SPAWNING GRAVELS OF RAINBOW TROUT IN GLEN AND GRAND CANYONS, ARIZONA

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ABSTRACT

Stream gravels were sampled in the Colorado River and tributaries in Grand Canyon National Park, Arizona, to assess the quality and extent of gravels available for spawning rainbow trout. Average median diameters of potential (i.e., unspawned) spawning gravels in tributaries (22 mm) fell at the coarse end of the range of averages reported in the literature, while the average for mainstem gravels above Lee's Ferry (12 mm) fell just below the range. Fine sediment content of the tributary gravels compared favorably with those reported in the literature for rainbow trout spawning gravels, but mainstem gravels had higher levels of sediment finer than 0.85 mm. However, both tributary and mainstem gravels satisfied generalized standards for fine sediment content drawn from emergence studies. Thus, tributary gravels can be considered as excellent, mainstem gravels above Lee's Ferry as adequate. Paired samples of redd and unspawned gravel in tributaries indicate that spawning fish reduced the percentage of fine sediment (< 0.85 mm) from 6% to 2% on average; they also increased the average size and improved sorting. Mainstem gravels above Lee's Ferry lie below Glen Canyon Dam and have no source of recruitment, so a long-term reduction in suitably-sized spawning gravels and a progressive armoring of the bed with cobbles may occur.

INTRODUCTION

All salmonids (salmon and trout) deposit their eggs in freshwater gravels to incubate. After hatching, the young remain in the gravel for a week to a month, then emerge as free-swimming fry (Northcote 1969). To be suitable for spawning, gravels must be small enough to be movable by the spawning fish, yet sufficently free of interstitial fine sediment that oxygen-bearing water can flow freely through them, past the incubating eggs (Allen, 1969, Reiser and Bjornn 1979). In the course of digging a redd (a nest in the gravel), the female agitates the bed so that fine sediment is washed away by the current, resulting in a cleaning of the gravel in the redd (Kondolf 1988).

Since closure of Glen Canyon Dam in 1963, an important rainbow trout fishery has developed in the Colorado River in the Grand Canyon (used here to designate the entire reach from Glen Canyon Dam down to Lake Mead, encompassing Glen, Marble, and Grand Canyons). The trout fishery is especially productive in the reach near Lee's Ferry, where consistently cold waters released from the dam have produced a nearly complete change in species composition from native warmwater fishes to introduced trout.

This study was undertaken as a part of a larger research effort in which the fisheries resources of the Colorado River system in the Grand Canyon, and the effects of fluctuating flows upon them, were examined in detail (Maddux *et al.* 1987). Spawning by Colorado River rainbow trout in tributaries had been recognized before this study, but the quality of those gravels in the tributaries had not been assessed. Spawning in the mainstem had been suspected, but its importance had not previously been documented, nor had the quality of mainstem gravels available for spawning been quantified.

The size composition of spawning gravels has been shown to be related to successful incubation and emergence in field studies elsewhere (e.g., Koski 1966, Tagart 1984) and in laboratory experiments

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(e.g., Phillips *et al.* 1975, Tappel and Bjornn 1983). Thus, assessment of the quality of gravels available to spawning salmonids is an important component to understanding factors that may limit reproductive success.

The objectives of this study were to characterize the gravels available for trout spawning in the Colorado system in the Grand Canyon, to compare these gravels with standards of gravel quality developed from the literature, and to quantify the size modification produced by redd construction. The quantity of gravel available for spawning is also an important factor, but its determination was beyond the scope of the present study. Results indicate that gravels in tributaries are of excellent quality, while gravels in the mainstem are adequate. We are indebted to Martha Hahn-O'Neil of the National Park Service for arranging our collecting permit and to Humphrey Summit Association for logistical support.

STUDY AREA

The Colorado River flows for over 400 km and drops more than 650 m from Glen Canyon Dam to Lake Mead. The combination of its large discharge [long-term average flow at Lee's Ferry is 480 m^3/s (Anderson and White 1979)] and its high gradient make the Colorado in the Grand Canyon a river of exceptional power. The mainstem is characterized by alternating long runs (average gradients typically 0.05% or less) and short, steep rapids (average gradients typically 0.5 to 1.7%; Leopold 1969).

The flow of the Colorado River in the Grand Canyon is increased on average less than 5% by tributary inflow, so water temperature and water quality in the river largely reflect the properties of the hypolimnetic waters released from Lake Powell; water temperature at Lee's Ferry ranges only from 6° to 12°C and increases on average by less than 2°C over the 385 km from Lee's Ferry to Diamond Creek (Maddux *et al.* 1987).

Tributary streams can be regarded as belonging to one of three types: low gradient perennial streams with large drainage areas and relatively fine-grained sediment loads at their mainstem confluences; steep, spring-fed perennial streams; and steep ephemeral streams. By virtue of their high gradients, the latter two types are competent to transport boulders during flash floods and associated debris flows (Cooley *et al.* 1977, Webb *et al.* 1988), and their mainstem confluences are typically marked by violent rapids. In contrast, rapids are subdued or absent at the confluences of low gradient tributaries.

The composition and distribution of fish species in the Grand Canyon has been profoundly altered by Glen Canyon Dam. The consistently cold water released from the dam, coupled with stocking efforts, has changed the system from one dominated by native warmwater species to introduced trout (Carothers and Minckley 1981). Of the trout, the most successful have been rainbow trout *(Salmo gairdneri)* and to a lesser extent, brown trout *(S. trutta).* Brook trout *(Salvelinus fontinalis)* distributions appear to reflect stocking and migration, with only limited natural reproduction. Warmwater species are nearly absent at Lee's Ferry, but increase in abundance downstream. Both introduced and native species utilize tributaries, but at different times of the year. Adult trout migrate into the tributaries in the spring and summer (Maddux *et al.* 1987). The tributaries utilized by trout for spawning habitat are of the second type described above, i.e., steep spring-fed, perennial streams. Steep, ephemeral streams are unsuitable because they dry up, and low-gradient perennial streams are unsuitable because their mobile bed material is predominantly fine-grained.

The use of tributary habitats by spawning trout has been recognized for some time (Carothers and Minckley 1981) in part because redds are easily seen in the beds of clear shallow tributaries. Mainstem spawning was suspected but its contribution was not demonstrated until Maddux *et al.* (1987) (1) observed redds in this reach and (2) conducted dye tests on fish to determine the hatchery contribution to the population.

During unusually low releases from Glen Canyon Dam, Maddux *et al.* (1987) observed high densities of redds on gravel bars above Lee's Ferry, excavated numerous redds, and encountered eggs. They also examined over 1500 rainbow trout at Lee's Ferry for the tetracycline dye characteristic of stocked fish. Based on this study, they concluded that natural reproduction was responsible for 27.5% percent of the population in this reach. The nearest tributary spawning habitat is Nankoweap Creek, 80 km downstream; data from mark-recapture studies indicate that movement of this many fish so far upstream was improbable. Thus, Maddux *et al.* (1987) (1) demonstrated that trout use mainstem gravels for spawning, and (2) independently established that this natural reproduction accounted for an important part of the fishery above Lee's Ferry.

METHODS

Gravel samples were collected from redds and from unspawned gravels in 6 tributaries and on 4 mainstem gravel bars (Fig. 1). Samples 1-21 were collected in December 1985 on a river expedition from Lee's Ferry to Diamond Creek; samples 22-24 were collected in October 1984 between Glen Canyon Dam and Lee's

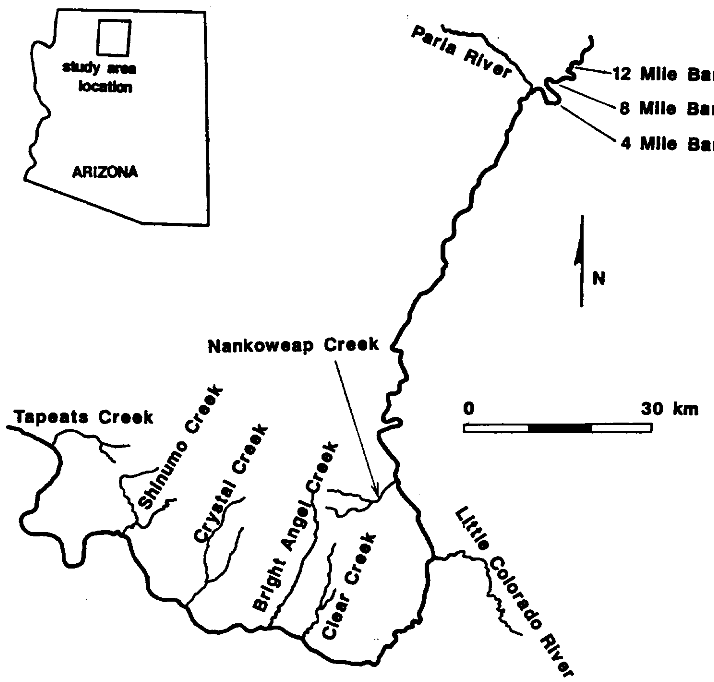

Figure 1. Location map of gravel samples, Colorado River and tributaries, Grand Canyon National Park. River miles refer to distance downstream from Lee's Ferry.

Ferry (bar designations refer to mileage upstream of Lee's Ferry). All tributary samples were collected within a few hundred meters of the mainstem confluence. Identification of redds was based on their morphology and the lighter color of the clean gravel in them, distinct from the surrounding undisturbed gravel, and was confirmed by encountering eggs in gravel samples.

Samples 1-21 were collected with a 25-cm diameter plastic bucket with the bottom removed. This was the only sampler sufficiently portable for use on a raft trip, but it was limited in operation to water depths of 0.5 m or less. The sampler was forced into the substrate and bed material was removed down to the depth at which eggs were no longer encountered or at which substrate became impenetrable, usually 10-15 cm below the bed surface.

Undisturbed gravel adjacent to the redds was also sampled to document the initial size distribution of the gravel, before modification by the spawning fish. In Tapeats Creek and Nankoweap Creek, the streambed gravels were sufficiently extensive and homogenous that adjacent samples could be confidently assumed to represent the same gravels as in the redds, only without modification from redd construction. In Clear, Crystal, and Shinumo Creeks, the channels were so small and bed material so heterogeneous that the assumption could be made with less confidence.

Samples 1-21 ranged in size from 6.6 kg to 17 kg in total weight, averaging 11.9 kg. These samples are smaller than recommended for accurate representation of the coarsest fractions (Church *et al.* 1987), but probably yield reasonably accurate measures of central tendency. Fine sediment suspended in the cylinder was sampled by filling a 250 ml bottle with the muddy water and recording the volume of water inside the cylinder. Total suspended solids were measured in the laboratory and total weight of the suspended solids was computed and added to the finest fraction in sieve analysis.

Gravel samples were dried in the sun or over a campfire. Fractions down to 4 mm in size were sieved in camp, weighed on a triple beam balance, and discarded; finer fractions were retained for sieving in the laboratory. Weights retained on each sieve were converted to percentages and summed to develop cumulative size distributions. Different sets of sieves were utilized for samples 1-21 and samples 22-24, as reflected in Appendix 1. The cumulative size distributions were plotted on semilogarithmic paper, following standard sedimentologic practice (Vanoni 1975). Water depth, velocity and water surface slope at each redd site for samples 1-21 are reported in Kondolf (1988).

Samples 22-24 were collected from bar surfaces exposed by low water levels. Because water was not flowing over the bed, the sampling strategy did not have to account for the problems of fine sediment washing downstream. The area to be sampled was outlined with a 25-cm diameter bucket, and the sample was removed with a shovel. The entire sample was taken to the laboratory, where it was dried, sieved, and weighed. Samples 22-24 ranged in size from 26 to 30 kg, averaging 28.9 kg.

Gravel sizes were compared with standards developed from a review of the literature (Kondolf 1988). Suitability of gravel for spawning depends on the size of the framework grains (whether the fish can move them) and on the fine sediment content. Framework size can be expressed by a measure of the central tendency of the distribution (such as the median), while fine sediment content has typically been expressed as the percentage finer than a given grain size. Framework size was assessed by comparison with published studies of gravel in rainbow trout redds. Fine sediment content was assessed by a similar comparison with published redd data and by application of criteria from results of published emergence studies.

RESULTS AND DISCUSSION

Size Distributions of Gravel Samples

Size descriptors (drawn from cumulative size distributions in Appendix 1) are presented in Table 1. Percentile values D16 and D84 refer to the sizes for which 16% and 84% of the sample is finer. Also listed in Table 1 are the geometric mean, dg, the geometric sorting index of geometric standard deviation, sg, and skewness, sk (Vanoni 1975), computed as:

$$dg = (D16\ D84)^{0.5}$$
$$sg = (D84/D16)^{0.5}$$
$$sk = \log(dg/D50)/\log(sg).$$

Table 1. Size Descriptors for Gravel Samples, Colorado River and Tributaries.

Sample No. / Site		River Mile (a)	Size Descriptors (mm) D16	D50	D84	dg (mm)	sg	sk	Percent < than: 0.85mm	3.35mm
TRIBUTARY REDDS										
GC-1	Nankoweap Ck	52	3.7	15.5	45	12.9	3.49	-0.15	3.1	15.5
GC-2	Nankoweap Ck	52	10.0	22.5	43	20.7	2.07	-0.11	0.3	3.1
GC-7	Clear Ck	84	2.6	18	54	11.8	4.56	-0.28	4.7	20.5
GC-9	Clear Ck	84	9.5	39	106	31.7	3.34	-0.17	1.2	5.8
GC-12	Crystal Ck	98	18	47	80	37.9	2.11	-0.29	nd	nd
GC-13	Crystal Ck	98	8.6	34	59	22.5	2.62	-0.43	0.8	3
GC-15	Shinumo Ck	108	8	40.5	66	23.0	2.87	-0.54	1	7.1
GC-16	Shinumo Ck	108	14	64	122	41.3	2.95	-0.40	0.5	4.8
GC-18-9	Tapeats Ck	134	5.5	19.8	61	18.3	3.33	-0.06	2.3	9.1
AVERAGE			8.9	33.4	71	24.5	3.04	-0.27	1.5	7.7
STD DEV			4.6	15.2	25.7	9.8	0.7	0.2	1.5	6.2
TRIBUTARY UNSPAWNED										
GC-5	Nankoweap Ck	52	2.0	12.5	37	8.6	4.30	-0.26	6.6	22.4
GC-3-4	Nankoweap Ck	52	2.9	9.5	28	8.9	3.11	-0.06	2.5	20
GC-8	Clear Ck	84	2.4	17.0	65	12.5	5.20	-0.19	7.6	23.9
GC-10	Clear Ck	84	11.0	46.0	94	32.2	2.92	-0.33	6.1	12.3
GC-11	Bright Angel Ck	88	2.0	25.0	71	11.9	5.96	-0.42	8.4	20.6
GC-14	Crystal Ck	98	7.0	21.0	44	17.5	2.51	-0.20	3.7	7
GC-17	Shinumo Ck	108	2.6	28.0	76	14.1	5.41	-0.41	6.8	18.9
GC-20-1	Tapeats Ck	134	3.2	16.3	57	13.4	4.25	-0.13	10.4	17.3
AVERAGE			4.1	21.9	59	14.9	4.21	-0.25	6.5	17.8
STD DEV			3.0	10.8	20.6	7.1	1.2	0.1	2.3	5.2
MAINSTEM REDDS										
GC-6	Nankoweap Ck fan	52	6.8	25	58	19.9	2.92	-0.21	2.3	8
GC-22	Four-mile bar	-4	1.1	10	28	5.5	5.05	-0.36	8	19
GC-23	Eight-mile bar	-8	1	11	32	5.7	5.66	-0.38	10	18.5
Average of Samples 22-23			1.1	10.5	30.0	5.6	5.4	-0.4	6.8	15.2
MAINSTEM UNSPAWNED										
GC-24	Twelve-mile bar	-12	0.5	16	55	5.2	10.49	-0.47	15	25

Notes: (a) River mile locations <0 refer to distance (in miles) upstream of Lee's Ferry

Median diameter, D50, and geometric mean, dg, are probably the most commonly employed measures of central tendency for particle size distributions. Stream gravels of the size typically used by spawning salmonids are usually negatively skewed; that is, their size distributions are not perfectly lognormal but are characterized by tails extended into fine sediment sizes (Kondolf 1988). This is reflected in negative values of skewness and by a tendency for D50 to exceed dg. The geometric sorting index, sg, reflects how well fluvial processes have collected similar-sized particles together by virtue of their similar settling velocities. If a deposit is dominated by a small range of grain sizes, it is "well-sorted" and has a low value of sg. If a wide range of grain sizes is more evenly represented, the deposit is "poorly sorted" or "well graded" and has a high value of sg.

Box-and-whisker plots of the size distributions (Figure 2; modified after Tukey 1977) show that spawning gravels in the tributaries were coarser than those in the mainstem. In tributaries, median diameter averages 33 mm in redds, 21.9 mm in unspawned gravels (Table 1). Mainstem redd samples 22 and 23 had median diameters of 10 and 11 mm, respectively. There are too few mainstem samples to draw firm conclusions, but the fact that the mainstem samples were so similar in size despite being collected nearly 5 km apart suggests that mainstem gravels above Lee's Ferry may be less variable (over space) than tributary gravels.

Variability in tributary gravel size reflects differences among streams in the sizes of gravel available to spawners. The size of gravels available in a given stream is a function of geomorphic variables (e.g., basin relief and lithology, runoff characteristics, channel slope, and recent flash flood history) and their interaction particular to each site. Repeated visual observations of tributary spawning habitats over a period of 2 years (Maddux *et al.* 1987) indicated that fine sediment content of bed material in tributaries was highly variable over time, presumably reflecting changes wrought by flash floods.

Sorting was best among tributary gravels, especially the redd samples, the latter apparently reflecting the removal of fine sediments during spawning. The poor sorting of the mainstem unspawned sample (no. 24) and its extreme negative skewness both reflect its high fine sediment content.

The mainstem gravels above Lee's Ferry are relict deposits of the free-flowing Colorado River, derived from upstream sources. Unlike the steep tributaries, with their heterogeneous beds, conditions on the mainstem bars are relatively more uniform and gradients are lower. Thus, deposits may be more uniform

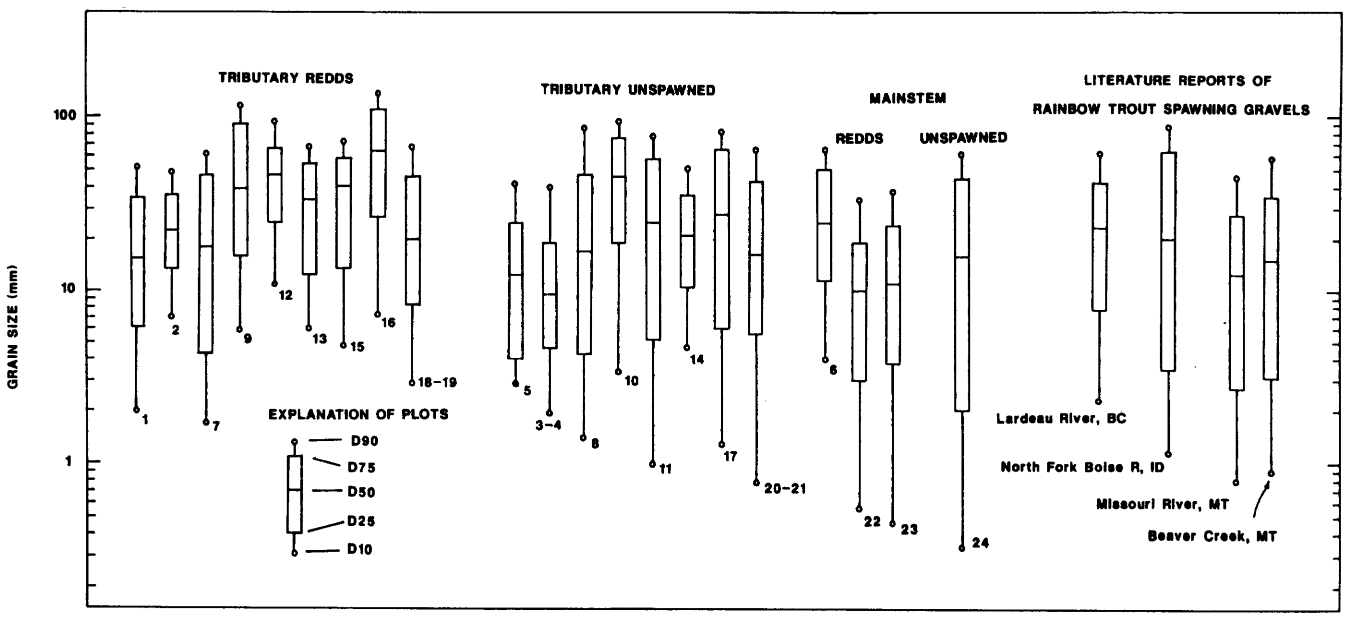

Figure 2. Size distributions of gravel samples from Colorado River and tributaries, Grand Canyon National Park, presented as box-and-whisker plots. For each sample, the rectangle (box) encompasses the middle 50% of the sample, from the D25 to D75 values, termed the "hinges." The median size, D50, is represented by a horizontal line through the box. Above and below the box are lines (whiskers) extending to the D90 and D10 values. Each plot is labeled with its sample number. Also shown are size distributions for rainbow trout spawning gravels reported in the literature, each designated by location. (Author, n, and fish length associated with each gravel reported in the literature are presented in Table 2.)

from site to site and contain higher levels of fine sediment. Mainsteam redd sample 6 was collected from fan deposits at the confluence of Nankoweap Creek, and its size characteristics were evidently determined more by the tributary flows that deposited it than by subsequent reworking from mainstem flows.

Comparison with Gravel Sizes Reported in Literature

Gravel sizes for redd and unspawned gravels have been reported for a variety of species and localities (Kondolf 1988). Most work has been done on the economically important Pacific salmon species, but resident trout have also been studied. Size distributions for gravels used by rainbow trout reported in three published studies are presented in Fig. 2 for comparison with our samples. All are averaged size distributions for potential spawning gravels; that is, they are composite size distributions from gravels that are known to be utilized by rainbow trout but did not come from actual redds. In Fig. 2, these gravels are identified by location; the reference from which they were drawn, the average length of the spawning female, the number of samples in the average, and selected size descriptors are presented in Table 2. For the purposes of comparison, the same information is presented for the gravels sampled in this study.

Of the size distributions reported in the literature, the coarsest are from the Lardeau River in British Columbia. The size of the gravels selected there may reflect, in part, the unusually large size of these Gerrard stock rainbow trout (G.F. Hartman, personal communication to G.M. Kondolf, 1987). However, when the table is viewed as a whole, a more general explanation suggests itself. The larger gravels are associated with smaller rivers and streams, presumably with higher gradients than the larger, low-gradient rivers. Beaver Creek, although small, was sampled near its confluence with the mainstem Missouri in what we presume was a reach of relatively low gradient. Thus, the sizes of gravel selected by spawning fish are influenced by the sizes locally available, which, in turn, are influenced by geomorphic variables.

Because the sizes reported in these published studies all reflected unspawned conditions, they are properly compared only with samples of unspawned gravels, not from redds, because the redd gravels would have been modified during redd construction, as discussed below. Tributary gravels sampled in this study were on the coarse end of the range reported in the literature (Table 2). Median diameters averaged 21.9 mm in the unspawned tributary gravel, contrasted with median diameters of from 12.5 to 23.5 mm reported in the other studies. The only sample of unspawned gravel in the mainstem above Lee's Ferry (no. 24) had a median diameter of 16 mm, well within the range of values derived from the literature.

Framework sizes of the tributary gravels appear to be consistent with those reported for rainbow trout elsewhere. The relative coarseness of the gravels reflects the characteristics of the tributaries used by spawning fish: perennial streams with high gradients and generally coarse bed material.

The average median diameter of the gravel samples obtained from redds on the mainstem bars above Lee's Ferry (nos. 22-23) was lower than any of the literature-derived averages, not so much because these gravels lack large particles, but because they possess an abundance of fine sediment. The fraction of sediment

Table 2. Rainbow trout spawning gravel reported in literature and this study.

Location	Reference	Fish Size(cm)	n	D50 (mm)	dg (mm)	sg	sk	Percent less than 0.85mm	Percent less than 3.4mm
Lardeau, R, BC	Hartman and Galbraith (1970)	75	6	23.5	14.7	3.6	-0.37	6.3	15.2
N Fk Boise, R, ID	Platts *et al.* (1979)	30	45	20	12.4	6.5	-0.25	7	24
Missouri R, MT	Spoon (1985)	44	27	12.5	8.3	4.6	-0.27	11.1	nd
Beaver Ck, MT	Spoon (1985)	44	19	15	9.3	4.9	-0.3	9.8	nd
Colorado R, AZ:	This study								
tributary redds		40	9	33.4	24.5	3.04	-0.27	1.5	7.7
tributary unspawned		40	8	21.9	14.9	4.21	-0.25	6.5	17.8
mainstem redds (22-23)		45	2	10.5	5.6	5.4	-0.4	6.8	15.2
mainstem unspawned (24)		45	1	16	5.2	10.5	-0.47	15	25

finer than 0.85 mm in the literature-derived distributions ranged from 7 to 11.3%. Unspawned gravels in the Grand Canyon tributaries averaged 6.2% finer than 0.85 mm, while mainstem redds above Lee's Ferry (samples 22-23) averaged 6.8% finer than 0.85 mm, the mainstem unspawned sample (no. 24) had 15% over 0.85 mm.

Results of numerous emergence studies were compiled by Kondolf (1988) to yield generalized standards for acceptable fine sediment content: the percentage finer than 0.85 mm should be under 14, and the percentage finer than 3.35 mm should be under 30. All except sample 24 satisfy the former standard; all samples satisfy the latter standard. Sample 24 is unspawned, so criteria from emergence studies (using redds or simulated redds) are not properly applied directly, because it can be expected that the fine sediment fraction will be reduced during spawning. Redd samples from this reach (samples 22 and 23) have less than 14% finer than 0.85 mm, and therefore satisfy the standard. Thus, mainstem gravels above Lee's Ferry do not compare favorably with rainbow trout spawning gravels reported in the literature but satisfy standards drawn from emergence studies.

Size Modification by Spawning Fish

Where possible, tributary gravel samples were collected in pairs of redd and adjacent, unspawned samples. These pairs consisted of the following samples (listed as spawned-unspawned): 1-5, 2-3&4 (avg), 7-8, 9-10, 13-14, 16-17, 18&19-20&21. With the assumption that the adjacent gravels were representative of conditions at the redd site before spawning, changes effected by spawning can be computed by comparing size distributions for the redd and unspawned samples. As noted above, we had more confidence that adjacent samples were representative of initial redd site conditions in Nankoweap and Tapeats Creek, with their larger gravel deposits, than in the other tributaries.

The comparison of the paired samples indicates that spawning fish reduced the average fraction finer than 4 mm from 19% to 11%, the average fraction finer than 0.85 mm from 6% to 2%. Primarily as a result of this reduction of fine sediment, the mean diameter increased (on average) from 21.5 to 30.4 mm, and sorting improved (sg decreased from 4.0 to 3.3). Thus, spawning trout in the tributaries substantially improved the quality of their spawning gravel in the course of redd construction.

Abundance of Spawning Gravel

The foregoing sections deal primarily with the quality of spawning gravels in the Colorado River and tributaries in the Grand Canyon. Less information is available to specify the quantity of available spawning gravels, but it is a topic that merits consideration, especially in view of potential impacts on this resource from operation of Glen Canyon Dam.

Tributary spawning gravels are limited in extent because of the small size of the channels and the often patchy distribution of gravels. Moreover, many of the tributary gravels may be unavailable at low stage because of migration barriers. Our observations indicate that available gravels in tributaries and their fan deposits in the mainstem (e.g., sample 6) are utilized intensively. No long term net change in abundance of these gravels is expected because their recruitment

Table 3. Changes in gravel composition produced by spawning as measured by comparing redd and adjacent, unspawned gravels.

Samples (GC)	Location	Initial Size Descriptors D50 (mm)	sg	Percent less than 3.4mm	0.85mm	Change in Size Descriptors D50 (mm)	sg	Percent < than 3.4mm	0.85mm
1,5	Nankoweap Ck	12.5	4.3	22.4	6.6	3	-0.81	- 6.9	-3.4
2-4	Nankoweap Ck	9.5	3.11	20.0	1.6	13	-1.04	-16.9	-1.3
7-8	Clear Ck	17	5.2	23.9	6.9	1	-0.64	- 3.4	-2.2
9-10	Clear Ck	46	2.92	12.3	4.9	- 7	0.42	- 6.5	-3.7
13-14	Crystal Ck	21	2.51	7.0	3.7	13	0.36	- 4.0	-2.9
16-17	Shinumo Ck	28	5.41	18.9	6.8	36	-2.46	-14.1	-6.3
18-21	Tapeats Ck	16.3	4.25	17.3	10.4	3.5	-0.92	- 8.2	-8.1
Average all samples		21.5	4.0	17.4	5.8	8.9	-0.73	- 8.6	-4.0
Average Nankoweap & Tapeats		12.8	3.9	19.9	6.2	6.5	-0.9	-10.7	-4.3

from the tributary basins should not change, although short-term variations due to flash floods and reworking of flood deposits is normal.

Mainstem spawning gravel above Lee's Ferry is extremely limited and intensively utilized. Examination of bars exposed in October 1984 and April 1987 during unusually low releases from Glen Canyon Dam showed that redds covered nearly the entire surface at some sites. Unlike the tributaries and their fans, the mainstem above Lee's Ferry has no source of gravel recruitment. Gravel from the upper Colorado River basin are trapped in Glen Canyon Dam, and there are no tributary sources above Lee's Ferry. Thus, the mainstem spawning gravel resource in this productive trout fishery must be regarded as threatened over the long term by transport of gravel downstream without replenishment from upstream. The result of these processes below large dams in other rivers has been a reduction in suitably-sized spawning gravel and a progressive armoring of the bed by cobbles (e.g., Buer *et al.* 1981).

CONCLUSIONS

1. Potential rainbow trout spawning gravels are coarser in tributaries to the Colorado River (median diameters averaged 21.9 mm) than in the mainstem above Lee's Ferry (median diameters averaged 12.3 mm).

2. Tributary gravel sizes are highly variable from tributary to tributary. Limited sampling suggests that mainstem gravels above Lee's Ferry display less spatial variability.

3. The size of tributary gravels falls at the coarse end of the range reported in published studies of rainbow trout spawning gravels, while mainstem gravels above Lee's Ferry fall just below the range.

4. Tributary gravels compare favorably in fine sediment content with rainbow trout spawning gravels reported in the literature and satisfy generalized standards drawn from emergence studies. Mainstem gravels above Lee's Ferry do not compare favorably with rainbow trout spawning gravels reported in the literature but satisfy generalized standards drawn from emergence studies.

5. Based on (3) and (4), tributary gravels can be regarded as of excellent quality, mainstem gravels above Lee's Ferry as adequate.

6. Paired samples of redd and unspawned gravel in tributaries indicate that spawning fish reduced the percentage of fine sediment ($<$ 0.85 mm) from 6% to 2% on average; they also increased the median diameter and improved sorting. This reduction in fine sediment content represents a significant improvement in gravel quality effected by the spawning fish.

7. No net long-term changes are anticipated in tributary spawning gravels, although migration barriers may develop when the river is at very low stage, making the tributary gravels inaccessible to the fish.

8. Mainstem gravels above Lee's Ferry have no source of recruitment. As gravels are transported downstream during high flows and are not replenished from upsteam, a long-term reduction in suitably-sized spawning gravels and a progressive armoring of the bed with cobbles may occur.

LITERATURE CITED

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Appendix 1. Cumulative size distributions for gravel samples, Colorado River and tributaries.

Sample No. and Site	Redd/ Adj	Cumulative Percent Finer than Indicated Size (mm) 0.063	0.25	0.85	2	4	9.5	12.5	19	25.4	32	45	64	90	128	180
GC-1 Nankoweap Ck	redd	0.3	0.6	3.2	10.2	17.2	34.2	42.5	58.4	69.2	72.2	84.4	97.3	100.0	100.0	100.0
GC-2 Nankoweap Ck	redd	.0	0.1	0.3	1.4	4.0	15.1	22.0	40.1	57.4	69.9	86.6	100.0	100.0	100.0	100.0
GC-3 Nankoweap Ck	adj	0.1	0.2	1.6	9.5	25.7	62.9	71.5	83.9	88.0	88.8	92.2	100.0	100.0	100.0	100.0
GC-4 Nankoweap Ck	adj	0.5	1.0	3.4	10.9	21.1	41.6	48.8	65.5	76.5	80.4	91.5	93.1	100.0	100.0	100.0
GC-5 Nankoweap Ck	adj	0.3	1.0	6.6	15.9	24.6	42.4	50.1	64.8	74.6	78.8	92.8	100.0	100.0	100.0	100.0
GC-6 Mainstem, N Ck fan	redd	0.1	0.5	2.3	4.9	9.3	21.7	26.5	38.3	50.6	54.9	69.6	88.1	100.0	100.0	100.0
GC-7 Clear Ck	redd	0.7	1.6	4.7	12.0	23.9	39.1	43.4	51.0	58.8	61.8	72.8	91.2	100.0	100.0	100.0
GC-8 Clear Ck	adj	2.0	3.8	6.9	14.1	24.1	38.3	43.0	51.6	61.7	64.6	72.8	84.5	90.3	100.0	100.0
GC-9 Clear Ck	redd	0.1	0.1	1.2	3.5	6.8	16.3	19.9	29.3	36.9	44.5	54.6	71.3	75.0	100.0	100.0
GC 10 Clear Ck	adj	1.3	2.2	4.9	7.9	10.7	14.8	18.3	25.2	33.6	38.2	49.4	68.9	80.9	100.0	100.0
GC-11 Bright Angel Ck	adj	1.1	2.5	8.4	15.7	22.1	32.5	36.7	44.6	50.5	54.1	66.0	79.4	100.0	100.0	100.0
GC-12 Crystal Ck	redd	0.0	0.0	0.0	0.0	3.7	9.1	11.4	17.0	24.1	29.8	46.1	72.5	88.6	100.0	100.0
GC-13 Crystal Ck	redd	0.3	0.5	0.8	1.3	4.2	18.3	25.1	36.3	45.0	49.3	58.1	88.0	88.0	100.0	100.0
GC-14 Crystal Ck	adj	0.5	1.9	3.7	4.9	8.2	22.4	29.3	45.5	61.3	71.6	84.7	100.0	100.0	100.0	100.0
GC-15 Shinumo Ck	redd	0.1	0.2	1.0	3.9	8.4	18.3	22.8	31.2	35.3	40.7	57.2	82.5	100.0	100.0	100.0
GC-16 Shinumo Ck	redd	.0	0.1	0.5	2.6	5.7	12.1	14.8	20.2	24.6	26.5	37.9	50.4	65.1	86.0	100.0
GC-17 Shinumo Ck	adj	0.9	2.4	6.8	13.8	20.6	31.2	35.6	43.2	48.9	51.9	60.8	74.6	100.0	100.0	100.0
GC-18 Tapeats Ck	redd	.0	0.4	2.3	5.1	10.8	28.9	35.5	47.6	57.6	64.4	77.6	83.7	100.0	100.0	100.0
GC-19 Tapeats Ck	redd	0.1	0.5	2.3	5.2	11.4	30.6	37.9	49.9	56.0	59.4	65.9	83.6	100.0	100.0	100.0
GC-20 Tapeats Ck	adj	0.6	3.9	10.6	14.5	19.3	38.9	45.4	57.0	63.7	66.7	76.0	85.5	100.0	100.0	100.0
GC-21 Tapeats Ck	adj	0.4	3.7	10.1	13.6	18.6	34.6	39.8	53.0	62.5	66.5	77.7	93.6	100.0	100.0	100.0

	Redd/ Adj	0.045	Cumulative Percent Finer Than Indicated Size (mm) 0.25	0.5	1	1.7	3	6	11	22	51
GC-22 Mainstem, 4-mi bar	redd	0	3	9	14.9	18.3	24.6	36.8	53.5	78.6	100
GC-23 Mainstem, 8-mi bar	redd	0.1	5.2	11.2	16.6	19.1	23.6	34.3	49.8	72.3	100
GC-24 Mainstem, 12-mi bar	adj	0.2	4	16	22.7	24.5	27.6	32.8	41.8	57.6	79.2