

Spawning by California Golden Trout: Characteristics of Spawning Fish, Seasonal and Daily Timing, Redd Characteristics, and Microhabitat Preferences

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Abstract.—We investigated the spawning biology of California golden trout *Oncorhynchus mykiss aguabonita*, an endemic subspecies of rainbow trout, in the Golden Trout Wilderness, California. We investigated the influence of stream temperature on the seasonal and daily timing of spawning, measured characteristics of completed redds, and quantified microhabitat use and preferences by spawning females. We also quantified size at sexual maturity, degree of sexual size dimorphism, and the operational sex ratio during the spawning season. Golden trout spawning began after peak stream discharge in mid-May, when maximum daily water temperatures consistently exceeded 15°C and continued for approximately 3 weeks. Stream temperatures also influenced the daily timing of spawning activity, with highest activity in the afternoon when stream temperatures approached the daily maximum. Among sexually mature fish (>95 mm), males were significantly larger than females, and ripe males were 3–9 times more abundant than ripe females. Females spawning early in the season were larger and constructed their redds in larger substrates than later-spawning females. Redds were characterized by very small substrates, and females showed distinct preferences for particular substrate sizes, water depths, and water velocities. Females selected spawning sites characterized by mean substrate sizes of 4–12 mm, water depths of 5–20 cm, and water velocities of 30–70 cm/s. Compared to spawning microhabitat preferences of other salmonids, female golden trout used smaller substrates, shallower water depths, and dug shallower nests. These differences may be the result of the unusually small size of golden trout in our study population, relative to salmonids used in previous studies of spawning microhabitat.

Stream-dwelling salmonids are widely distributed throughout North America and are sensitive to human-caused habitat alterations (e.g., Meehan 1991). Spawning habitat is easily disturbed by a variety of management activities (Moring 1982; Platts et al. 1989; Platts 1991), and its availability and quality often influences population structure of salmonids (Witzel and MacCrimmon 1981; Chapman 1988; Beard and Carline 1991; Hicks et al. 1991). Detailed descriptions of spawning habitat requirements are critical for accurate prediction of changes in salmonid populations resulting from habitat changes and for design of habitat restoration projects.

The original distribution of California golden trout *Oncorhynchus mykiss aguabonita* was limited to the South Fork Kern River and Golden Trout Creek in the southern Sierra Nevada, California

(Behnke 1992). This subspecies of rainbow trout *O. mykiss* is a popular sportfish and has been widely introduced throughout western North America (Fisk 1983). Because of perceived threats to population viability in its native habitat, the U.S. Fish and Wildlife Service (USFWS) is considering listing the California golden trout as a “threatened” species under the U.S. Endangered Species Act (K. Stubbs, USFWS, personal communication). California golden trout are affected by predation by and competition with introduced brown trout *Salmo trutta* and habitat degradation due to livestock grazing (Inyo National Forest 1965; Knapp and Matthews, unpublished).

The natural history and habitat requirements of California golden trout remain poorly understood, although studies show that in their native habitat golden trout grow slowly (Knapp and Dudley 1990) and are found in high densities (Platts and McHenry 1988; Knapp and Matthews, in press). Stefferud (1993) provided information on the

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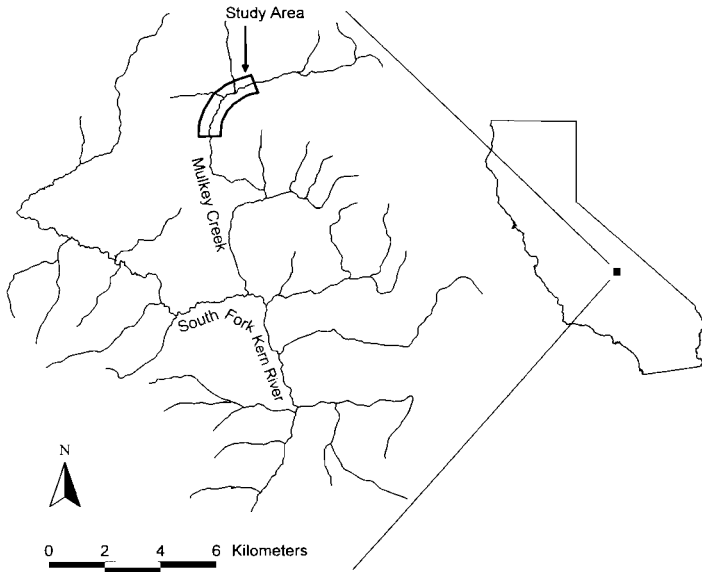


FIGURE 1.—Map of the golden trout study area on Mulkey Creek, California.

spawning biology of California golden trout. His qualitative observations suggested that temperature influences the timing of both seasonal and daily spawning, that large females spawn before small females, and that redds of early spawning females are constructed in larger substrates than later spawning females. Stefferud (1993) also provided limited information on redd characteristics, including substrate sizes, water depths, and water velocities. If effects of habitat alteration on this subspecies are to be better understood, additional quantitative data on reproductive ecology, timing of spawning, and spawning microhabitat preferences are needed.

This study was designed to provide quantitative information on four components of the spawning biology of California golden trout:

- (1) characteristics of spawning fish (size of males and females at sexual maturity, degree of sexual dimorphism, and ratio of breeding males to breeding females);
- (2) factors influencing the timing of spawning (the effect of stream temperature and discharge on seasonal and daily timing of spawning activity and the influence of fish size on seasonal timing of spawning);
- (3) characteristics of redds (the particle size characteristics of redds, including differences between redds constructed early and late in the spawning season, and the average number of egg pockets within redds, average egg pocket

depth, and average number of eggs per pocket);

- (4) microhabitat use and preferences of spawning females (comparison of substrate sizes, water depths, and water velocities used relative to those available to spawning females).

Study Area

Mulkey Creek is a tributary to the upper South Fork Kern River and lies at the southern end of the Sierra Nevada, Inyo National Forest, California ($118^{\circ}15'N$, $36^{\circ}22'W$; Figure 1). The upper South Fork Kern River watershed, including Mulkey Creek, is contained within the Golden Trout Wilderness, an area characterized by large subalpine meadows and low-gradient streams. The South Fork Kern River is one of two watersheds harboring native populations of California golden trout. A barrier approximately 5 km upstream from the Mulkey Creek–South Fork Kern River confluence originally restricted golden trout to the lower portion of Mulkey Creek, but golden trout were introduced into upper Mulkey Creek (Mulkey Meadow) sometime before 1876 (Pister 1991) and are currently the only fish species present (Knapp and Matthews, in press).

Our study site was on Mulkey Creek, 2 km above the lower end of Mulkey Meadow (elevation, 2,850 m; Figure 1), and contained approximately 3 km of stream. This section of Mulkey Creek is generally wide and shallow, with rela-

tively unstable streambanks. Bank instability has been attributed in large part to cattle grazing (Knapp and Matthews, in press). Stream substrates in the study reach are primarily sand and gravel. Discharge of Mulkey Creek in 1994 was low (Knapp, unpublished data) resulting from snowfall that was approximately 55% below average during winter 1993–1994 (CADWR 1994).

Methods

Timing of Spawning and Characteristics of Spawning Fish

Data collection.—To determine the effect of stream temperature and discharge on the seasonal timing of spawning, we measured stream temperature, discharge, and number of active redds daily throughout the 1994 spawning season (April 16–June 29). Two Omnidata² model ES-60 temperature probes (accurate within $\pm 0.25^\circ\text{C}$) recorded daily minimum, maximum, and average water temperatures. Because both thermistors provided nearly identical temperature records, we present temperature data from one randomly chosen probe. Discharge was measured at two permanent transects perpendicular to water flow at the downstream end of the study reach. Water depth and velocity were measured every 1–8 d (mean, 2.5 d) at 20-cm increments along each transect. We calculated discharge for each transect by multiplying the stream width by average water depth and average water velocity. Results with this method were very similar to those of the more laborious method of summing the discharges for each of numerous cells across a transect (Gordon et al. 1992). To calculate mean discharge, we averaged values from both transects.

We marked all new redds and monitored enlargement of established redds within the entire study reach daily. Redds were distinguished by their characteristic pit and tailspill (Ottaway et al. 1981; Grost et al. 1991a; Thurow and King 1994). A numbered tag was placed next to each new redd at the upstream edge of the pit. If the redd was enlarged on following days, indicating additional excavation (e.g., Chapman 1988), we marked the new upstream edge of the pit with another tag to allow monitoring of redd activity on subsequent days. We defined "daily redd activity" as the number of new redds plus the number of redds that

had been enlarged since the previous day. We were unable to differentiate true redds (containing eggs) from false redds (no eggs) during these visual surveys, but because more than 90% of excavated redds contained eggs (see Methods: redd characteristics), any bias associated with including false redds should be small.

To determine the effect of stream temperature on the daily timing of spawning activity, we measured stream temperature and the number of occupied redds in a 300-m section of the study reach during 2 d. Occupied redds were those attended by at least one fish and were counted from a distance of 5–10 m (fish on redds did not appear to be affected by the observer's presence until the observer approached to within 2 m of redds). On May 20, we recorded temperature (using a handheld thermometer accurate to $\pm 1^\circ\text{C}$) and number of occupied redds at 0850, 1030, 1300, 1630, and 1745 hours and on May 26 at 0850, 1030, 1300, 1500, and 1745 hours. We did not collect data either earlier in the morning or at night because previous observations indicated that redds were never occupied then.

To determine whether fish size influenced the seasonal timing of spawning, we captured and assessed reproductive status of 128–263 trout on each of four dates during the spawning season (May 2, 16, 25, and June 2). We captured trout by electrofishing. We distinguished one class of reproductive males and two classes of reproductive females. Males and females were categorized as "ripe" if they released milt or eggs when gentle pressure was applied to the abdomen. Females that did not release eggs but had swollen abdomens and large mature eggs that could be felt through the abdominal wall were categorized as "not ripe." The fact that the number of "not ripe" females declined dramatically over the spawning season (100% of females on May 2; 3% of females on June 2) indicates that they became ripe and spawned in the 1994 season, justifying their categorization as "reproductive." Fish that did not release gametes and did not have swollen abdomens were classified as "nonreproductive." We measured fork length of all sampled fish and released them at the site of capture. Data on fish size and reproductive status were also used to determine size at sexual maturity, degree of sexual size dimorphism, and operational sex ratio (the ratio of breeding males to breeding females at any one period; Alcock 1989:549).

Statistical analysis.—Because stream temperature, discharge, and spawning activity were mea-

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sured on consecutive days, they do not represent independent samples and are therefore not suitable for statistical analyses. Therefore, we relied on graphical methods to evaluate the effects of stream temperature and discharge on the seasonal timing of spawning. The number of occupied redds counted five times on each of 2 d also do not represent independent samples, and we therefore relied on graphical methods to evaluate the effects of stream temperature on the daily timing of spawning.

To evaluate the influence of fish size on the seasonal timing of spawning, we compared the size of ripe males and ripe females over the reproductive period. Because male and female sizes were normally distributed and variances were not significantly different between sampling dates, we used one-way analysis of variance (ANOVA) to test for differences in mean size (H_0 = size of males and females remains constant over the spawning season). Male size was compared over all four sampling dates. Female size was compared over the later three sampling dates (there were no ripe females on the first sampling date), and because only four ripe females were captured on the last sampling date, the number of females on the third and fourth sampling dates were combined.

We compared the size of sexually mature males and females (size of ripe males versus size of ripe and not ripe females) using a two-sample *t*-test for unequal variances (H_0 = the mean size of sexually mature males and females is equal). We used this test because sizes of sexually mature males and females were normally distributed, but variances in male versus female size were significantly different.

Redd Characteristics

Data collection.—To determine the number of egg pockets per redd, egg pocket depth, and number of eggs per pocket, we excavated 29 redds by hand on June 4 and June 8. We excavated redds by kneeling in the stream just below the redd and starting from the downstream end of the tailspill, slowly removing substrate to a depth of approximately 100 mm. A net was positioned immediately downstream of the excavation site to capture dislodged eggs. When an egg pocket was discovered, the distance from the undisturbed redd surface to the deepest eggs (egg pocket depth) was measured to the nearest 5 mm with a ruler. After complete excavation of each egg pocket, eggs in the net were counted and discarded. Excavation was continued until we reached the upstream edge of the pit.

To determine the substrate size composition of

redds and whether substrate sizes used by females changed during the spawning season, we sampled substrates from redds on five dates throughout the spawning season (May 14, 19, 20, 27, and June 4). Redds cored on each date were randomly chosen from the pool of all redds begun during the previous 4 d. We cored redds by inserting a 15-cm-diameter cylinder (Knapp and Vredenburg, in press) into the upstream half of the tailspill to a depth of 50 mm (the average egg pocket depth; see Results: redd characteristics). This portion of the redd contains the majority of egg pockets in other trout species (Grost et al. 1991a). All substrate from within the core was excavated by hand and placed in resealable plastic bags for transport to the laboratory. We found eggs in the core in 61% of the samples and in the redd (but not in the core) in 30% of the samples. Nine percent of the samples were discarded when no eggs were found in the core or in the redd. Samples were dried for a minimum of 12 h at 70°C until a constant weight was attained. Samples were agitated on a mechanical shaker for 10 min through 10 standard testing sieves (mesh openings = 50, 25, 12.5, 9.5, 6.3, 3.35, 1.7, 0.85, 0.42, 0.21 mm). The fraction of each sample that passed through all sieves was classified as smaller than 0.21 mm. Each size fraction was weighed to the nearest 0.1 g on an electronic balance, and geometric mean diameter (D_g) and percent fines were calculated for each sample. Geometric mean diameter was calculated using the product-of-moments formula given by Lotspeich and Everest (1981). Percent fines were calculated as the percentage of sediment smaller than 0.85 mm (Young et al. 1991a).

Statistical analysis.—to determine whether substrate sizes used by females changed during the spawning season, substrate sizes from cores taken May 14, 19, and 20 were compared with substrate sizes from cores taken May 27 and June 4. Because geometric mean substrate diameters and percent fine sediment were not normally distributed, we compared D_g and percent fine sediment across dates using the Kruskal–Wallis (KW) nonparametric one-way ANOVA (H_0 = substrate sizes used by spawning females remain constant over the spawning season). When differences among dates were significant ($P \leq 0.05$), we made pairwise comparisons between dates using the Tukey test applied to the ranked data.

Spawning Microhabitat Characteristics

Data collection.—To quantify microhabitats used by spawning females, we measured substrate

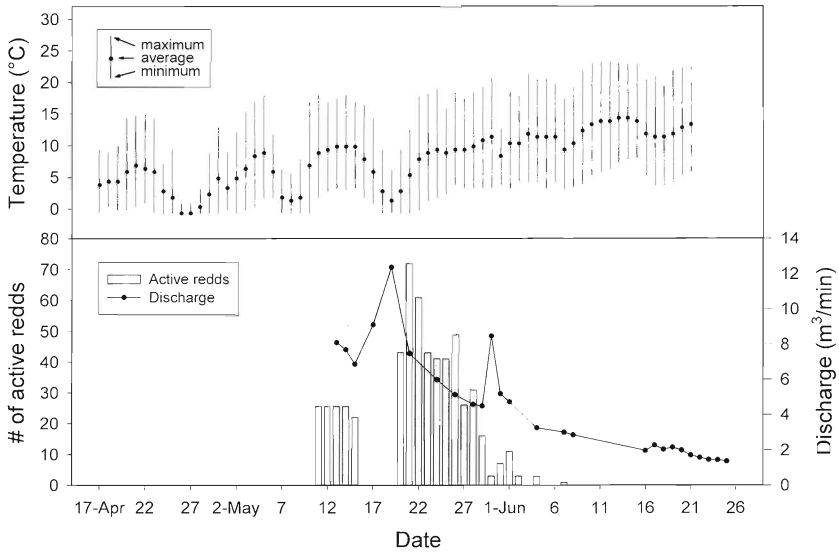


FIGURE 2.—Water temperature, stream discharge, and number of active golden trout redds measured over the 1994 spawning season.

size composition and water depth of redds, and water velocity over redds in the study reach. We quantified the substrate size composition used by spawning females using core samples taken during the spawning season (May 14, 19, 20, 27, and June 4; see Methods: redd characteristics). To determine the size of substrates available to females, we used samples collected throughout the study reach in 1993 (Knapp and Matthews, in press). To compare substrate sizes used by females with substrate sizes available, we assumed that substrate size distributions had not changed between the 2 years. Although we acknowledge that this assumption is a limitation of our study design, we believe that it is unlikely to affect the general nature of our results for two reasons. First, the below-average precipitation of the 1993–1994 winter resulted in very low peak flows that were insufficient to cause bed-load transport (Knapp, personal observation). Therefore, a major redistribution of sediment between the 2 years is improbable. Second, although the lack of a large flushing flow could have allowed fine sediments to increase between the 1993 and 1994 sampling dates, small changes in the amount of sediment in the smallest particle size categories would be unlikely to cause large changes in the geometric mean particle diameter.

Substrate cores collected in 1993 were taken by shovel in the deepest water along each of 75 transects evenly spaced throughout the study reach and arranged perpendicular to flow. The shovel was

inserted 15 cm deep in the substrate and then lifted from the stream. Our assumption that samples taken with the cylinder and the shovel were comparable was based on recent studies (Grost et al. 1991b; Young et al. 1991b). We processed samples using the same methods as in 1994.

We measured water depth and velocity at the upstream edge of the pit for all redds ($N = 326$) on the day the redds were first observed. Water depth was measured to the nearest 1 cm with a wading rod. We measured water velocity at 60% of the water depth to the nearest 1 cm/s using an electromagnetic current meter. At this depth, velocity approximates mean water column velocity (Gordon et al. 1992), and most published descriptions of salmonid spawning habitat characterize water velocity in this way (Bjornn and Reiser 1991). Therefore, our measurements should be comparable to those of numerous previous studies. To determine the water depths and velocities available to spawning females, we measured water depth and velocity along 364 transects evenly spaced throughout the study reach and perpendicular to flow. We took measurements at five equally spaced points along each transect on May 26 and May 28–31. Stream discharges during this sampling period were similar to those during high spawning activity (6.6 m³/min for redds, 5.7 m³/min for transects; ranges for redds and transects were both 4.5–8.5 m³/min; Figure 2). Therefore, we assumed that our measurements of available water depths and ve-

locities were representative of those encountered by most spawning females.

We calculated female preferences for substrate size, water depth, and water velocity by dividing the proportion of habitat used within a substrate size, water depth, or water velocity increment by the proportion of habitat available in the same increment (Bovee 1986). Index values greater than 1 indicate selection by females, and values less than 1 indicate avoidance. Other researchers have suggested that this method may remove some of the influence of habitat availability on habitat use curves (Baldrige and Amos 1982; Moyle and Baltz 1985).

To ensure that differences in stream discharge during measurement of water depths and velocities used versus those available did not result in systematic biases in microhabitat preference curves, we conducted a second analysis using only microhabitat use and availability data collected over a restricted range of stream discharges (4.5–6.0 m³/min). As a result of this restriction, we used water depth and velocity data only for redds first observed on May 24–29, May 31, and June 1, and habitat availability data collected on May 26, 28, 29, and 31 (Figure 2). We did not recalculate substrate sizes used versus those available because substrate size should be relatively unaffected by the range of stream discharges measured during this study.

Statistical analysis.—To determine whether the substrate sizes, water depths, and water velocities used by spawning females differed from those available, we compared values for these variables measured at redds (i.e., used by females) and along transects (i.e., available to females). Because mean substrate sizes, water depths, and water velocities were not normally distributed, we made comparisons using Kruskal–Wallis (KW) nonparametric one-way ANOVA (H_0 = females use substrate sizes, water depths, and water velocities in proportion to their availability).

To evaluate the extent to which differences in stream discharge biased microhabitat preference indices, we compared mean water depth and water velocity calculated from the full sample versus the restricted sample (H_0 = water depth and water velocity are equal between the full and restricted samples). Comparisons were made with Kruskal–Wallis nonparametric one-way ANOVA because data were not normally distributed. We also compared mean water depth and velocity used versus that available as calculated from the restricted sample. Because data on water depth and velocity

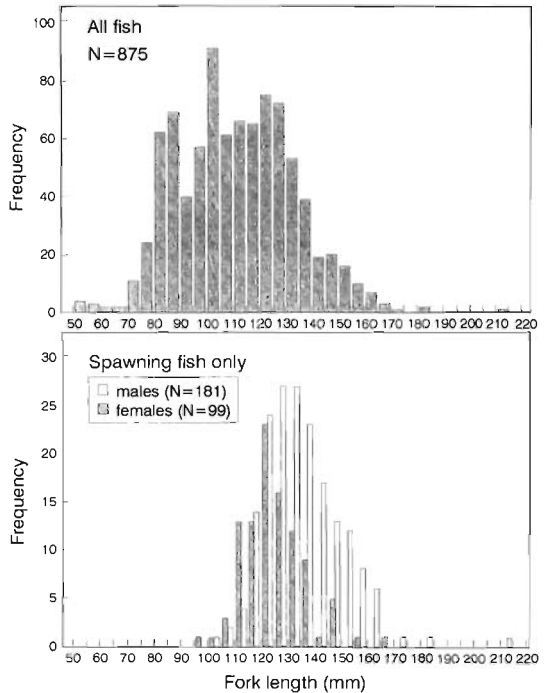


FIGURE 3.—Size-frequency histograms for all golden trout (upper figure) and spawning fish only (lower figure) during the 1994 spawning season. Sample sizes (N) are given for each figure. Among spawning fish, males were significantly larger than females.

were not normally distributed, we made comparisons using Kruskal–Wallis nonparametric one-way ANOVA (H_0 = females use water depths and water velocities in proportion to their availability).

Results

Characteristics of Spawning Fish

Our 1994 data showed that male and female golden trout in Mulkey Creek reach sexual maturity at approximately 95–100 mm (Figure 3). Spawning males were significantly larger than spawning females ($t = 6.3$, $P < 0.0001$; Figure 3); this difference remained highly significant when the 215-mm male was excluded from the analysis. Operational sex ratios (OSR) became increasingly skewed toward males over the spawning season. Early in the season (May 14–18), the OSR was 3.1:1 (ripe males : ripe females). In midseason (May 25) and late season (June 2), OSRs were 5.3:1 and 9:1, respectively.

Timing of Spawning

Golden trout began spawning in the study reach on May 12, and the last redd was constructed on

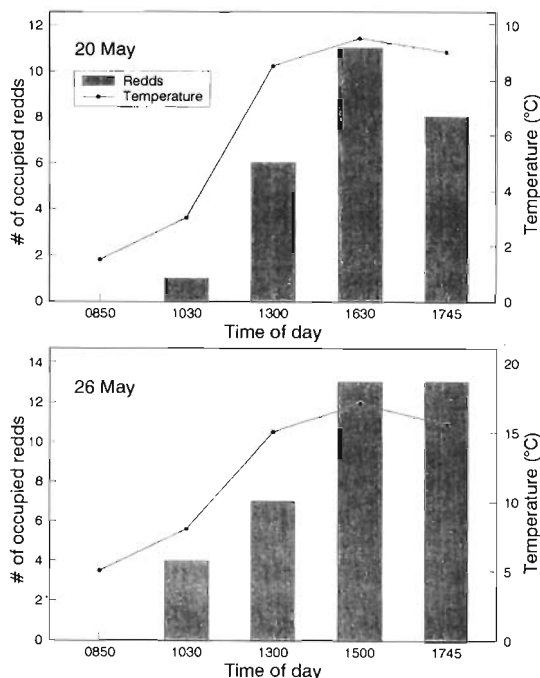


FIGURE 4.—Daily timing of spawning activity (number of occupied redds) by golden trout as a function of stream temperature on 2 d during the 1994 spawning season.

June 8. The start of the spawning season was associated with increasing water temperature. Redd construction did not begin until maximum water temperatures consistently exceeded 15°C and average water temperatures consistently exceeded 8°C (Figure 2). After spawning began, redd construction ceased when temperatures declined below these thresholds (e.g., May 16–19; Figure 2). However, because discharge also changed in conjunction with water temperature, the relative roles of these factors in reducing spawning activity are unclear. Although we lack discharge measurements before spawning began, decreasing stream discharge during the spawning season indicates that golden trout spawn primarily after peak runoff (Figure 2).

The daily timing of spawning activity was influenced by water temperature (Figure 4). No redds were occupied in early morning when water temperatures were at their daily minimum. As the stream temperature increased, the number of occupied redds also increased and peaked between 1500 and 1630 hours when stream temperatures reached the daily maximum (Figure 4).

Fish size influenced the seasonal timing of

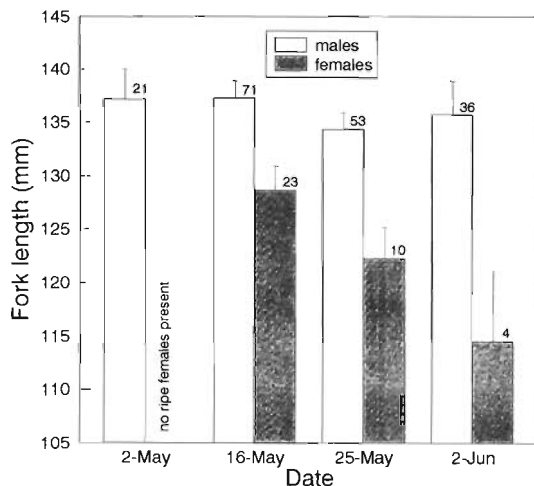


FIGURE 5.—Seasonal timing of spawning by golden trout as a function of the size of individual males and females. Data are presented as the mean \pm 1 SE, and sample sizes are given above each bar. Early spawning females were significantly larger than later-spawning females; there was no relationship between date and size of males.

spawning for females but not for males (Figure 5). Ripe females captured early in the spawning season were significantly larger than ripe females captured in the middle and at the end of the season ($F = 5.4$; $df = 1, 35$; $P < 0.03$). The average size of ripe males did not change over the spawning season ($F = 0.45$; $df = 3, 177$; $P > 0.7$; Figure 5).

Redd Characteristics

Redds were active an average of 1.7 d (range, 1–6), and 4% of redds had other redds superimposed on them. Excavated redds had an average of two egg pockets (range = 1–4, $N = 65$) and 22 eggs per pocket (range, 6–51; $N = 58$). The bottom of egg pockets averaged 50 mm deep (range, 40–60 mm; $N = 65$). Redds were composed primarily of fine gravel and sand and contained very little substrate larger than 25 mm (Figure 6). Geometric mean diameter of substrates from redds was 5.7 mm ($N = 82$; range, 2.8–11.3 mm; $SD = 1.6$ mm). The average percent of substrates smaller than 6.3 mm was 47.0% (range, 23.1–73.0%; $SD = 10.4\%$), and the average percent of substrates smaller than 0.85 mm was 9.5% (range, 2.9–17.4%; $SD = 3.7\%$).

Substrate size composition of cores taken from redds completed early, midway, and late in the spawning season differed significantly ($KW = 9.1$; $df = 2, 79$; $P < 0.02$; Figure 7). Cores taken on

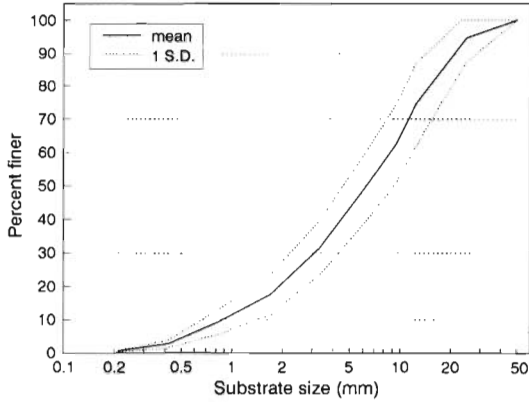


FIGURE 6.—Cumulative particle size distribution of substrates from golden trout redds. Substrate size is plotted on a logarithmic scale. Particle size is presented as the mean \pm 1 S.D.

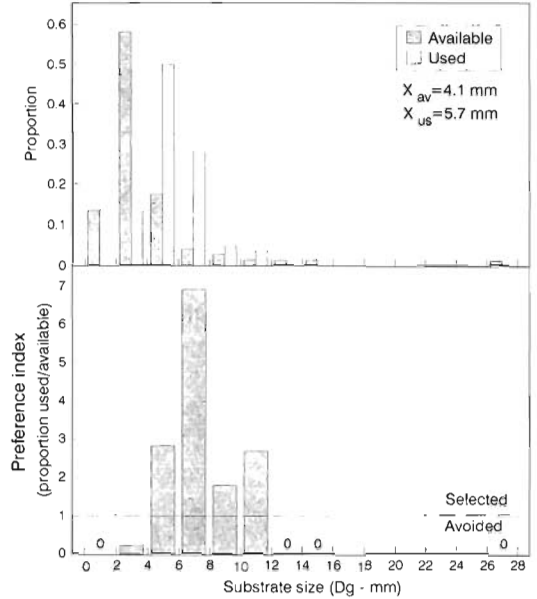


FIGURE 8.—Substrate sizes (geometric mean diameters, D_g) available to and used by spawning female golden trout (upper figure) and substrate sizes selected by spawning female golden trout (lower figure). Mean substrate sizes available (\bar{X}_{av}) and used (\bar{X}_{us}) are given. Preference index was calculated by dividing the proportion of habitat used within a substrate size increment by the proportion of habitat available in the same increment. Index values greater than 1 indicate selection by females and values less than 1 indicate avoidance. A zero indicates that a particular substrate size increment was available but was not used. A lack of either a bar or a zero indicates that a substrate size increment was not available.

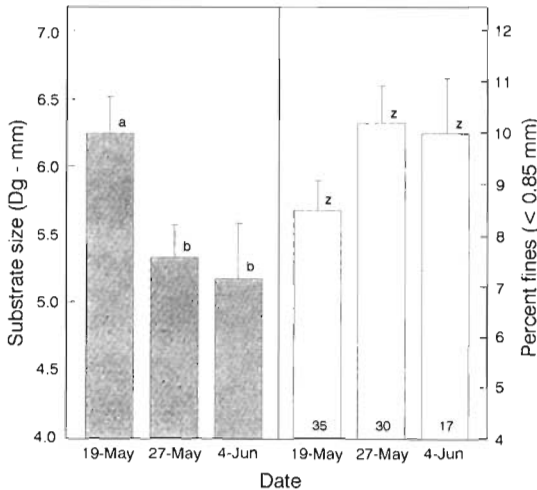


FIGURE 7.—Substrate geometric mean diameter (D_g) and percent fines of golden trout redds completed early, midway, and late in the spawning season. The 19 May sample date includes cores taken on May 14, 19, and 20. Means (+SEs) are presented, and sample sizes for each date are given inside the open bars. Among dates for each variable, means without a letter in common are significantly different ($P < 0.05$).

Spawning Microhabitat Use

The geometric mean substrate diameter used by female golden trout was significantly larger than that available in the study reach: 5.7 mm versus 4.1 mm ($KW = 45.7$; $df = 1, 155$; $P < 0.0001$; Figure 8). The fish selected substrates with $D_g = 4-12$ mm and avoided those with D_g smaller than 4 mm and larger than 12 mm (Figure 8). Geometric mean substrate diameters of 6-8 mm were most frequently selected.

Average water depths at redds were significantly shallower than those available: 12.2 cm versus 17.8 cm ($KW = 33.2$; $df = 1, 2,144$; $P < 0.0001$; Figure 9). Females selected depths of 5-20 cm and avoided those less than 5 cm and greater than 20 cm (Figure 9). Water depths of 10-15 cm were most frequently selected.

Average water velocities at redds were significantly faster than those available: 43.0 cm/s versus

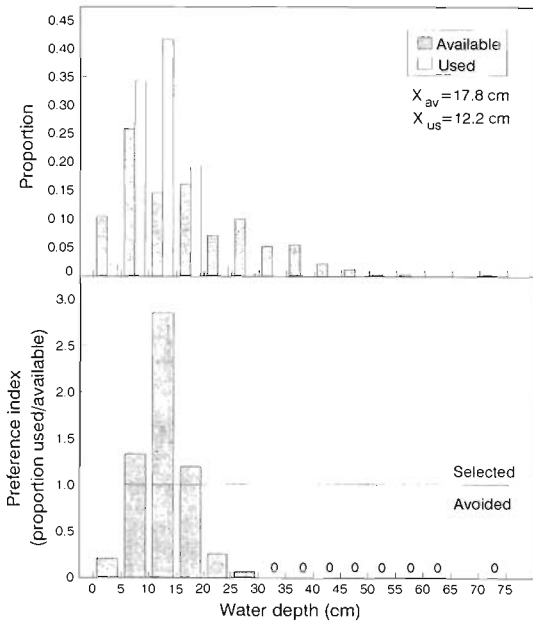


FIGURE 9.—Water depths available to and used by spawning female golden trout (upper figure) and water depths selected by spawning female golden trout (lower figure). Mean water depths available (\bar{X}_{av}) and used (\bar{X}_{us}) are given. Preference index was calculated by dividing the proportion of habitat used within a water depth increment by the proportion of habitat available in the same increment. Index values greater than 1 indicate selection by females and values less than 1 indicate avoidance. A zero indicates that a particular water depth increment was available but was not used, and the absence of either a bar or a zero indicates that a water depth increment was not available.

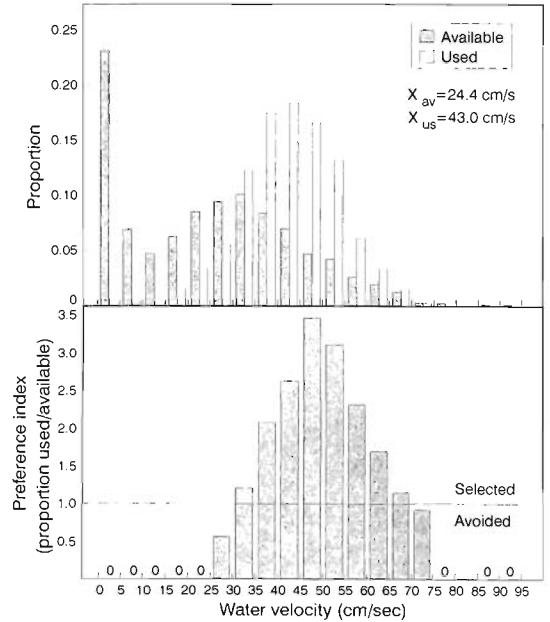


FIGURE 10.—Water velocities available to and used by spawning female golden trout (upper figure) and water velocities selected by spawning female golden trout (lower figure). Mean water velocities available (\bar{X}_{av}) and used (\bar{X}_{us}) are given. Preference index was calculated by dividing the proportion of habitat used within a water velocity increment by the proportion of habitat available in the same increment. Index values greater than 1 indicate selection by females and values less than 1 indicate avoidance. A zero indicates that a particular water velocity increment was available but was not used, and the absence of either a bar or a zero indicates that a water velocity increment was not available.

24.4 cm/s (KW = 263.4; df = 1, 2,144; $P < 0.0001$; Figure 10). Females selected water velocities of 30–70 cm/s and avoided those less than 30 cm/s and greater than 70 cm/s (Figure 10). Females selected a wide range of water velocities but selected those of 45–55 cm/s most frequently.

The mean water depths and velocities available and used were largely unchanged when we restricted the availability and use data to sample dates with very similar stream discharges. Comparisons of microhabitat availability and use from the full versus restricted sample showed that only water depth used by females was changed significantly or our restricting the data (water depth from unrestricted versus restricted data: 12.2 cm versus 13.2 cm; KW = 4.34; df = 1, 419; $P < 0.05$; all other comparisons: $P > 0.6$). Water depth and velocity preference curves were unchanged by our restricting the availability and use data. Spawning females used water depths that were significantly

shallower than those available (KW = 3.9; df = 1, 1,413; $P < 0.05$) and used water velocities that were significantly faster than those available (KW = 92.7; df = 1, 1,413; $P < 0.001$).

Discussion

Golden trout spawning biology shows many similarities to that of other nonanadromous *Oncorhynchus* species, and it also shows some characteristics that to our knowledge have not been previously reported for salmonids. Golden trout in Mulkey Creek showed a marked sexual dimorphism in size, spawning males being significantly larger than spawning females. Sexual dimorphism is common in many anadromous salmonids (e.g., Beacham and Murray 1987; Keenleyside and Dupuis 1988; Quinn and Foote 1994), but we were unable to find any published reports of this pattern in nonanadromous species. The marked size difference in golden trout may be a consequence of

intrasexual competition among males for access to spawning females. Operational sex ratios skewed toward males often result in strong male-male competition (Emlen and Oring 1977) in which larger males typically have an advantage over smaller males (Keenleyside and Dupuis 1988; Quinn and Foote 1994). Strong male-male competition is likely in golden trout, given our observations of as many as five males competing for access to a single female. During these interactions, large males always occupied the position closest to the spawning female.

Water temperature appeared to influence the seasonal timing of spawning. Golden trout began spawning when maximum water temperatures consistently exceeded 15°C. This temperature threshold is similar to that reported for golden trout in Mulkey Creek by Stefferud (1993) and for Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (16°C; Thurow and King 1994) but is higher than the threshold temperature for Gila trout (*O. gilae* (8°C; Rinne 1980). The range of water temperatures during golden trout spawning (15–21°C) is at the upper end of the range of spawning temperatures reported for other stream-dwelling salmonids (2.2–20°C; Bjornn and Reiser 1991) and is higher than those for anadromous salmonids (4.4–13.9°C; Bjornn and Reiser 1991). Discharge may also influence the seasonal timing of spawning, as most spawning in Mulkey Creek occurred as flows subsided. A similar pattern was reported by Thurow and King (1994) for Yellowstone cutthroat trout.

Although the effect of water temperature on the seasonal timing of spawning is relatively well documented, few studies have evaluated the effect of water temperature on daily timing of spawning activity. In golden trout, the number of occupied redds increased with increasing water temperature, and the number of occupied redds was highest in late afternoon when stream temperatures reached their daily maximum. These results support the qualitative observations on golden trout by Stefferud (1993). Rinne (1980) also reported that occupation of redds by Gila trout was highest in the afternoon. However, neither we nor Rinne (1980) or Stefferud (1993) accounted for changes in light levels during the day, and because light intensity is certainly correlated with both water temperature and time of day, light intensity and not water temperature could conceivably be responsible for the correlation between time of day and redd occupation (e.g., if golden trout spawn only during periods of high light levels). If this were the case,

we would expect to find a similar number of occupied redds at times with similar light levels (e.g., a fixed number of hours after sunrise and before sunset on a particular day). For example, in Figure 4, the number of occupied redds at 1030 hours should be equal to the number of redds at 1500 hours because these times are approximately 5 h after sunrise (0541 hours) and five h before sunset (1957 hours), respectively. The much lower levels of spawning at 1030 hours than at 1500 hours suggests that water temperature was more likely responsible for the observed pattern of redd occupancy.

An understanding of microhabitat characteristics (e.g., substrate size, water depth, and water velocity) used by spawning salmonids is important for determining the effect on salmonid populations of land management practices that might perturb these features. Redds of golden trout were characterized by an abundance of sand and fine gravel; the geometric mean particle diameter in redds was 5.7 mm (median particle diameter of about 6 mm). This is smaller than mean substrate sizes previously reported for golden trout redds (Stefferud 1993), and is smaller than mean particle diameters reported from redds of any other salmonid species for which we could find comparable data. For example, the median particle diameter of redd substrates is approximately 11 mm for Yellowstone cutthroat trout (Thurow and King 1994), 10–30 mm for brown trout (Grost et al. 1991a; Kondolf and Wolman 1993), 10–50 mm for rainbow trout (Kondolf et al. 1989; Kondolf and Wolman 1993), and 6–10 mm for brook trout *Salvelinus fontinalis* (Kondolf and Wolman 1993). The median particle diameters for anadromous salmonids are even larger (7–80 mm; Kondolf and Wolman 1993).

Water depths and velocities used by spawning female golden trout were similar to those reported previously for this species (Stefferud 1993). Water depths over redds were also similar to those observed for Gila trout (Rinne 1980) but were shallower than those reported for most other salmonids (e.g., Smith 1973; Shirvell and Dungey 1983; Witzel and MacCrimmon 1983; Parsons and Hubert 1988; Grost et al. 1990; Thurow and King 1994). Water velocities used by spawning salmonids are highly variable even within species (e.g., Shirvell and Dungey 1983; Grost et al. 1990), and the range of water velocities at golden trout redds overlapped those reported for other salmonids (Smith 1973; Shirvell and Dungey 1983; Witzel and MacCrimmon 1983; Parsons and Hubert 1988; Grost et al. 1990; Thurow and King 1994).

In addition to being constructed of smaller substrates and in shallower water depths than have been recorded for most other salmonids, golden trout egg pockets in Mulkey Creek were also unusually shallow (range, 40–60 mm) compared to previously reported egg pocket depths. For example, bottom depths of egg pockets were 100–250 mm for coho salmon *O. kisutch* (van den Berghe and Gross 1984), 20–230 mm for brown trout (Grost et al. 1991a), and 55–120 mm for brook trout (Young et al. 1989).

The smaller substrates, shallower water depths, and shallower egg pockets of golden trout redds in Mulkey Creek relative to redds of other salmonids is likely due in part to the smaller size of fish in our study. Females of large-bodied species can construct redds in larger substrates than females of small-bodied species, and this body size constraint often results in large females using a wide range of substrate sizes and small females using a narrower range of smaller substrate sizes (Crisp and Carling 1989; Kondolf and Wolman 1993). The interpretation that the small size of golden trout in our study population may have resulted in the uncharacteristically small substrates we found in redds is supported by our observation that early spawning (i.e., larger) females used larger substrates than later-spawning (i.e., smaller) females.

Although body size appears to constrain the substrate sizes used by spawning golden trout and may be partially responsible for the unusually small substrates found in golden trout redds, the comparison of substrate sizes available versus used suggests that female golden trout selected the largest substrates available. Therefore, the small substrates found in golden trout redds likely result from both the sandy substrates typical of Mulkey Creek (Knapp and Matthews, in press) and constraints imposed by the fishes' small body size.

Spawning female golden trout use shallow water depths probably because their small body size allows them to use shallower depths than larger species (Crisp and Carling 1989; Bjornn and Reiser 1991). Similarly, the shallow egg pockets of golden trout redds probably result from nest depth being constrained by the small size of golden trout used in this study, because egg-burial depth is typically an increasing function of fish size (van den Berghe and Gross 1984; Crisp and Carling 1989).

Our observations that the size of spawning golden trout females changed over the reproductive season and that female size can influence habitat use (this study; Crisp and Carling 1989; Bjornn and Reiser 1991; Kondolf and Wolman 1993) sug-

gests that researchers attempting to characterize spawning habitat use by measuring microhabitat characteristics over only part of the spawning season (e.g., Stefferud 1993; Thurow and King 1994) may include only a subset of the microhabitats actually used by a species. The growing number of studies reporting that female size influences the timing of reproductive activity in various fish species (cutthroat trout *O. clarki*: Ball and Cope 1961, as cited in Gresswell et al. 1994; mottled sculpin *Cottus bairdi*: Downhower and Brown 1981; largemouth bass *Micropterus salmoides*: Miranda and Muncy 1987; dwarf perch *Micrometrus minimus* Schultz et al. 1991) supports our assertion that spawning microhabitat preferences may be accurately characterized only if microhabitat use is measured over the entire spawning season.

The habitat of golden trout in the Golden Trout Wilderness, including Mulkey Creek, is being affected by present levels of livestock grazing (Knapp and Matthews, in press). Our results on the spawning biology of golden trout will aid in the design of future research to quantify the effect of grazing on spawning habitat. For example, in future research, we plan to use artificial redds to determine the relation between substrate quality and embryo survival (Gustafson-Marjanen and Moring 1984; MacKenzie and Moring 1988). Because attributes of natural redds are believed to influence embryo survival (Chapman 1988), our data on golden trout redd characteristics will enable us to construct artificial redds that closely resemble natural redds. In addition, our data on preferences by female golden trout for particular water depths, water velocities, and substrate sizes will help define habitat requirements for this species and appropriate restoration efforts.

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