ. 15*, 51 pp., Dep. of Recreat. and Conserv., Fish. Res. Sect., Victoria, British Columbia, 1970.

Helle, J. H., Biological characteristics of intertidal and freshwater spawning of pink salmon at Olsen Creek, Prince William Sound, Alaska, 1962–63, *Spec. Sci. Rep. Fish. 602*, 19 pp., U.S. Fish and Wildlife Serv., Washington, D. C., 1970.

Hobbs, D. F., Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters, *N. Z. Mar. Dep. Fish. Bull.*, *6*, 104 pp., 1937.

Ibbeken, H., The mystery of bimodality: Falsification of current concepts, proposal of a new one, in *Dynamics of Gravel Bed Rivers*, John Wiley, New York, 1992.

Inman, D. L., Measures for describing the size distribution of sediments, *J. Sediment. Petrol.*, *22*, 125–145, 1952.

Knott, J. M., and S. W. Lipscomb, Sediment discharge data for selected sites in the Susitna River basin, Alaska, 1981–82, *U.S. Geol. Surv. Open File Rep.*, *83–870*, 45 pp., 1983.

Kondolf, G. M., Salmonid spawning gravels: A geomorphic perspective on their size distribution, modification by spawning fish, and criteria for gravel quality, Ph.D. dissertation, Dep. of Geogr. and Environ. Eng., Johns Hopkins Univ., Baltimore, Md., 1988.

Kondolf, G. M., S. S. Cook, H. R. Maddux, and W. R. Persons, Spawning gravels of rainbow trout in Glen and Grand Canyons, Arizona, *J. Ariz. Nev. Acad. Sci.*, *23*, 19–28, 1989.

Kondolf, G. M., G. F. Cada, M. J. Sale, and T. Felando, Distribution and mobility of potential salmonid spawning gravels in steep boulder-bed streams of the eastern Sierra Nevada, *Trans. Am. Fish. Soc.*, *120*, 177–186, 1991.

Kondolf, G. M., M. G. Wolman, and M. J. Sale, Modification of fluvial gravel size by spawning salmonids, *Water Resour. Res.*, this issue.

Koski, K. V., The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams, M.S. thesis, 84 pp., Oreg. State Univ., Corvallis, 1966.

Krumbein, W. C., Flood gravel of San Gabriel Canyon, California, *Geol. Soc. Am. Bull.*, *51*, 636–676, 1940.

Krumbein, W. C., Flood deposits of Arroyo Seco, Los Angeles County, California, *Geol. Soc. Am. Bull.*, *53*, 1355–1402, 1942.

Lisle, T. E., Sediment transport and resulting deposition in spawning gravels, North Coastal California, *Water Resour. Res.*, *25*, 1303–1319, 1989.

Lotspeich, F. B., and F. H. Everest, A new method for reporting and interpreting textural composition of spawning gravel, *Res. Note PNW-369*, U.S. For. Serv. Pac. Northw. Exp. Stat., Corvallis, Oreg., 1981.

Maddux, H. R., D. M. Kulby, J. C. deVos, Jr., W. R. Persons, R. Staedicke, and R. L. Wright, Effects of varied flow regimes on aquatic resources of Glen and Grand Canyons, final report, contract No. 4-AG-40-01810, 291 pp., U.S. Bur. of Reclam., Denver, Colo., 1987.

McNeil, W. J., and W. H. Ahnell, Success of pink salmon spawning relative to size of spawning bed materials, *Spec. Sci. Report Fish. 469*, 15 pp., U.S. Fish and Wildlife Serv., Washington, D. C., 1964.

Morris, D. A., and A. I. Johnson, Summary of hydrological and physical properties of rock and soil materials as analyzed by the hydrological laboratory of the US Geological Survey 1948–1960, *U.S. Geol. Surv. Water Supply Pap.*, *1839-D*, 39 pp., 1967.

Orcutt, D. R., B. R. Pulliam, and A. Arp, Characteristics of steelhead trout redds in Idaho streams, *Trans. Am. Fish. Soc.*, *97*, 42–45, 1968.

Peterson, R. H., Physical characteristics of Atlantic salmon spawning gravels in some New Brunswick streams, *Fish. Mar. Serv. Tech. Rep.*, *785*, 28 pp., 1978.

Pettijohn, F. J., *Sedimentary Rocks*, 3rd ed., 628 pp., Harper and Row, New York, 1975.

Platts, W. S., M. A. Shirazi, and D. H. Lewis, Sediment particle sizes used by salmon for spawning with methods for evaluation, *U.S. EPA Rep. EPA 600/3-79-043*, Corvallis, Oreg., 1979.

Plumley, W. J., Black Hills terrace gravels: A study in sediment transport, *J. Geol.*, *56*, 526–577, 1948.

Reiser, D. W., and T. A. Wesche, Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations, *Water Resour. Ser. 64*, Wyo. Water Resour. Res. Inst., Univ. of Wyo., Laramie, 1977.

Schlee, J., Upland gravels of southern Maryland, *Geol. Soc. Am. Bull.*, *68*, 1371–1410, 1957.

Scrivener, J. C., and M. J. Brownlee, Analysis of Carnation Creek gravel quality data 1973 to 1981, in *Proceedings of the Carnation Creek Workshop, A 10-Year Review*, edited by G. F. Hartman, pp. 154–173, Pacific Biological Station, Nanaimo, British Columbia, 1982.

Shirazi, M. A., and W. K. Seim, Stream system evaluation with emphasis on spawning habitat for salmonids, *Water Resour. Res.*, *17*, 592–594, 1981.

Shirazi, M. A., W. K. Seim, and D. H. Lewis, Characterization of spawning gravel and stream system evaluation, Salmon-spawning gravel: A renewable resource in the Pacific Northwest?, *Rep. 39*, pp. 227–278, State of Wash. Water Res. Cent., Wash. State Univ., Pullman, 1981.

Spoon, R. L., Reproductive biology of brown and rainbow trout below Hauser Dam, Missouri River, with reference to proposed hydroelectric peaking, M.S. thesis, 144 pp., Mont. State Univ., Bozeman, 1985.

Tukey, J. W., *Exploratory Data Analysis*, 688 pp., Addison-Wesley, Reading, MA, 1977.

Van den Berge, E. P., and M. R. Gross, Female size and nest depth in coho salmon (*Oncorhynchus kisutch*), *Can. J. Fish. Aquat. Sci.*, *41*, 204–206, 1984.

Vanoni, V. A. (Ed.), *Sedimentation Engineering*, 745 pp., American Society of Civil Engineers, New York, 1975.

Vining, L. J., J. S. Blakely, and B. M. Freeman, An evaluation of the incubation life-phase of chum salmon in the Middle Susitna River, Alaska, *Rep. 5*, Alaska Dep. of Fish and Game Winter Habitat Invest., Anchorage, 1985.

Vronskiy, B. B., Reproductive biology of the Kamchatka River chinook salmon (*Oncorhynchus tschawytscha* (Walbaum)), *J. Ichthyol.*, *12*, 259–273, 1972.

Warner, K., Natural spawning success of land-locked salmon (*Salmo salar*), *Trans. Am. Fish. Soc.*, *92*, 161–164, 1963.

Wilbur, R. L., Grey literature: A professional dilemma, *Fisheries*, *15*, 2–6, 1990.

Witzel, L. D., Relation of gravel size to spawning site selection and alevin production by *Salvelinus fontinalis* and *Salmo trutta*, M.S. thesis, Univ. of Guelph, Ont., 1980.

G. M. Kondolf, Department of Landscape Architecture, College of Environmental Design, The University of California, Berkeley, CA 94720.

M. G. Wolman, Department of Geography and Environmental Engineering, Johns Hopkins University, Baltimore, MD 21218.

(Received April 28, 1992;
revised February 2, 1993;
accepted February 15, 1993.)