

Livestock Grazing, Golden Trout, and Streams in the Golden Trout Wilderness, California: Impacts and Management Implications

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Abstract.—Impacts of livestock grazing on California golden trout *Oncorhynchus mykiss aguabonita* and their habitat were studied inside and outside of livestock exclosures in the Golden Trout Wilderness, California. In two consecutive years, the majority of stream physical characteristics showed large differences between grazed and ungrazed areas, and the directions of these differences were consistent with the recovery of exclosed streams and riparian areas from impacts caused by livestock grazing. Ungrazed areas consistently had greater canopy shading, stream depths, and bank-full heights and smaller stream widths than grazed areas. California golden trout were very abundant in the study sites; their densities and biomasses were among the highest ever recorded for stream-dwelling trout in the western United States. California golden trout density and biomass per unit area were significantly higher in ungrazed than in grazed areas in three of four comparisons. Differences between grazed and ungrazed areas were less consistent when density and biomass were calculated on the basis of stream length. Our results suggest that current levels of livestock grazing are degrading the stream and riparian components of the study meadows to the detriment of golden trout populations.

Grazing of domestic livestock is the most widespread land use in western North America (Wagner 1978). In the western United States, grazing occurs on the majority of federal lands, including national forests, national wildlife refuges, lands administered by the U.S. Department of Interior's Bureau of Land Management (BLM), and some national parks. In the western states, grazing affects 64 million hectares administered by the BLM and 53 million hectares administered by the U.S. Forest Service (Armour et al. 1994). Impacts of livestock grazing on stream and riparian ecosystems are widespread (for recent reviews, see Kauffman and Krueger 1984; Platts 1991; Fleischner 1994) and are particularly acute in the arid western states. In arid climates, lush vegetation is often found only near stream corridors and as a result, livestock tend to congregate in these areas (Roath and Krueger 1982; Gillen et al. 1984). Although western riparian zones are the most productive habitats in North America (Johnson et al. 1977), at least 50% of these ecosystems are degraded as a consequence of livestock grazing (Armour et al. 1994). A recent

review of conditions on U.S. Forest Service lands also concluded that most riparian ecosystems are in need of restoration (USGAO 1988).

Livestock grazing directly affects three general components of stream and riparian ecosystems: streamside vegetation; stream channel morphology, including the shape of the water column and streambank structure; and water quality (Platts 1979; Kauffman and Krueger 1984). These impacts can alter the population structure of resident fish, particularly salmonids (Platts 1991). Although the spatial and temporal variability of stream salmonids may often obscure any population changes caused by land management practices (Hall and Knight 1981; Platts and Nelson 1988), a recent review reported that 15 of 19 studies showed that stream fish were diminished in the presence of livestock grazing (Platts 1991).

In 1993 and 1994, we conducted a study of grazing impacts to streams in the Golden Trout Wilderness, California, using a series of livestock exclosures. The 133,500-ha Golden Trout Wilderness (GTW) was created in 1977, in part to protect the habitat of the two subspecies of golden trout *Oncorhynchus mykiss* sspp. The Little Kern golden

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trout *O. m. whitei*² is native to the Little Kern River and is currently listed as a threatened species under the federal Endangered Species Act (Behnke 1992). The California golden trout *O. m. aguabonita* is native to the South Fork Kern River and Golden Trout Creek (Behnke 1992), and most of its native range lies within the GTW. The basic ecology of the California golden trout remains poorly understood, although recent research on stream populations in the GTW shows that individuals are long lived, slow growing, and exist at high densities (Knapp and Dudley 1990). The California golden trout has been the subject of much management interest because of its status as California's state fish, its limited natural distribution, and several perceived threats to its viability, including introduction of nonnative brown trout *Salmo trutta* and habitat degradation caused by livestock grazing. Because of these threats, the California golden trout is being considered for federal listing as a threatened species.

Although much attention has been focused on damage caused by past livestock grazing in the GTW (e.g., T. A. Felando, Inyo National Forest, unpublished report, 1982), very little is known about whether current levels of livestock grazing are causing additional degradation of stream and riparian ecosystems. Therefore, we quantified a series of riparian, stream, and fishery variables inside and outside three grazing exclosures to address the following questions: (1) Are stream and riparian habitat variables different between areas inside and outside of exclosures? and (2) Are the density and biomass of golden trout different between areas inside and outside of exclosures?

Study Area

The GTW is at the southern end of the Sierra Nevada, California (118°15'N, 36°22'W). This study was confined to the eastern portion of the GTW in the Inyo National Forest. This area was largely unaffected by Pleistocene glaciation (Odion et al. 1988) and is characterized by large subalpine meadows (up to approximately 7.5 km²). These meadows are found primarily along the South Fork Kern River and a major tributary, Mulkey Creek. Meadows are dominated by sagebrush *Artemisia cana*, but streamside zones are typically dominated by sedge *Carex* spp. and willow *Salix* spp. (Odion et al. 1988; Sarr 1995). Over

90% of the annual precipitation falls as snow (Major 1977), and the remainder mostly occurs during summer thunderstorms.

Livestock have grazed the area now contained within the GTW since at least 1860, and there are reports of 200,000 sheep in the area during a year between 1860 and 1890 (Felando, unpublished report) and of 10,000 cattle in the late 1800s (Inyo National Forest 1982). Past overgrazing has resulted in widespread riparian degradation (Albert 1982; Felando, unpublished report), and large-scale restoration efforts have been implemented by the U.S. Forest Service (Inyo National Forest) during the past 70 years.

Mulkey and Ramshaw meadows are currently grazed by approximately 950 cow-calf pairs (in 1993, 235 in Mulkey and 700 in Ramshaw; in 1994, 235 in Mulkey and 730 in Ramshaw). Mulkey Meadow is typically grazed for several weeks in July and again in September. In Ramshaw Meadow, cattle are generally trailed through in late July with only light grazing and are gathered into the meadow for a week of high-intensity grazing in October.

The fish fauna of this watershed is composed of two native species, the California golden trout and Sacramento sucker *Catostomus occidentalis*. However, we encountered only California golden trout during our surveys. These populations are self-sustaining, are not subject to management activities (e.g., fish stocking), and experience very light angling pressure.

The Inyo National Forest constructed exclosures in several GTW meadows in 1983 and 1991 to protect stream segments from grazing impacts. Our study sites were inside and outside three grazing exclosures in Ramshaw Meadow (2,660 m; Figure 1) and Mulkey Meadow (2,850 m; Figure 2). Cattle rarely trespass inside these exclosures (D. Hubbs, Inyo National Forest, unpublished data), and we consider stream sections inside the exclosures to have been ungrazed since exclosures were constructed. All stream reaches used in our study were typical of those found in low-gradient meadows (types C-4 and E-4 of Rosgen 1994).

Study Design

An inherent problem with studies that use exclosures to investigate the impacts of livestock grazing is treatment (i.e., exclosure) replication. The most statistically robust study design would incorporate numerous randomly placed exclosures. Such a design is difficult to achieve because of the limited availability of grazed sites with sim-

² Although the systematics of western salmonids remains controversial, we use the most recent classification and common names as described by Behnke (1992).

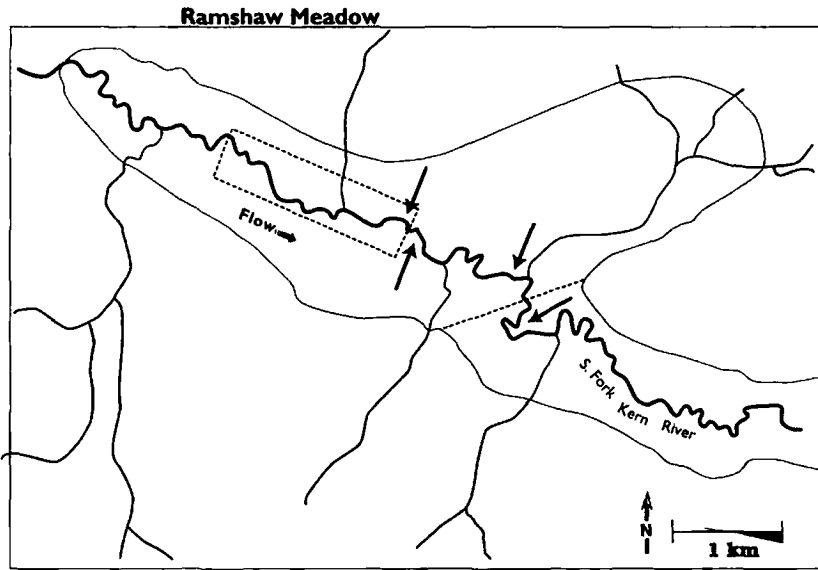


FIGURE 1.—Map of Ramshaw Meadow. The upper enclosure is depicted by the dotted rectangle and the lower drift fence enclosure is depicted by the dotted line across the stream and meadow. Arrows show study sites inside and outside enclosures. Shaded area is forest surrounding the meadow.

ilar site potential and the cost of constructing multiple enclosures (Platts and Wagstaff 1984); as a result, we are aware of very few studies that have used such a design (Buckhouse et al. 1981; Kauffman et al. 1983; Platts and Nelson 1985a). Much more common are grazing studies that take advantage of enclosures placed by land management

agencies to protect particular stream sections from grazing impacts (Rinne 1988). These studies frequently are based on comparisons of stream characteristics inside and outside of a single enclosure (Keller and Burnham 1982; Platts and Nelson 1985b; Odion et al. 1988; Kondolf 1993). However, statistical analyses based on differences in-

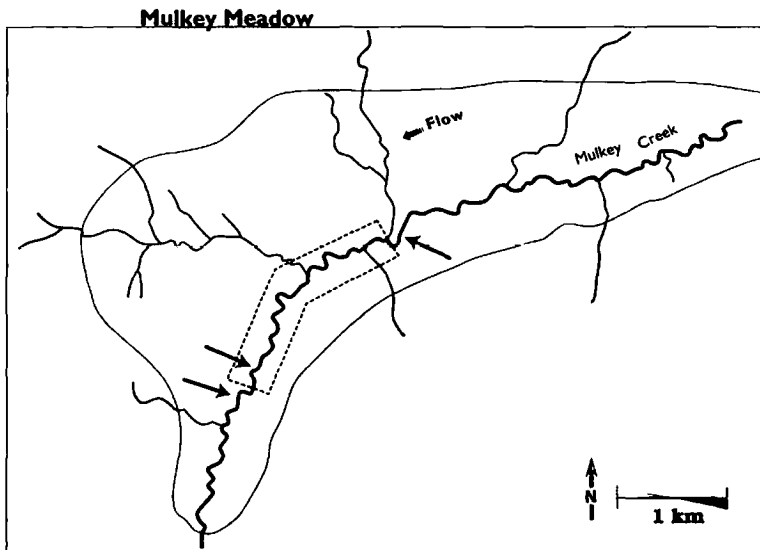


FIGURE 2.—Map of Mulkey Meadow. The enclosure is depicted by the dotted rectangle. Arrows show study sites below, inside, and above the enclosure. Shaded area is forest surrounding the meadow.

side and outside of single exclosures are generally pseudoreplicated, making interpretations of differences problematic (Hurlbert 1984). Despite this flaw and other shortcomings inherent to exclosure studies (Rinne 1988), unreplicated exclosures often provide the only avenue available for the study of grazing impacts. Indeed, such studies provide the bulk of available information on the effects of livestock grazing on stream and riparian ecosystems (Platts 1991).

The design of our study was similarly constrained by the availability of grazing exclosures. Although we could have used our three exclosures as replicate treatments, we chose not to because the exclosures were placed nonrandomly (violating assumptions underlying statistical tests) and because of the low statistical power resulting from a sample size of three. This low statistical power would have increased the likelihood of type II error, the finding of no significant difference when a true difference exists. As a result, we chose to make separate grazed versus ungrazed comparisons for each exclosure.

The location of exclosures also constrained our placement of grazed and ungrazed study sites. Although it may have been statistically more appropriate to place habitat transects along the entire stream length inside the exclosures and over similar distances outside exclosures, we were prevented from using this design because the exclosures contained several very different stream channel types. Because comparison of stream and riparian conditions across disparate channel types could obscure any differences in the sites due to grazing, we reduced the spatial heterogeneity of sites used in our grazed versus ungrazed comparisons by locating study sites as close together as possible (only Rosgen's C-4 and E-4 channel types were included). This design reduced the spatial scale of the study, however.

Despite the shortcomings of our study design, the exclosures represent the only means of assessing grazing impacts on streams and California golden trout in the GTW. We believe our data contribute meaningfully to the management of California golden trout populations and their habitat.

Methods

Study sites.—Ramshaw Meadow contains two grazing exclosures (Figure 1). The lower exclosure was built in 1991 to keep cattle from grazing the entire lower portion of Ramshaw Meadow. Approximately 700 cattle are trailed through the exclosure every year in early and late summer but

affect only a very small portion of the exclosure. Study sites were 100 m below (ungrazed site) and 100 m above (grazed site) the upstream end of the exclosure. The exclosure in upper Ramshaw Meadow was built in 1983. The ungrazed site was just inside the lower end of the exclosure and the grazed site was 100 m downstream of the exclosure (Figure 1). We located the ungrazed site at the exclosure fence line instead of 100 m upstream to allow comparisons with data that had been collected at this location in 1984.

The exclosure in Mulkey Meadow was built in 1991. We located study sites 100 m downstream of the exclosure (grazed site), 100 m above the downstream end of the exclosure (ungrazed site), and 100 m above the upstream end of the exclosure (grazed site) (Figure 2).

Stream physical characteristics.—We quantified stream physical characteristics and surveyed fish populations within each study site during August 20–30, 1993, and August 16–24, 1994. All sites contained 125 m of stream, and at each site we measured characteristics along each of 25 transects spaced 5 m apart and arranged perpendicular to stream flow (Simonson et al. 1994). At each transect, we measured channel width, channel depth, stream width, stream depth, bank-full height, bank overhang, bank angle, and bank water depth. These variables are potentially sensitive to land use activities, such as livestock grazing, that influence channel stability. We defined channel width as the cross section containing the stream that is distinct from the surrounding area due to breaks in the general slope of the land, lack of upland vegetation, and changes in the composition of substrate materials (Platts et al. 1983). Channel width was measured to the nearest 10 cm. Channel depth, the distance from the top of the channel to the water surface, was measured to the nearest 5 cm. Stream width, the width of the present water surface not including islands, was measured to the nearest 5 cm. We measured unvegetated stream width, the total stream width minus the width of any bands of emergent vegetation along each bank, to the nearest 5 cm. This vegetation is typically the beaked sedge *Carex rostrata* (= *C. utriculata*), a species that rapidly colonizes stream margins in the absence of grazing in Mulkey and Ramshaw meadows and that may play an important role in channel stabilization and stream narrowing (Rosgen 1994; Sarr 1995). Unvegetated stream width was measured only in 1994. Although bank-full height is generally defined as the height reached by a stream on average every 1.5 years (Gordon et

al. 1992), this measure is unlikely to be strongly influenced by land management practices. Instead, we defined bank-full height as the height above the current water level at which the banks lose their ability to contain the stream (Gordon et al. 1992); it was measured to the nearest 5 cm.

We quantified streambank morphology by measuring bank angle, bank overhang, and bank water depth of both banks along each transect. We measured bank angle to the nearest 5° using a clinometer on a 1.5-m rod placed against the bank slope (Platts et al. 1983). Overhanging banks have bank angles of 0–89°, and laid-back banks have bank angles of 90–180°. If banks were overhanging, the extent of overhang was measured to the nearest 5 cm from the deepest bank undercut to the furthest point of bank protrusion. We defined bank water depth as the water depth 15 cm from each bank and measured it to the nearest 5 cm.

To quantify instream characteristics, we measured vegetative canopy shading, substrate composition, and, at equally spaced points along each transect, water depth, water velocity, and height of any aquatic vegetation. Canopy shading was measured at each bank and in midstream by facing up and downstream with a densiometer (Platts et al. 1983). Water depth, water velocity, and height of submerged vegetation were measured at 10 equally spaced points along each transect in 1993, and at 5 equally spaced points in 1994. The reduced number of points in 1994 was necessitated by extremely low flows that would have caused points to be too close together (often <10 cm). Water depth and height of submerged vegetation were measured to the nearest 1 cm. Water velocity was measured with a Marsh-McBirney³ model 2000 current meter, and each measurement represented a 10-s average. Velocities at each point were measured at 60% of the water depth with a top-setting wading rod.

In 1993, we quantified substrate particle size distributions (geometric mean diameter— D_g of Platts et al. 1979—and percent fines) by taking a core sample with a shovel at the deepest point along each transect. The shovel was inserted into the substrate to a depth of 15 cm and then lifted from the stream (Grost et al. 1991). Samples were placed into resealable plastic bags for transport to a laboratory, where they were dried for a minimum of 72 h to a constant weight and separated into 11

size-fractions with a mechanical shaker. In 1994, we measured substrate particle size distributions by measuring the substrate contacted by the upstream edge of the wading rod base at each of the five equally spaced points along each transect. Particles 1 mm or larger in diameter were measured to the nearest millimeter. Particles smaller than 1 mm were classified as fine sand (0.5 mm) or silt (0.1 mm). We used this technique in 1994 instead of the shovel sampler because of the difficulty of transporting heavy samples out of the remote study areas and the time-consuming nature of the sifting process.

To quantify the size-structure of riparian willows, we counted and measured heights of all willows within 2 m of each streambank at each site in 1994. Willow heights were measured to the nearest 1 cm.

Of the 14 measured variables, most were expected to respond relatively quickly and in a predictable direction to removal of livestock from the streamside zone (Platts 1991). For these variables, we predicted the following changes in ungrazed areas inside exclosures relative to grazed areas outside exclosures.

- (1) Total stream width and unvegetated stream width will have decreased as vegetation invaded the channel and banks stabilized.
- (2) Bank-full height will have increased as vegetation colonized point bars and captured sediment.
- (3) Canopy shading will have increased as willow and sedge species recolonized streambanks.
- (4) Bank angle will have decreased and bank overhang and bank water depth will have increased as banks stabilized and were transformed from laid-back to undercut configurations.
- (5) Stream water depth will have increased as stream width decreased and constricted stream flow.

Several additional measured variables were expected to change very slowly in response to livestock exclosure or were not anticipated to change in a predictable direction. We included these in our study to allow post hoc determinations of whether sites inside and outside of exclosures were similar. Large differences in most or all of these variables would suggest that paired sites differed before exclosures were built. Channel width and channel depth were expected to respond to the removal of livestock grazing, but these changes were likely to be measurable only over a period of several decades and not the 2–11 year time scale used

³ Trade names and commercial enterprises are mentioned solely for information. No endorsement by the U.S. Forest Service is implied.

in this study (Kondolf 1993). For two additional variables, substrate size and water velocity, we did not predict any direction of change. Although substrate size would be expected to increase after the removal of livestock as a consequence of a reduction in delivery of fine sediments to the stream, livestock grazing has continued upstream of the exclosures. Therefore, even if fine sediment inputs were reduced within the exclosures, we expected these changes to be masked by continued inputs from upstream (Rinne 1988).

Although we do not have preexclosure data for most sites, we did have a detailed map (accurate to 10 cm) drawn in 1984 of the stream section inside the upper Ramshaw exclosure (T. L. Dudley and R. A. Knapp, unpublished data). To determine whether stream width inside the upper Ramshaw exclosure had changed since the time of exclosure construction in 1983, we compared the mean stream width from the map with the mean stream width at the site in 1993 and 1994. To extract total stream widths from the 1984 map, we drew 25 transects on the map, each perpendicular to stream flow and spaced 5 m apart. At each transect, we measured the total stream width with a ruler and converted these measurements to their actual dimensions (1 cm = 1 m). If stream width had not changed since 1984 (i.e., no recovery had occurred), the mean stream width as measured from the 1984 map should have been similar to the stream width measured in 1993 and 1994.

Fish population characteristics.—We surveyed fish populations using standard electrofishing depletion techniques (Van Deventer and Platts 1983). To facilitate electrofishing, we divided each 125-m site into five 25-m sections with block nets. We conducted three passes through each section with a Smith-Root type XII electrofisher that produced 400 V and a pulse frequency of 90 Hz. The length of time that the electrofisher was running on each pass was similar within a section to ensure a similar electrofishing effort on each pass. Captured fish were measured for fork length to the nearest 1 mm and weighed on an electronic balance to the nearest 0.1 g. Fish were released into the section from which they were captured after the final pass within the section was completed.

The number of fish in each site was estimated from the rate of depletion by maximum-likelihood estimation techniques (Microfish, version 3.0 software; Van Deventer and Platts 1985). The depletion data used in the maximum-likelihood estimations were obtained by adding all fish from the first pass in sections 1–5 (= total number of fish

in pass 1), the number of fish from the second pass in sections 1–5 (= total number of fish in pass 2), and the number of fish from the third pass of sections 1–5 (= total numbers of fish in pass 3) (Van Deventer and Platts 1985). Capture probabilities were similar among size-classes—in 1993 they were 0.50 for adults (≥ 100 mm) and 0.36 for age-0 fish (55 mm) (paired *t*-test, $N = 7$, $P > 0.09$); in 1994 they were 0.59 and 0.52, respectively ($P > 0.2$)—and all size-classes were pooled for the population estimates. The number of fish per square meter was calculated for each 125-m site by dividing the estimated number of fish per site by the stream surface area (average stream width $\times$ 125 m). The estimated total weight of fish in each section was extrapolated from the mean weight of fish captured. We calculated fish weight per square meter by dividing the estimated total weight per site by the stream surface area.

On the basis of a recent review of livestock impacts on stream fish populations (Platts 1991), we predicted that California golden trout density (number/125 m, number/m²) and biomass (g/125 m, g/m²) should be greater in ungrazed than grazed areas. Although recent evidence shows that trout of some species move considerable distances (Young 1995a) and that movement may confound studies of habitat-related differences in trout population structure when sites are close to each other (Young 1995b), other research indicates that adult California golden trout rarely move more than a few meters (Matthews 1996). In addition, numerous grazing studies have documented differences in trout populations in adjacent study sites inside and outside exclosures (Platts 1991).

Statistical analysis.—To provide an overview of the differences between sites inside and outside the three exclosures, we tallied the number and direction of differences in physical stream characteristics. If livestock grazing outside exclosures had not influenced stream characteristics, an equal number of changes in variables should have agreed and disagreed with expectations. Differences from equality were evaluated with the binomial test. To determine the magnitude of differences between paired grazed and ungrazed sites, we also treated the upper Ramshaw, lower Ramshaw, and Mulkey exclosures as separate analyses. Most physical stream variables could not be normalized for particular sites, so we relied primarily on nonparametric Kruskal–Wallis one-way analyses of variance (ANOVA) to test for differences in values inside and outside of exclosures. One- or two-tailed tests were used according to the null hy-

pothesis being tested. Because of the pseudo-replication problems inherent in statistical comparisons of single sites inside and outside of an enclosure (e.g., artificially inflated sample sizes; Hurlbert 1984), we present *P*-values for comparisons of site characteristics only to provide a relative measure of the magnitude of differences, and not to draw conclusions based solely on statistical significance ($P \leq 0.05$).

Fish data were analyzed as estimated density (number/125 m and number/m²) and biomass (g/125 m and g/m²) per site with modified *t*-tests. The estimated number of fish per 125 m was compared between grazed and ungrazed sites with the following *t*-test formula (Keller and Burnham 1982):

$$t = \frac{(\text{number}_1) - (\text{number}_2)}{\sqrt{(\text{SE}_1)^2 + (\text{SE}_2)^2}};$$

subscript 1 refers to the grazed site of a pair, subscript 2 to the ungrazed site; standard errors were calculated by the maximum-likelihood model. Degrees of freedom were calculated with the formula:

$$df = n \left\{ \frac{\left(\frac{1}{n} \sum \text{var}_1 + \frac{1}{n} \sum \text{var}_2 \right)^2}{\left(\frac{1}{n} \sum \text{var}_1 \right)^2 + \left(\frac{1}{n} \sum \text{var}_2 \right)^2} \right\};$$

n = number of sections, and var is variance. Fish weight per 125 m was compared between sites with the *t*-test formula:

$$t = \frac{|(\text{weight}_1) - (\text{weight}_2)|}{\sqrt{(\text{SE}_1 \cdot X_{wt1})^2 + (\text{SE}_2 \cdot X_{wt2})^2}},$$

where (weight₁) and (weight₂) are the estimated weight of fish in site 1 and site 2, (SE₁) and (SE₂) are the standard errors of (number₁) and (number₂) calculated by the maximum-likelihood model, and *X*_{wt1} and *X*_{wt2} are the average individual fish weights in sites 1 and 2. Multiplying the standard error by the average individual fish weight was necessary to scale the standard error to fish weight. Comparisons of the number of fish per square meter and weight of fish per square meter were made with formulas similar to those given above except that (number_{*i*}) and (SE_{*i*}), and (weight_{*i*}) and (SE_{*i*} · *X*_{wt*i*}) were first divided by the stream surface area of site *i* to scale these variables to area.

As with the habitat data, analysis of the fish data involved statistical comparisons of single sites inside and outside of an enclosure and are therefore pseudoreplicated. As a result, we present *P*-values

TABLE 1.—Differences in stream physical characteristics in relation to predicted changes between paired sites inside (ungrazed) and outside (grazed) enclosures in 1993 and 1994.

Enclosure comparison (ungrazed versus grazed)	Difference consistent with prediction	No differ- ence	Differ- ence opposite from prediction
Upper Ramshaw, 1993	6	1	0
Upper Ramshaw, 1994	8	0	0
Lower Ramshaw, 1993	3	2	2
Lower Ramshaw, 1994	7	0	1
Mulkey (versus site below), 1993	7	0	0
Mulkey (versus site below), 1994	5	0	3
Mulkey (versus site above), 1993	7	0	0
Mulkey (versus site above), 1994	8	0	0
All, 1993	23	3	2
All, 1994	28	0	4

associated with comparisons of fish population characteristics only to provide a relative measure of the magnitude of differences and not to draw conclusions based solely on statistical significance ($P \leq 0.05$).

Results

Stream Physical Characteristics

All of the protected sites showed differences in stream physical characteristics that were consistent with changes expected following the removal of livestock from streamside zones. In 1993, of 28 comparisons between paired ungrazed and grazed sites for variables that we predicted would change in a particular direction, 23 (82%) differed in the predicted direction, 3 (11%) showed no change, and 2 (7%) changed in directions opposite to what was predicted (Table 1). In 1994, of the 32 comparisons made, 28 (88%) differed in the predicted direction and 4 (12%) changed opposite to predictions (Table 1). The difference between the numbers of confirmed and contradicted predictions was statistically significant in both years (1993, 23 versus 2; $P < 0.001$; 1994, 28 versus 4; $P < 0.001$). Canopy shading and bank water depth showed the greatest number of predicted differences, showing differences in all comparisons in 1993 and 1994. Water depth, stream width, and bank-full height showed differences in the predicted directions in 75–100% of the comparisons, and unvegetated stream width and bank angle showed the predicted differences in 75% of the comparisons. Bank overhang showed the predicted differences in 50–75% of the comparisons.

Of the variables with no predicted direction of

change, only channel depth and width showed consistent differences between inside and outside the exclosures. Channel depth was shallower in grazed sites in all of the 1993 comparisons and in 75% of the 1994 comparisons. Channel width was greater in grazed areas in all of the 1993 and 1994 comparisons. Substrate size, percent fine sediment, and water velocity showed no consistent differences between inside and outside of exclosures.

Stream physical habitat results were very similar between 1993 and 1994 (Table 1); therefore, we present detailed stream physical characteristics for each site for 1994 only.

Upper Ramshaw Meadow

In 1994, one of the four variables for which there was no predicted direction of change (channel width, channel depth, substrate size, and water velocity) showed a large difference (defined as one exceeding 20%) between sites inside and outside the upper Ramshaw exclosure (Table 2): channel width was 47% greater below than inside the exclosure. Of the variables that we expected to change in a predicted direction as a result of livestock exclusion, all showed differences consistent with changes expected after the cessation of livestock grazing, and six of the eight differences were larger than 20% (Table 2). Bank-full height, bank overhang, and bank water depth were 75–100% greater inside than outside the exclosure. Canopy shading was 250% greater inside the exclosure than outside.

In 1994, stream width was 34% narrower inside the exclosure than outside (Table 2). To determine whether this difference was the result of a change (i.e., recovery) that had occurred inside the exclosure since 1984, we compared the stream width inside the exclosure obtained from the 1984 channel map to the 1993 and 1994 field measurements of stream width. Stream width inside the exclosure in 1984 was significantly wider than stream width in both 1993 and 1994 (1984, 345 cm; 1993, 271 cm; 1994, 230 cm; ANOVA on log-transformed data; $P < 0.0001$). Differences in stream width between 1993 and 1994 were not significant (Tukey pairwise comparison of means; $P > 0.05$). Therefore, stream width had narrowed significantly inside the exclosure since 1984 (i.e., recovery was occurring).

Willows were much more abundant within the exclosure: 264 willows were counted inside the exclosure and 11 willows were counted below the exclosure (Figure 3A). Willows inside covered a much wider range of heights than those below the

exclosure (inside, 5–220 cm; below, 10–70 cm). Also, willows 5–20 cm tall were abundant inside the exclosure but nearly absent below the exclosure.

Lower Ramshaw Meadow

One of the four variables for which there was no predicted direction of change showed a large difference between sites inside and outside the lower Ramshaw exclosure (Table 2): substrate size was 59% larger above than inside the exclosure. Of the eight variables that we expected to change in a predicted direction as a result of livestock exclusion, seven showed differences in the predicted directions, and four of these differences were larger than 20% (Table 2). Unvegetated stream width and total stream width were 31 and 19% narrower inside the exclosure than above the exclosure, respectively, and stream depth, bank water depth, and canopy shading were 30–50% greater inside than above the exclosure. The difference in bank angle was in the opposite direction of what we predicted (bank angle was larger in the ungrazed site), but this difference was small (5%).

As in upper Ramshaw Meadow, willows were much more abundant within the lower exclosure; 222 willows were counted inside the exclosure and 22 willows were counted above the exclosure (Figure 3B). Willows inside the exclosure also showed a much wider size range than those outside the exclosure (inside, 5–170 cm; above, 10–60 cm).

Mulkey Meadow

One of the four variables for which there was no predicted direction of change showed a large difference between sites inside and below the Mulkey exclosure (Table 2): water velocity was 40% higher below the exclosure than inside it. Of the variables that we expected to change in a predicted direction as a result of livestock exclusion, five differed in the predicted direction, and three of these differences were larger than 20% (Table 2). Canopy shading, bank water depth, and stream depth were 25–33% greater inside than below the exclosure. Three variables differed in the opposite direction from our predictions, but all of these differences were smaller than 20% (Table 2). Stream width and unvegetated stream width were 12 and 10% wider inside the exclosure than outside, and bank overhang was 17% less inside the exclosure.

In the comparison of physical characteristics between sites inside and above the exclosure, three of the four variables for which there was no predicted direction of change showed large differ-

TABLE 2.—Means (SEs) of stream physical characteristics outside (grazed) and inside (ungrazed) the upper Ramshaw, lower Ramshaw, and Mulkey exclosures in 1994.

Variable	Grazed	Ungrazed	Percent difference ^a	N	P ^b
Upper Ramshaw exclosure versus below exclosure					
Channel depth (cm)	61 (2)	69 (2)	13	25	0.008
Channel width (cm)	899 (39)	613 (34)	47	25	<0.001
Substrate size (mm)	4.7 (0.4)	4.6 (0.4)	2	125	0.90
Water velocity (cm/s)	17 (1)	19 (1)	12	125	0.30
Stream width (cm)	309 (19)	230 (11)	34+	25	<0.001
Unvegetated stream width (cm)	290 (17)	200 (10)	45+	25	<0.001
Bank-full height (cm)	16 (2)	28 (2)	75+	25	<0.001
Canopy shading (%)	10 (2)	35 (3)	250+	25	<0.001
Bank angle (degrees)	145 (5)	124 (5)	14+	50	<0.001
Bank overhang (cm)	2 (1)	4 (1)	100+	50	0.07
Bank water depth (cm)	8 (1)	16 (1)	100+	50	<0.001
Stream depth (cm)	12 (1)	14 (1)	17+	125	0.03
Lower Ramshaw exclosure versus above exclosure					
Channel depth (cm)	47 (1)	44 (2)	6	25	0.14
Channel width (cm)	569 (40)	583 (38)	2	25	0.14
Substrate size (mm)	3.5 (0.3)	2.2 (0.3)	59	125	<0.001
Water velocity (cm/s)	16 (1)	15 (1)	7	125	0.94
Stream width (cm)	283 (18)	238 (8)	19+	25	0.09
Unvegetated stream width (cm)	276 (19)	210 (9)	31+	25	0.01
Bank-full height (cm)	18 (2)	20 (2)	11+	25	0.42
Canopy shading (%)	14 (2)	21 (3)	50+	25	0.19
Bank angle (degrees)	114 (7)	120 (8)	5-	50	0.38
Bank overhang (cm)	7 (2)	8 (2)	14+	50	0.87
Bank water depth (cm)	10 (1)	13 (1)	30+	50	0.02
Stream depth (cm)	10 (1)	14 (1)	40+	125	<0.001
Mulkey exclosure versus below exclosure					
Channel depth (cm)	56 (2)	64 (1)	14	25	0.002
Channel width (cm)	489 (36)	426 (17)	15	25	0.39
Substrate size (mm)	6.1 (0.9)	6.5 (0.9)	6	125	0.37
Water velocity (cm/s)	14 (1)	10 (1)	40	125	0.01
Stream width (cm)	130 (11)	146 (10)	12-	25	0.17
Unvegetated stream width (cm)	111 (9)	122 (11)	10-	25	0.50
Bank-full height (cm)	15 (2)	18 (2)	20+	25	0.30
Canopy shading (%)	24 (2)	32 (3)	33+	25	0.05
Bank angle (degrees)	114 (6)	112 (6)	2+	50	0.60
Bank overhang (cm)	7 (2)	6 (2)	17-	50	0.55
Bank water depth (cm)	16 (2)	21 (2)	31+	50	0.03
Stream depth (cm)	16 (1)	20 (1)	25+	125	0.01
Mulkey exclosure versus above exclosure					
Channel depth (cm)	41 (2)	64 (1)	56	25	<0.001
Channel width (cm)	759 (33)	426 (17)	78	25	<0.001
Substrate size (mm)	8.2 (1)	6.5 (0.9)	26	125	0.007
Water velocity (cm/s)	9 (1)	10 (1)	11	125	0.72
Stream width (cm)	162 (7)	146 (10)	11+	25	0.04
Unvegetated stream width (cm)	140 (7)	122 (11)	15+	25	0.02
Bank-full height (cm)	11 (1)	18 (2)	63+	25	0.01
Canopy shading (%)	2 (1)	32 (3)	1,500+	25	<0.001
Bank angle (degrees)	152 (4)	112 (6)	36+	50	<0.001
Bank overhang (cm)	1 (1)	6 (2)	500+	50	0.06
Bank water depth (cm)	10 (1)	21 (2)	110+	50	<0.001
Stream depth (cm)	10 (1)	20 (1)	100+	125	<0.001

^a A "+" after the percent difference indicates the direction of the difference is consistent with changes expected after the removal of livestock; a "-" after the percent difference indicates that the difference is opposite to the changes expected after the removal of livestock; the lack of a symbol indicates that there was no predicted direction of change.

^b Comparisons are pseudoreplicated. Therefore, *P*-values are given only for comparison of relative magnitudes of differences.

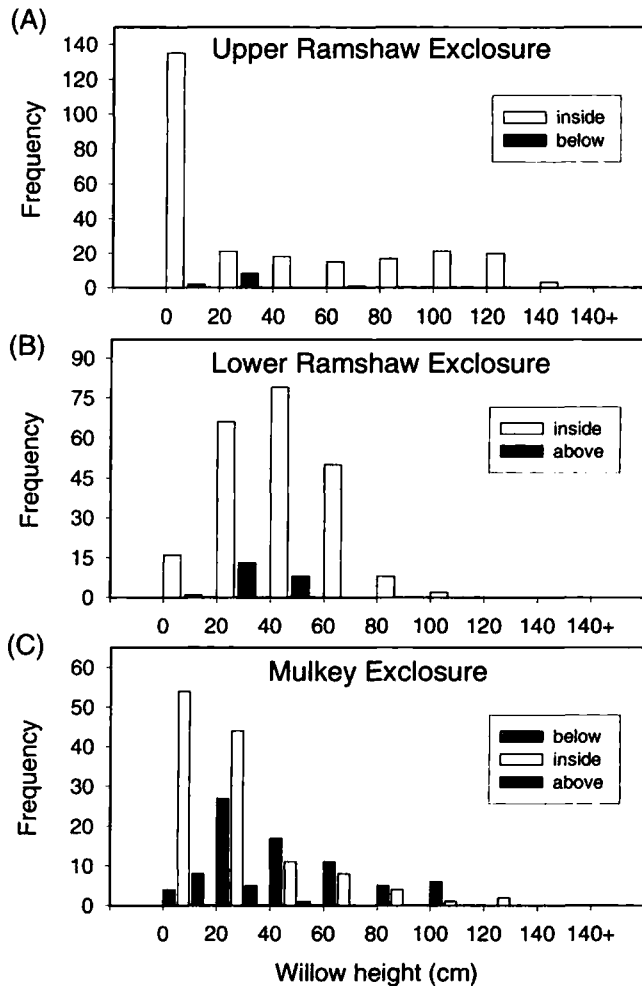


FIGURE 3.—Size-frequency histograms of willows (A) inside and below the upper Ramshaw exclosure, (B) inside and above the lower Ramshaw exclosure, and (C) below, inside, and above the Mulkey exclosure. Frequency of willows is presented in 20-cm size ranges.

ences (Table 2). Above the exclosure, the channel was 56% shallower and 78% wider, and substrate size was 26% larger, than inside the exclosure. Of the variables that we expected to change in a predicted direction as a result of livestock exclusion, all eight showed differences in the predicted directions, and six of the differences were larger than 20% (Table 2). Bank water depth and stream depth were 100–110% greater inside than above the exclosure. In addition, canopy shading was 15 times greater and bank overhang was 5 times greater inside than above the exclosure.

Willows were more abundant within the exclosure than either above or below the exclosure; 124 willows were counted inside the exclosure, 14 above the exclosure, and 70 below the exclosure

(Figure 3C). The size range of willows inside and below the exclosure was greater than the size range above the exclosure (inside, 5–140 cm; below, 10–120 cm; above, 5–60 cm). Small (5–20 cm) willows were much more abundant inside the exclosure than either above or below the exclosure.

Fish Population Characteristics

Three electrofishing passes through each 25-m section allowed the capture of nearly all fish in a 125-m site. There were small differences between actual and estimated total fish per section and low SEs around population estimates. The SE associated with the estimated number of fish per site was 3.6% of the estimate in 1993 ($N = 7$; range, 2.3–4.8%) and 2.8% of the estimate in 1994 ($N = 7$;

range, 1.3–6.5). The average capture probability was 0.50 in 1993 ($N = 7$; range, 0.40–0.59) and 0.56 in 1994 ($N = 7$; range, 0.41–0.63).

California golden trout were very abundant in the study streams. Densities ranged from 1.3 to 2.7 fish/m² (370–692 fish/125 m) and biomasses ranged from 15.8 to 21.2 g/m² (3,186–6,779 g/125 m). Fish population characteristics were similar between 1993 and 1994; therefore, we present only data from 1994. The outcome of statistical analyses of fish population characteristics depended in part on whether density and biomass were calculated on a unit-area or unit-stream-length basis. When density and biomass were calculated on a unit-area basis, California golden trout density and biomass were significantly ($P \leq 0.05$) higher inside than outside exclosures in three of the four comparisons and not significantly different in one comparison (Figures 4, 5). In contrast, when density and biomass were calculated on a unit-stream-length basis, California golden trout density and biomass were significantly higher inside than outside the exclosure in one comparison, significantly lower inside than outside in one comparison, and not significantly different in the remaining two comparisons (Figures 4, 5). At the upper Ramshaw exclosure, the number and weight of California golden trout per square meter were significantly higher inside than below the exclosure (Figures 4A, 5A). The number and weight of fish per 125 m, however, were significantly lower inside than below the exclosure (Figures 4A, 5A). The number and weight of fish per square meter were significantly higher inside than above the lower Ramshaw exclosure, but the number and weight of fish per 125 m did not differ significantly between sites (Figures 4B, 5B). At the Mulkey exclosure, California golden trout densities calculated on a unit-area and unit-stream-length basis both were significantly higher inside the exclosure than below the exclosure, but not significantly different from the densities above the exclosure (Figure 4C). California golden trout biomasses calculated on a unit-area and unit-stream-length basis both were significantly higher inside the exclosure than above the exclosure but not significantly different from those below the exclosure (Figure 5C).

Discussion

Our study was hampered by the small number of exclosures available, their nonrandom placement, and the resulting pseudoreplication of our sampling design (Hurlbert 1984). Although we acknowledge that extrapolations from our data to

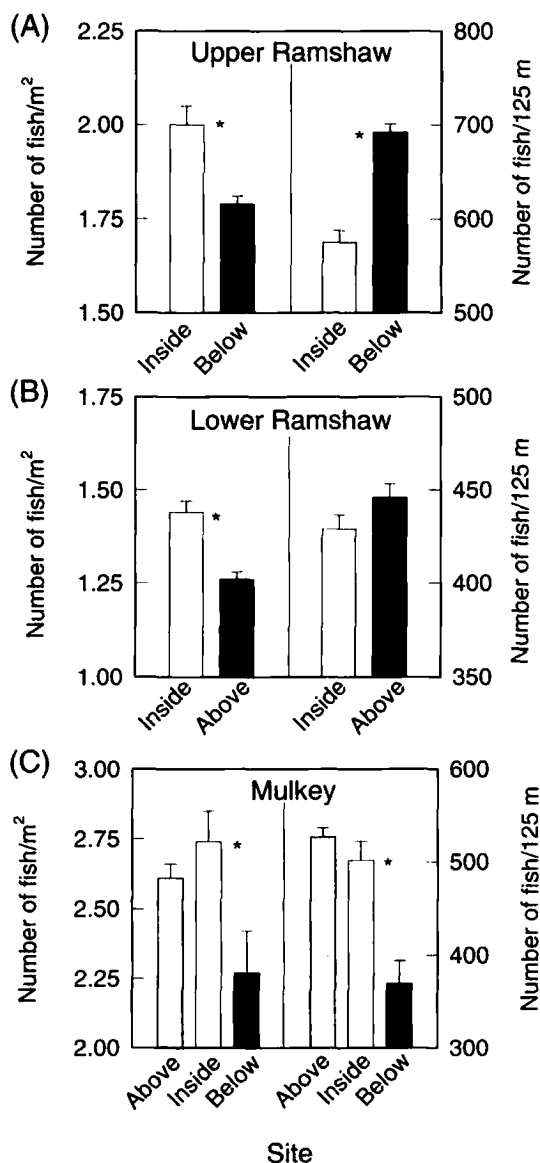


FIGURE 4.—California golden trout population density calculated as number of fish/m² (left-side bars) and number of fish/125 m of stream (right-side bars) (A) inside and below the upper Ramshaw exclosure, (B) inside and above the lower Ramshaw exclosure, and (C) below, inside, and above the Mulkey exclosure. An asterisk between paired bars indicates that the difference is statistically significant ($P \leq 0.05$).

other portions of the study meadows should therefore be made cautiously, the exclosures represent the only possible means of quantitatively assessing current levels of livestock grazing on California golden trout and their habitat at a time when such

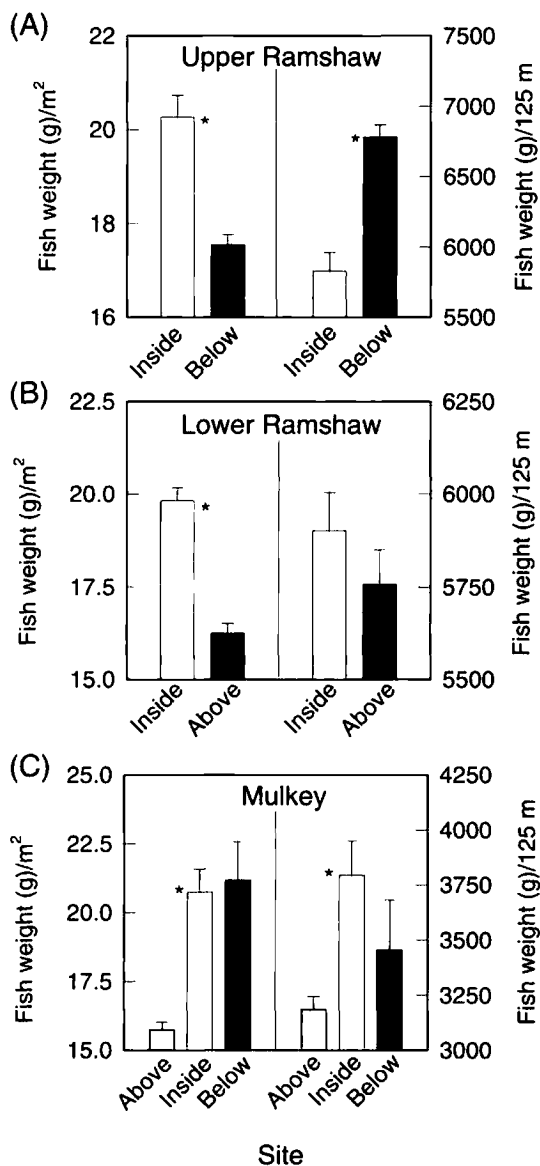


FIGURE 5.—California golden trout population biomass calculated as fish weight (g)/m² (left-side bars) and fish weight (g)/125 m of stream (right-side bars) (A) inside and below the upper Ramshaw exclosure, (B) inside and above the lower Ramshaw exclosure, and (C) below, inside, and above the Mulkey exclosure. An asterisk between paired bars indicates that the difference is statistically significant ($P \leq 0.05$).

data are critically needed to aid in determining the status of this subspecies.

Stream Physical Characteristics

Our comparison of stream physical characteristics inside and outside exclosures in Ramshaw

and Mulkey meadows strongly suggest that the observed differences are the result of livestock grazing. The consistent differences in numerous physical characteristics between inside and outside sites, including increased streamside vegetation, stream narrowing and deepening, and increased bank stability, are consistent with recovery from grazing-induced damage (Platts 1991). Differences were particularly large at the Mulkey and upper Ramshaw exclosures, where recovery from past grazing is resulting in a more confined, narrow stream (conversion from a type C to a type E channel; Rosgen 1994) lined with abundant mesic and hydric vegetation.

On the basis of the magnitude of differences inside and outside exclosures for each of our measured stream physical characteristics, vegetation apparently responded most rapidly to grazing exclusion, and recovery of streambanks and channel morphology proceeded at a slower rate. Kondolf (1993) reported similar results in a subalpine meadow in the White Mountains, California. Measurements taken inside and outside a 24-year-old exclosure showed significant vegetative recovery, but no detectable recovery in stream channel morphology.

Among the most pronounced differences between protected and unprotected sites were the numbers and sizes of willows. The number of young (5–40-cm) willows was much higher inside than outside all exclosures, suggesting that livestock grazing is impeding willow recruitment. Odion et al. (1988) also found that willow plantings had significantly lower survival outside than inside exclosures in the GTW, and reduction in willow cover appears to be a common result of livestock grazing (Kauffman and Krueger 1984; Platts 1991). Therefore, although willows are currently quite sparse outside grazing exclosures in the GTW, this rarity may be a result of 130 years of livestock grazing and not a natural attribute of these meadows.

Past attempts to establish willows from cuttings have resulted in low survival even inside of GTW grazing exclosures (Odion et al. 1988). However, we observed a large number of young willows inside exclosures. Taken together, these results suggest that the most effective means of establishing willows in the GTW is by natural recruitment following livestock exclusion.

Of the stream physical habitat variables that we measured, several were expected to change only very slowly (20–100 years) or we could not predict in which direction they would change inside versus

outside exclosures. These variables were measured to allow post hoc determinations of whether sites inside and outside of exclosures were similar at the time of exclosure construction. Channel depth and channel width both showed consistent differences inside versus outside exclosures; channels were generally more incised and narrower inside exclosures. Although the differences in channel depth and width between some of our grazed and ungrazed sites suggest that some aspects of our sites may have been different at the time of exclosure construction, differences in channel depth and width alone are unlikely to account for the consistent differences in other stream characteristics between inside and outside sites at all exclosures. Instead, these differences are much more likely the result of recovery from livestock grazing inside exclosures.

Changes in stream physical characteristics similar to those found in our study are reported in other studies of grazing impacts on stream and riparian ecosystems. These include increased streamside vegetation (Marcuson 1977; Van Velson 1979; Duff 1983; Platts and Nelson 1985a; Kondolf 1993), stream narrowing and deepening (Duff 1983; Platts and Nelson 1985a), and increased streambank stability (Kauffman et al. 1983; Platts and Nelson 1985b; Rinne 1988).

Fish Population Characteristics

Our comparisons of California golden trout density and biomass show that the magnitude of differences between inside and outside exclosures is influenced by the method used to calculate these variables. When density and biomass were calculated as the number and weight of golden trout per square meter, densities and biomasses were generally significantly higher inside than outside the exclosures. When the density and biomass were expressed as the number and weight per 125 m of stream, however, there were no consistent differences inside versus outside exclosures. The contrasting results obtained when fish density and biomass were calculated based on unit area versus unit stream length are a consequence of the different stream widths (and therefore stream areas) inside and outside exclosures.

Comparisons of fish populations are generally made based on unit-area measurements (e.g., number/m², g/m², kg/ha; Keller and Burnham 1982; Platts and Nelson 1985b; Beard and Carline 1991; Larscheid and Hubert 1992), but authors have also used unit-volume measurements (e.g., g/m³; Platts and Nelson 1985a) and unit-stream-length mea-

surements (e.g., number/50 m, g/50 m; Rinne 1988). Because our paired sites were close together and discharges at paired sites should therefore be similar, we found no reason to use unit-volume measurements. Although both unit-area and unit-length measurements are justified in study designs such as ours, unit-area measurements may provide the more accurate portrayal of grazing impacts. Trout population size is frequently limited by the autotrophic food base (Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983). Because total autotrophic production should increase with increasing stream width but remain constant on a per-area basis, wide stream sections should have a larger total autotrophic food base than narrower stream sections. As a consequence, all other factors being equal, the number of fish per unit stream length should be an increasing function of stream width, whereas the number of fish per unit area should be unaffected by stream width. Therefore, unit-stream-length measurements are potentially confounded by effects associated with stream width, whereas unit-area measurements remove these effects. Based on this reasoning and our results showing that California golden trout density and biomass per square meter were generally greater in ungrazed than grazed sites, we conclude that livestock grazing in the study meadows is having negative effects on California golden trout populations.

Several other studies have also documented the negative consequences of livestock grazing on trout populations (Platts 1991). For example, Marcuson (1977) found that the biomass of brown trout was more than three times higher in an ungrazed stream section than in one that was grazed. Platts (1981) reported that fish densities were more than 10 times higher in a stream section subject to light grazing or no grazing relative to a heavily grazed section. Similarly, densities of rainbow trout *Oncorhynchus mykiss* and brook trout *Salvelinus fontinalis* were higher in an ungrazed than in a grazed stream section (Keller and Burnham 1982). Although these effects are generally attributed to reductions in the quality of physical stream habitat, cumulative effects of grazing can further reduce trout populations by altering stream discharge regimes and by increasing water temperatures (Van Velson 1979; Platts and Nelson 1989; Li et al. 1994).

The results of our fish population surveys show that in spite of the effects of livestock grazing, California golden trout exist at extremely high densities in Mulkey and Ramshaw meadows (1.3–

2.7 fish/m²). In comparison with salmonid densities in 277 streams reviewed by Platts and McHenry (1988), the California golden trout populations in our study sites were among the densest ever reported for trout in the western United States and were an order of magnitude more dense than the average trout density for all ecoregions in the western United States (0.25 fish/m²; Platts and McHenry 1988). Because it is unclear whether Platts and McHenry (1988) included age-0 fish in their density estimates, we made the same comparison after removing age-0 fish from our density calculations. Densities of California golden trout in Mulkey and Ramshaw meadows (1.2–2.0 fish/m²) remained among the greatest in the western United States. Biomass of California golden trout in our study streams (15.8–21.2 g/m²) is also among the highest recorded and is 3–4 times higher than the average trout biomass of streams in the western United States (5.4 g/m²; Platts and McHenry 1988).

Livestock Grazing and Wilderness Management

Our study provides evidence that areas in Ramshaw and Mulkey meadows grazed by livestock are in poorer condition than areas inside exclosures and that this degradation is negatively impacting California golden trout. If stream condition in our grazed sites is representative of the condition of streams subjected to grazing throughout the GTW (and we believe it is), our study raises the question of whether such degradation is appropriate in a designated wilderness. Under the Wilderness Act of 1964, "an area of wilderness . . . which is protected and managed so as to preserve its natural conditions and which . . . generally appears to have been affected primarily by the forces of nature, with the imprint of man's work substantially unnoticeable" (Kloepfer et al. 1994). Although national forests do not have the authority to curtail livestock grazing solely because of wilderness designation (Kloepfer et al. 1994), they do have the authority to make changes in livestock grazing programs to reduce unacceptable impacts. The Inyo National Forest apparently recognizes the impact of livestock grazing on stream and riparian ecosystems in the GTW, but past efforts to rehabilitate degraded stream habitats in the GTW relied primarily on expensive structural remedies (Laituri et al. 1987; Felando, unpublished report) that have met with very limited success. One of the simplest and most cost-effective means of reducing grazing impacts is to rest areas or reduce livestock numbers (Platts 1991), and we suggest that the Inyo Na-

tional Forest consider these management options to reduce impacts on stream and riparian ecosystems in the GTW. The restoration of these ecosystems will increase meadow stability (Odion et al. 1988), improve habitat for native California golden trout, and enhance conditions for a wide range of other riparian-dependent species (Johnson et al. 1977; Szaro and Rinne 1988).

Acknowledgments

Phil Pister deserves accolades for his extensive work on California golden trout and for bringing attention to their plight. Roland Knapp was supported during this research by a cooperative agreement with the U.S. Forest Service Pacific Southwest Research Station (agreement PSW-92-0041CA). The Fish Habitat Relationship Program through the regional office of the U.S. Forest Service provided additional financial assistance, and we are especially grateful to Lynn Decker, Pacific Southwest Region Fish Program Manager, for her support. We also acknowledge Donald Sada for his role in designing portions of the stream physical habitat and fish sampling protocol. We thank Ed Ballard, Jim Muck, Randall Osterhuber, and Vance Vredenburg of the U.S. Forest Service and Melanie Paquin of the University of California, Davis, for assisting with the field work. Sara Chubb, former Inyo National Forest fish biologist, and Del Hubbs, Inyo National Forest range conservationist, were helpful in setting up the study. The comments of Sylvia Mori (Pacific Southwest Research Station Statistician) and four reviewers of an earlier version of the manuscript greatly improved our presentation. Dennis and Jody Winchester of Cottonwood Packers and their mules made wilderness research possible.

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