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EFFECTS OF STREAM CHANNEL MORPHOLOGY ON GOLDEN TROUT SPAWNING HABITAT AND RECRUITMENT

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Abstract. Populations of stream-dwelling salmonids (e.g., salmon and trout) are generally believed to be regulated by strong density-dependent mortality acting on the age-0 life stage, which produces a dome-shaped stock-recruitment curve. Although this paradigm is based largely on data from anadromous species, it has been widely applied to stream-resident salmonids despite the fact that the processes limiting or regulating stream-resident populations remain poorly understood. The purpose of the present study was to determine whether stream channel morphology affects the availability of spawning habitat for California golden trout, and whether spawning habitat availability influences the production of age-0 trout and recruitment into the adult population.

Wide stream reaches contained significantly more spawning habitat and a higher density of nests and age-0 trout than did narrow reaches. In contrast to the idea that salmonid populations are regulated by density-dependent mortality of age-0 fish, we found that the mortality of age-0 trout was largely density independent. In addition, over most of the range of observed fish densities, the density of a particular cohort was positively correlated between years for age-0, age-1, and age-2 trout. Therefore, our golden trout study population was limited by spawning habitat, with spawning habitat availability influencing the production of age-0 trout as well as recruitment into the adult population.

Grazing by cattle has widened the study streams, and our current findings help to explain why stream sections subject to grazing had more spawning habitat and higher golden trout densities than ungrazed sections. Individual growth rates of golden trout are apparently negatively density dependent, and these grazing-related increases in trout density have likely resulted in decreased growth rates. Our study demonstrates that it is only by gaining an understanding of how processes operate that we will be able to predict the effects of habitat alteration on populations.

Key words: *golden trout; livestock grazing; recruitment; reproduction; salmonids; Sierra Nevada; spawning habitat; stream alteration; stream morphology.*

INTRODUCTION

A central goal of ecology is the identification of factors that influence the distribution and abundance of organisms. At the most basic level, populations are regulated by births, deaths, emigration, and immigration. The values of these demographic parameters are a function of the suite of biotic and abiotic factors that constitute an organism's habitat. Recruitment, the addition of new individuals to populations or to successive life-cycle stages within populations (Caley et al. 1996), provides a link between birth rates and the dynamics of juvenile and adult components of populations. The influence of recruitment on population dynamics has been the focus of much research in a wide variety of organisms, including plants (Elton 1958, Cavers and Harper 1967, Davis 1981, Eriksson and Ehrlen 1992, Hurtt and Pacala 1995, Tilman 1997), invertebrates (Connell 1985, Menge and Sutherland 1987, Olafsson et al. 1994, Wiernasz and Cole 1995, Noda and Nakao 1996, Peterson et al. 1996), and fishes (Ricker 1954, Freeman et al. 1988, Fogarty et al. 1991, Doherty and Fowler 1994*a*, Johnston et al. 1995, Caley et al. 1996).

Recruitment dynamics have been particularly well studied in fishes, due perhaps to the commercial and recreational importance of this group of animals (e.g., Huppert and Fight 1991, Cushing 1995). Theoretically, rates of recruitment can limit or regulate adult populations (Caley et al. 1996), and this suggestion is supported by a large body of evidence showing that patterns of recruitment are frequently reflected in the age structure of adult populations (e.g., coral reef fishes: Victor 1983, Wellington and Victor 1985, Dowerty and Fowler 1994*a*; stream fishes: Freeman et. al. 1988, Beard and Carline 1991, Johnston et al. 1995) and that

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variable recruitment results in variations in adult population size (Williams 1980, Victor 1983, Doherty and Fowler 1994*b*). Despite the likely role of recruitment in structuring many fish populations (e.g., Caley et al. 1996), our understanding of the factors influencing the production and recruitment of early life stage fishes and the extent to which these processes affect the adult component of populations remains limited.

Stream-dwelling salmonids (e.g., salmon and trout) have several attributes that make them good candidates for the study of factors affecting recruitment and population dynamics. First, because of the physical confines of the stream environment, all life stages can be accurately sampled using relatively simple techniques (Van Deventer and Platts 1983). Second, because of the commercial and economic importance of stream-dwelling salmonids, the basic life history of these species is relatively well understood (Bjornn and Reiser 1991, Meehan and Bjornn 1991). Lastly, stream-dwelling salmonids are sensitive to habitat changes (Hicks et al. 1991), and therefore provide an excellent opportunity to investigate the influence of habitat alteration on recruitment and population dynamics. An improved understanding of the mechanisms by which stream alterations affect spawning habitat, production of early life stages, and recruitment would greatly improve our ability to predict the consequences of habitat changes on salmonid populations (e.g., Gowan and Fausch 1996). Since stream ecosystems are currently being altered at a greater rate than during any other time in history (National Research Council 1992), such predictive abilities are critically important for efforts aimed at minimizing the effects of human activities.

Research on recruitment dynamics in salmonids have focused largely on anadromous species. Results from these studies have generally supported the paradigm that salmonid populations are regulated by strong density-dependent mortality acting on the age-0 stage soon after emergence from the gravel (Le Cren 1965, Allen 1969, Egglishaw and Shackley 1977, Elliot 1984*a*, Elliot 1985*a*, Everest et al. 1987, Gardiner and Shackley 1991, Crisp 1993). This density-dependent mortality typically results in a dome-shaped stock-recruitment curve, with egg density and age-0 fish density being positively correlated until reaching a maximum, after which further increases in egg density result in decreases in the density of age-0 fish (Ricker 1954, Elliot 1985*a*, Gardiner and Shackley 1991). This population regulation at the age-0 stage is believed to result from territory formation by newly emerged fish that places an upper limit on their density (Chapman 1966, Allen 1969, Elliot 1990, Grant and Kramer 1990).

Here we report on a 4-yr study of the California golden trout, *Oncorhynchus mykiss aguabonita,* designed to assess whether stream channel morphology influences the availability of spawning habitat, and whether spawning habitat affects the production of age-0 trout and subsequent recruitment to the adult population. The California golden trout is endemic to only two stream drainages in the southern Sierra Nevada, both within the Golden Trout Wilderness (GTW), and is currently being considered for listing under the federal Endangered Species Act. Of particular concern is the alteration of stream habitats by livestock grazing, and the effects of these changes on golden trout population densities (Inyo National Forest 1997).

Livestock have grazed the area now contained within the GTW since at least 1860. Past overgrazing resulted in widespread meadow erosion (Albert 1982, Odion et al. 1988), and although the number of cattle grazing the area today is far below historical levels (Sarr 1995), the present grazing intensity appears to be slowing recovery of stream and riparian ecosystems. For example, Knapp and Matthews (1996) found that stream reaches that had been protected from grazing were generally deeper, narrower, and had more riparian vegetation than reaches grazed by livestock. These results and those of Odion et al. (1988) and Sarr (1995) suggest that although meadow stream reaches in the GTW are generally wide and shallow today, they were likely to have been narrower and deeper prior to grazing by livestock. This conversion of stream channels from narrow and deep to wide and shallow results from stream bank destabilization and erosion (Rosgen 1994) and is one of the most commonly reported effects of livestock grazing on meadow streams (Platts 1991).

Despite livestock-induced alterations to stream channel morphology, golden trout exist at very high densities (Knapp and Matthews 1996). Indeed, golden trout density (number per linear distance of stream) is positively correlated with increasing stream channel instability (Knapp and Dudley 1990) and is often higher in areas subject to livestock grazing than in areas protected from grazing (Knapp and Matthews 1996). In addition, we have repeatedly observed that golden trout nests (redds) are found predominantly in relatively wide stream reaches (observations made during studies reported in Knapp and Vredenburg 1996).

To better understand the mechanisms underlying these patterns, we hypothesized that stream morphological changes associated with livestock grazing (e.g., bank instability and stream widening) increase both spawning habitat availability and the production of age-0 trout, and that higher densities of age-0 trout result in increased recruitment into the adult population. To examine this general hypothesis, we tested the following three predictions: (1) the availability of golden trout spawning habitat and density of redds is higher in wide stream reaches than in narrow stream reaches; (2) the density of age-0 fish is higher in wide stream reaches than in narrow stream reaches, and is an increasing function of redd density; and (3) the size of a particular cohort is a positive function of the size of that cohort in the previous year for age-0, age-1, and age-2 fish. If all three predictions are supported, our results would directly link stream channel morphology to spawning

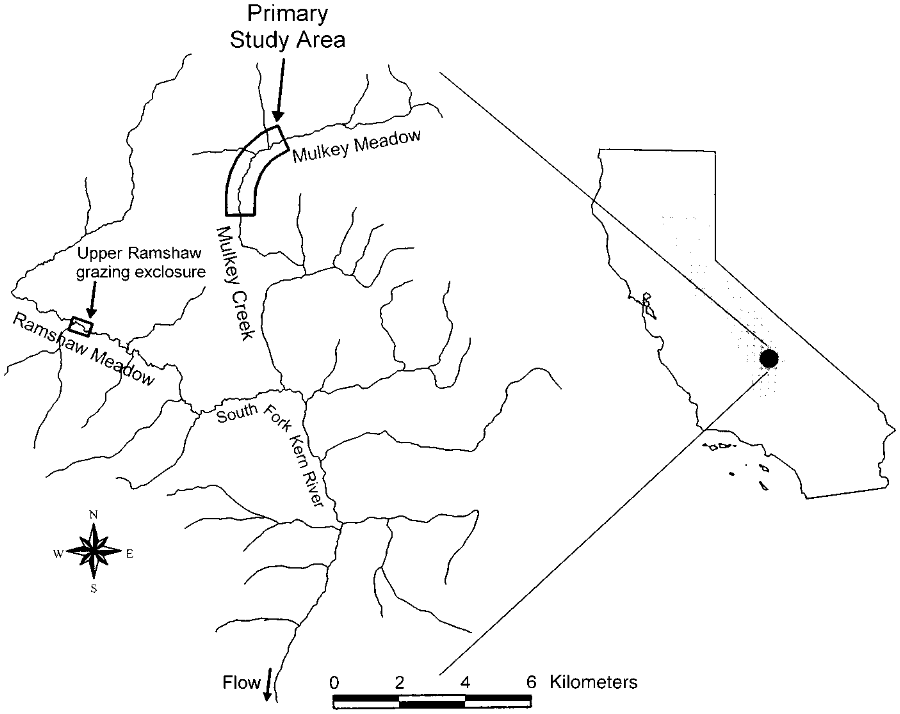

FIG. 1. Map of California showing the Sierra Nevada (shaded area) and the location of the South Fork Kern River watershed. The enlargement of the South Fork Kern River watershed shows the location of the primary study area on Mulkey Creek, and the Upper Ramshaw Meadow grazing exclosure on the South Fork Kern River.

habitat availability and recruitment, and would provide a mechanism by which changes in stream channel morphology caused by livestock grazing may increase the density of adults in this rare salmonid.

METHODS

Study sites

Our study sites were located in Mulkey and Ramshaw Meadows near the headwaters of the South Fork Kern River, Inyo National Forest, California, USA (118°15′ N, 36°22′ W; Fig. 1). The upper portion of this watershed, including the study area, is contained within the 133 500-ha Golden Trout Wilderness, designated in 1977 in part to protect habitat of the golden trout. The California golden trout is the only fish species present in Mulkey and Ramshaw Meadows (Knapp and Matthews 1996).

Our primary study site was located on Mulkey Creek at an elevation of ~2850 m, and contained 3.5 km of stream (Fig. 1). We chose the Mulkey Creek study area because of the relatively constant stream gradient and homogeneous vegetation in this portion of the meadow. A second study site was located around the upper Ramshaw Meadow livestock exclosure on the South Fork Kern River (elevation ≅ 2660 m; Fig. 1). This exclosure was constructed in 1983, and we selected 125-m study reaches located immediately inside and below the exclosure (see Knapp and Matthews 1996 for additional details). These sites were chosen because previously collected data indicated that these sites were similar at the time of exclosure construction (i.e., wide and shallow), but by 1994 the protected stream reach was substantially narrower and deeper than the grazed reach (Knapp and Matthews 1996).

Stream habitat and redd characterization

Data collection.—To test our prediction that stream channel morphology influences the amount of spawning habitat, we took advantage of the fact that lower Mulkey Creek is characterized by a series of wide and narrow reaches in an otherwise relatively uniform meadow environment. We compared channel morphology and spawning habitat between replicate wide and narrow reaches. In addition, we assessed the influence of livestock grazing on golden trout spawning habitat by comparing redd densities inside and outside the Upper Ramshaw Meadow livestock exclosure.

Within the Mulkey Creek study area, we divided the stream into discrete reaches based on the channel types of Rosgen (1994; Fig. 2). Based on channel characteristics (entrenchment, width/depth, slope), we divided the stream into five "E channel" reaches (Fig. 3A; low gradient, meandering riffle/pool stream with little sediment deposition, width/depth ratio <12; Rosgen 1994), five "C channel" reaches (Fig. 3B; low gradient, meandering, riffle/pool stream with point-bar deposition, width/depth ratio >12; Rosgen 1994), and seven reaches that were intermediate between E and C chan-

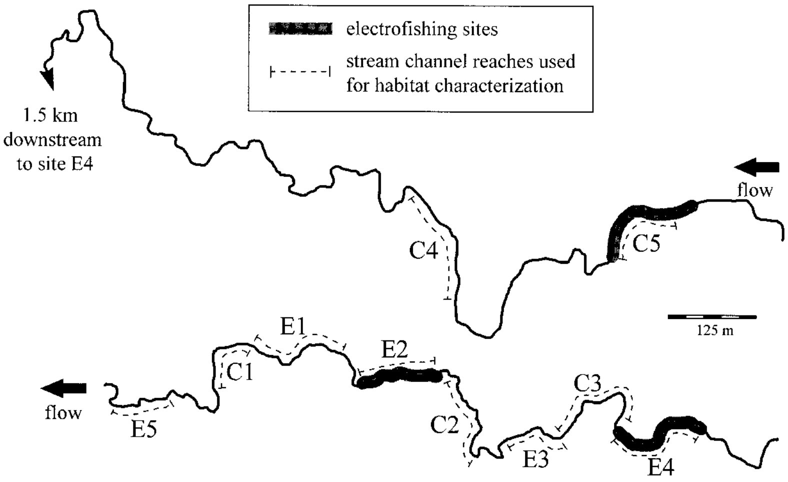

FIG. 2. Map of the Mulkey Creek study area showing the locations of the study stream reaches (C1–C5, E1–E5) and electrofishing sites. Wide ("C") reaches are broad and shallow; narrow ("E") reaches are confined and deep.

nels (some point-bar deposition, width/depth ratio ~12). We used the five E reaches and five C reaches (hereafter referred to as "narrow" and "wide" reaches, respectively) to quantify stream channel morphology and spawning habitat in relatively unaltered and altered channel types, respectively. The narrow and wide reaches ranged in length from 45–130 m (narrow reaches: range = 45–125 m, $\bar{X}$ = 82 m; wide reaches: range = 53–130 m, $\bar{X}$ = 85 m). All five narrow reaches and three of the wide reaches were located in close proximity to each other and were separated from the remaining two wide reaches by ~2.2 km of stream with intermediate channel morphology (Fig. 2). In most cases, narrow and wide study reaches alternated with each other, but in two cases two reaches of the same channel type were adjacent to each other (E1 and E2; C4 and C5; Fig. 2). In both cases, the reaches were separated from each other by a minimum of 40 m of intermediate channel type.

To determine the onset and termination of the spawning season, we counted redds in the study area six times between 1 May and 5 June. We measured characteristics of redds and study stream reaches in Mulkey Creek immediately after the spawning season to ensure that our measurements reflected those encountered by spawning trout (end of spawning season: 5 June; habitat measurements: 6–12 June). Channel slope over each reach was measured with an engineer's level and stadia rod (Platts et al. 1983). All other channel and in-stream characteristics of each reach were measured along transects spaced 2.5 m apart and arranged perpendicular to stream flow. At each transect, we measured stream width, bank angle, and stream bank vegetation cover. Stream width (excluding islands), was measured to the nearest 5 cm with a meter tape. We measured the angle of both banks to the nearest 5° using a clinometer on a 1.5-m rod placed against the bank slope (Platts et al. 1983); smaller angles indicate more bank overhang. Bank vegetation cover was estimated visually on both banks inside a 0.1-m^2 area extending from the stream edge to 50 cm away from the stream and 10 cm upstream and downstream of the transect. We also noted whether a redd was present within 1.25 m of each transect.

We measured water depth (to the nearest 2 cm), water velocity, and substrate size at five equally spaced points along each transect. Water velocity was measured with an electromagnetic current meter to the nearest 1 cm/s at 60% of the water depth (each measurement represented a 10-s average). We visually estimated the average substrate size within a 10 cm × 10 cm area centered at each point. Visual estimates of average substrate size were highly correlated with estimates from cores (n = 20, $r^2 = 0.93$, $P < 0.0001$, $y = 0.84x + 0.40$; R. A. Knapp, *unpublished data* for Mulkey Creek).

To quantify the microhabitats used for spawning by golden trout, we measured characteristics of each redd in all ten Mulkey Creek study stream reaches. We measured redd characteristics immediately preceding the measurement of reach characteristics. We located redds by walking slowly upstream on one bank, and scanning the stream bottom for the characteristic pit and "tailspill" of redds (Bjornn and Reiser 1991). After marking each redd with a numbered tag, we measured water depth, water velocity, and substrate size at the upstream edge of the redd pit. Measurements taken at the upstream edge of the pit should most closely reflect the pre-redd characteristics of the site (Parsons and Hubert 1988, Grost et al. 1991, Thurow and King 1994). We also counted the number of redds constructed inside and outside the upper Ramshaw Meadow livestock exclosure, and used the same technique for finding redds as was used in Mulkey Creek.

Data handling and statistical analysis.—Comparisons between sample means were made using the Kruskal-Wallis nonparametric analysis of variance (ANO-

VA). We used nonparametric tests because Wilk-Shapiro tests and rankit plots showed that data were generally not normally distributed and could often not be normalized using standard transformations (Sokal and Rohlf 1981). In addition, sample variances were frequently significantly different and could not be equalized. When making comparisons directly related to our three predictions (see *Introduction*) we used one-tailed tests; two-tailed tests were used in all other cases. Statistical analyses were performed using Statistix V. 4.1 software; the level of statistical significance was set at $P \leq 0.05$ for all comparisons.

In comparisons of habitat differences between narrow and wide reaches, ''reach'' was the replicate ($n = 10$), and response variables were averaged for each reach. Only one value for stream slope was obtained for each reach, so slopes of narrow and wide reaches were not averaged prior to analysis. To compare the characteristics of sites used by females for redd construction vs. sites available to females, we analyzed differences between the substrate size, water depth, and water velocity measured at redds ($n = 131$) vs. at transect-based microhabitat measurement points ($n = 1560$).

Choice of spawning site by golden trout and many other salmonids is determined primarily by substrate size, water depth, and water velocity (Bjornn and Reiser 1991, Knapp and Vredenburg 1996). Therefore, we used the mean ± 2 SD of substrate size, water depth, and water velocity measured at redds to produce a suitability criterion to compare spawning habitat availability in narrow and wide reaches. This criterion accurately predicts the presence or absence of redds within 1.5-m^2 stream units, with a misclassification error rate of $<5\%$ ($N = 205$; R. A. Knapp, *unpublished data*). Other classification criteria, including mean ± 1 SD, mean ± 1.5 SD, mean ± 2.5 SD, and range, have higher misclassification rates (R. A. Knapp, *unpublished data*) and were therefore not considered for use in this study. Using the mean ± 2 SD criterion, a microhabitat measurement point was considered suitable spawning habitat if it had a substrate size of 10–22 mm, a water depth of 4–18 cm, and a water velocity of 15–64 cm/s. If measurements of substrate size, water depth, or water velocity fell outside of these ranges, the point was considered unsuitable for spawning. The availability of spawning habitat between narrow and wide reaches was compared using the percentage of microhabitat measurement points that were suitable for spawning.

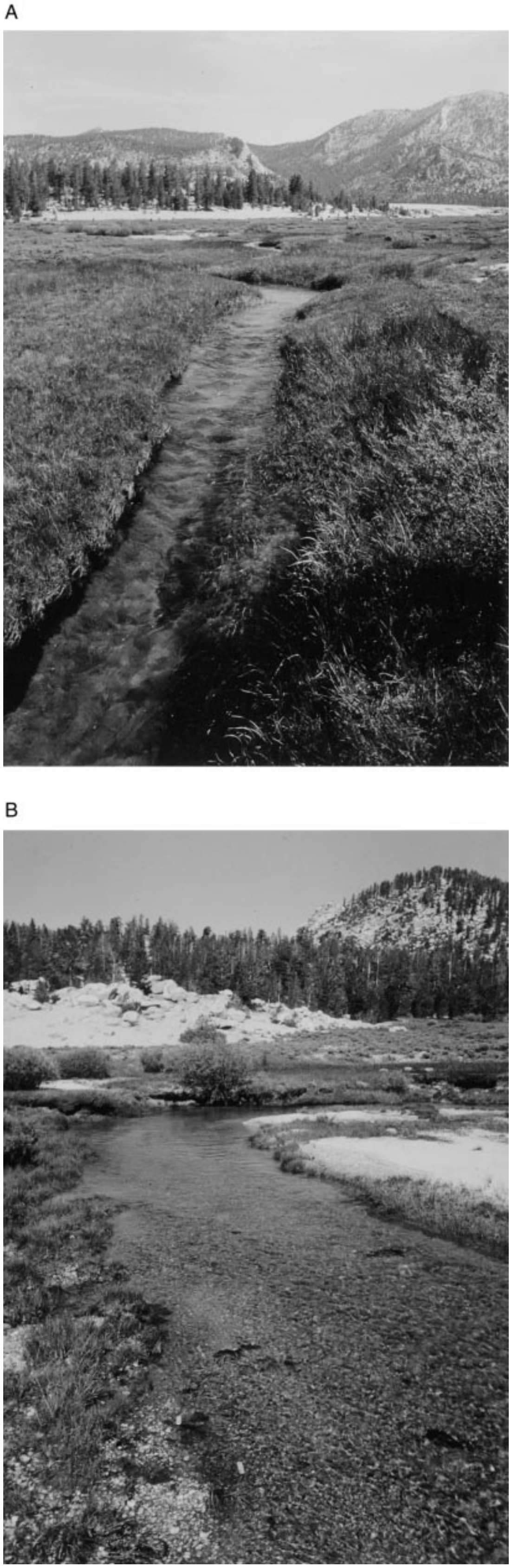

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FIG. 3. Photographs of (A) Reach E5 and (B) Reach C1 illustrating the differences in stream channel morphology between narrow and wide reaches on Mulkey Creek. Note the large amount of streamside vegetation that characterizes narrow reaches compared with the relatively sparse vegetation of wide reaches.

TABLE 1. Characteristics [mean (SE)] of wide and narrow stream reaches on Mulkey Creek.

Variable	Reach type: Wide	Reach type: Narrow	P†
Stream depth (cm)	18 (2)	30 (1)	0.009
Stream width (cm)	363 (18)	200 (6)	0.009
Width/depth ratio	22 (3)	7 (1)	0.009
Water velocity (cm/s)	40 (1)	37 (1)	>0.1
Substrate size (mm)	7.8 (0.6)	4.7 (0.7)	0.03
Vegetation cover (%)	40 (7)	87 (2)	0.009
Bank angle (degrees)	158 (3)	103 (5)	0.009
Slope (degrees)	0.18 (0.04)	0.17 (0.02)	>0.6

† All comparisons between the five wide reaches and five narrow reaches were made using the Kruskal-Wallis nonparametric one-way analysis of variance.

To determine whether any channel morphological features were associated with the presence or absence of spawning habitat, we compared bank vegetation cover, stream width, and bank angle measured at transects that contained at least one microhabitat measurement point with suitable spawning habitat vs. transects that lacked suitable spawning habitat. We made comparisons based on transects from narrow and wide reaches combined (number of transects with spawning habitat = 71, number of transects without spawning habitat = 241) and wide reaches only (number of transects with spawning habitat = 66, number of transects without spawning habitat = 92).

To compare redd abundance between narrow and wide reaches, we calculated redd densities for each stream reach on the basis of stream length (number/m of stream) and stream surface area (number/m^2). To determine whether any channel morphological features were associated with the presence or absence of redds, we compared bank vegetation cover, stream width, and bank angle measured at transects with and without redds. Comparisons were made between transects with and without redds for narrow and wide reaches combined (number of transects with redds = 51, number of transects without redds = 261), and for wide reaches only (number of transects with redds = 51, number of transects without redds = 107).

Production and recruitment of age-0 trout

Data collection.—To examine the relationship between redd density and the production of age-0 trout, we compared the number of age-0 fish in each Mulkey Creek study reach in August with the number of redds counted in the same study reaches in June. We conducted counts of age-0 fish ($\leq$60 mm; Knapp and Matthews 1996) in all ten Mulkey Creek study reaches on 3 August, after emergence of age-0 trout from redds was complete. Age-0 fish were counted by two observers crawling upstream along opposite banks. This visual census technique is commonly used to count age-0 salmonids (Moore and Gregory 1988, Bozek and Rahel 1991*a*), and results from visual counts are correlated with those obtained from more intensive electrofishing (Bozek and Rahel 1991*b*).

To determine whether the density of a particular cohort was correlated between years for age-0, age-1, and age-2 fish and to estimate the shape of stock-recruitment curves, we electrofished three 125-m stream sections in Mulkey Creek annually from 1993–1996 (Fig. 2). We surveyed fish populations in September of each year using an electrofisher and standard three-pass depletion techniques (Van Deventer and Platts 1983). During electrofishing, each 125-m section was isolated using block nets. The length of time that the electrofisher was running on each pass was similar within a section to ensure a similar electrofishing effort. Fork length of each fish was measured to the nearest 1 mm, and fish were released into the section from which they were captured after the final pass was completed. The number of age-0, age-1, and age-2 fish in each of the three electrofishing sections was estimated from the rate of depletion during passes 1–3 using maximum-likelihood estimation techniques (Microfish V. 3.0; Van Deventer and Platts 1985). Capture probabilities were similar among age classes.

Age-0, age-1, and age-2 fish were identified by their distinct size classes and age information based on otoliths (Knapp and Dudley 1990; R. A. Knapp and K. R. Matthews, *unpublished data* for the Mulkey Creek electrofishing sites) (1993: age-0 = 20–45 mm, age-1 = 55–89 mm, age-2 = 90–110 mm; 1994: age-0 = 20–50 mm, age-1 = 55–79 mm, age-2 = 80–100 mm; 1995: age-0 = 20–50 mm, age-1 = 60–89 mm, age-2 = 90–110 mm; 1996: age-0 = 25–59 mm, age-1 = 60–89 mm, age-2: 90–110 mm). We were not able to extend these analyses beyond age-2 trout, because extensive overlap in the sizes of age-3 and older fish made delineation of age classes impossible.

Data handling and statistical analysis.—We calculated densities of age-0, age-1, and age-2 trout on the basis of stream length (number/m of stream) and stream area (number/m^2). We compared the density of age-0 trout between the five wide reaches and five narrow reaches using the Kruskal-Wallis nonparametric ANOVA since the data could not be normalized. We used linear and nonlinear stock-recruitment models to investigate the relationship between (1) redd density and age-0 trout density (n = 10), (2) the density of age-0

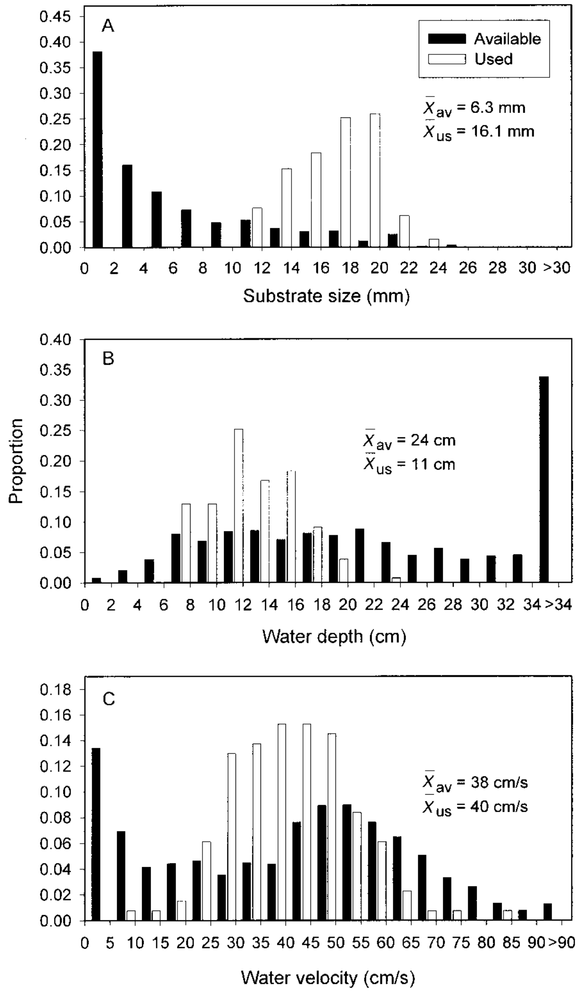

FIG. 4. Comparison of (A) substrate sizes, (B) water depths, and (C) water velocities available to and used by spawning female golden trout in Mulkey Creek. Mean parameter values available ($\bar{X}_{av}$) and used ($\bar{X}_{us}$) are given. Mean substrate size and water depth used by females was significantly different from the mean substrate size and water depth available. There was no difference between water velocities used by females and those available to them.

trout in year *t* and the density of age-1 trout in year *t* + 1 (n = 9), and (3) the density of age-1 trout in year *t* and the density of age-2 trout in year *t* + 1 (n = 9). Linear models were fit to the data using simple linear regression, and nonlinear Beverton-Holt and Ricker models (Ricker 1954, Beverton and Holt 1967, Elliot 1985*b*) were fit using the SigmaPlot V. 4.0 curve fitter. The general form of these equations is given in Table 2. The level of statistical significance was set at $P \leq 0.05$ for all comparisons. Because the two measures of trout density produced very similar stock-recruitment curves, we only present the curves based on the number of trout per meter.

RESULTS

Narrow and wide reaches in Mulkey Meadow were significantly different for all measured parameters except slope and water velocity (Table 1). ''Wide'' reaches were significantly broader and shallower than ''narrow'' reaches, and had larger substrates, less bank vegetation cover, and greater bank angles (i.e., banks were more unstable). For narrow and wide reaches combined, bank vegetation cover was negatively correlated with stream width ($n = 312$; $r = -0.54$; $P < 0.0001$) and bank angle ($n = 312$; $r = -0.66$; $P < 0.0001$).

In Mulkey Meadow, golden trout spawning began on 28 May and only a few females were still excavating redds on 5 June. No spawning was seen after 8 June. A total of 131 redds were constructed in the study area. In selecting spawning locations, females used substrates that were significantly larger than the average available substrates ($P < 0.0001$; Fig. 4A) and water depths that were significantly shallower than the average available water depth ($P < 0.0001$; Fig. 4B). Water velocities measured at redds were not significantly different from the average water velocities available to spawning females ($P > 0.8$; Fig. 4C).

Wide reaches contained significantly more spawning habitat than narrow reaches ($P < 0.005$; Fig. 5). For wide and narrow reaches combined, transects containing spawning habitat had lower bank vegetation cover ($P < 0.0001$), larger stream widths ($P < 0.0001$), and greater bank angles ($P < 0.0001$) than transects not containing spawning habitat. The relationships between (1) bank vegetation cover and presence or absence of spawning habitat and (2) stream width and presence or absence of spawning habitat remained highly significant when only wide reaches were included in the analysis (bank vegetation cover: $P < 0.003$; stream width: $P < 0.0003$); bank angle, however, was not significantly different between transects with and without spawning habitat when only wide reaches were included (bank angle: $P > 0.4$).

Redd density in the Mulkey Creek study reaches, measured either on the basis of stream length or stream area,

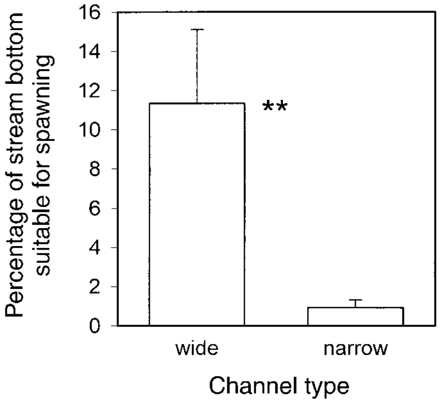

FIG. 5. Comparison of the percentage of the stream bottom that was suitable for spawning by golden trout for wide vs. narrow reaches in Mulkey Creek. Bars represent means, and error bars show 1 SE. Wide reaches contained significantly more spawning habitat than did narrow reaches (**: $P < 0.005$).

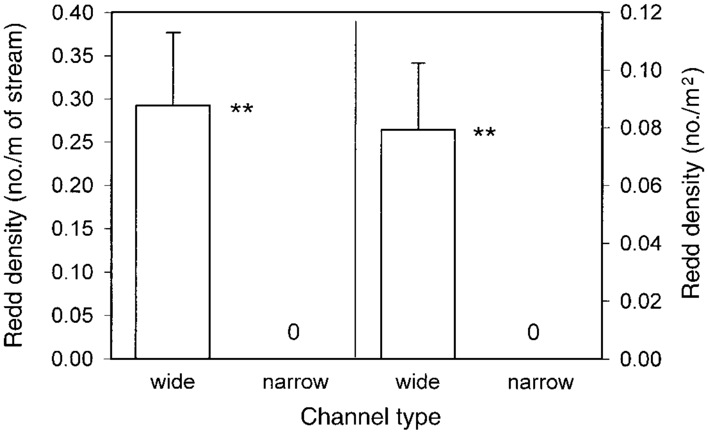

FIG. 6. Comparison of the density of golden trout redds (number/m of stream, number/m^2) for wide vs. narrow reaches in Mulkey Creek. Bars represent means and error bars show 1 SE. Zeros indicate that no redds were found. Wide reaches contained significantly higher redd densities than did narrow reaches (**: $P < 0.005$).

was also significantly greater in wide reaches than narrow reaches ($P < 0.003$; Fig. 6). Similarly, in Ramshaw Meadow, females constructed 52 redds in the 125-m reach below the livestock exclosure (0.42 redds/m) and no redds in the 125-m reach inside the exclosure. For the Mulkey Creek wide and narrow reaches combined, transects containing redds had lower bank vegetation cover ($P < 0.0001$; Fig. 7A), larger stream widths ($P < 0.0001$; Fig. 7B), and greater bank angles ($P < 0.0001$; Fig. 7C) than transects not containing redds. The relationships between (1) bank vegetation cover and presence or absence of redds and (2) stream width and presence or absence of redds remained highly significant when only wide reaches were included in the analysis (bank vegetation cover: $P < 0.002$; stream width: $P < 0.0001$); bank angle, however, was not significantly different between transects with and without redds when only wide reaches were included (bank angle: $P > 0.3$).

Wide reaches in Mulkey Creek contained a much higher density of age-0 trout than narrow reaches, and this was true regardless of whether density was calculated on the basis of stream length ($P < 0.005$; Fig. 8) or stream surface area ($P < 0.005$; Fig. 8). In addition, redd density was positively correlated with age-0 trout density in the 10 study reaches (Fig. 9). The linear, Beverton-Holt, and Ricker models all provided significant and similar fits to the data, accounting for >80% of the variation in age-0 trout density (Table 2A).

Based on the 1993–1996 electrofishing data, the density of age-0 trout in one year was a significant predictor of the density of age-1 trout the following year (Fig. 10A). The linear, Beverton-Holt, and Ricker models all provided significant fits to the data, but the Ricker model explained the greatest amount variation in the density of age-1 trout (Table 2B). This model produced an asymptotic relationship between these two age classes. All three functions were influenced by a single data point, however (age-0 trout density = 1.48 fish/m), and the exact shape of the curves is therefore uncertain. Similarly, the density of age-1 trout in one year was a significant predictor of the density of age-2 trout the following year (Fig. 10B), although only the Ricker model provided an acceptable fit to the data (Table 2C). This model suggested an asymptotic or weakly dome-shaped relationship between these two age classes, but this nonlinearity was due entirely to a single data point (age-1 trout density = 1.37 fish/m).

DISCUSSION

Our results provide strong support for the prediction that channel morphology controls the availability of golden trout spawning habitat. Wide stream reaches had large amounts of spawning habitat and high redd densities compared to narrow reaches. These differences in spawning habitat resulted in wide reaches having a higher density of age-0 trout than narrow reaches.

The prediction that the density of age-0 fish would be an increasing function of redd density was also supported. The similar fits to the data provided by linear, Beverton-Holt, and Ricker functions as well as the positive slopes of these curves over the entire range of redd densities suggests that mortality of age-0 golden trout between early June (end of the spawning season) and early August was either density independent (linear function) or only weakly density dependent (asymptotic function). Positive linear correlations between age-0 trout density and either spawning habitat availability or redd density have been reported for other stream salmonids (Beard and Carline 1991, Bozek and Rahel 1991*a*, Delacoste et al. 1993, Magee et al. 1996). These results are in marked contrast, however, to the paradigm that salmonid populations are regulated by strong density-dependent mortality of age-0 trout that produces a dome-shaped stock-recruitment curve (Le Cren 1965, Allen 1969, Egglishaw and Shackley 1977, Elliot 1984*a*, Elliot 1985*a*, Everest et al. 1987, Gardiner and Shackley 1991, Crisp 1993). Because a dome-shaped stock-recruitment function will have very different implications for recruitment dynamics and adult population size than will linear or asymptotic stock-

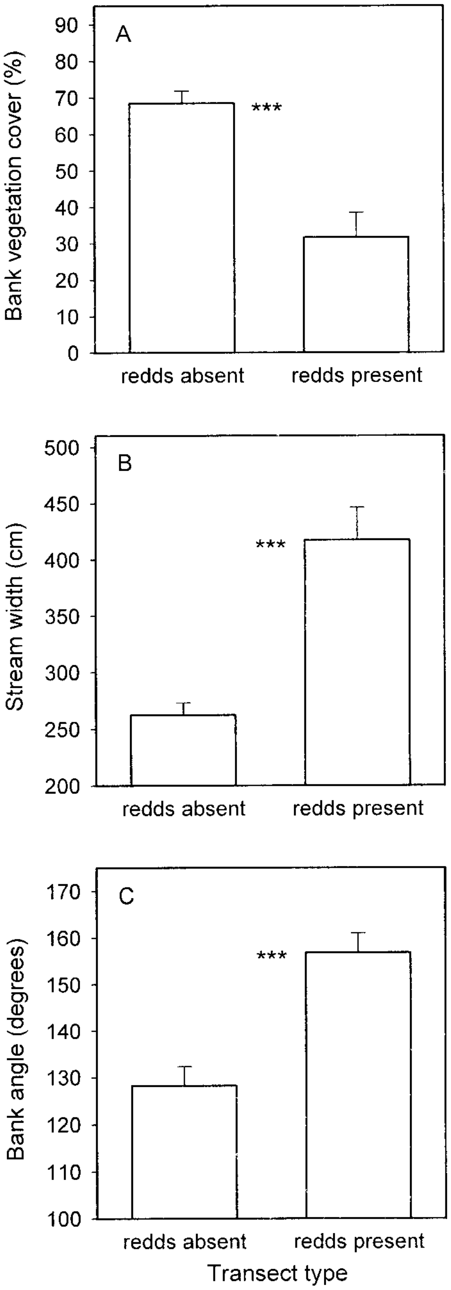

FIG. 7. Comparison of (A) bank vegetation cover, (B) stream width, and (C) bank angle from transects without redds vs. transects with redds in Mulkey Creek. Bars represent means, and error bars show 1 SE. A transect was considered to contain a redd if at least one redd was found within 1.25 m upstream or downstream of the transect. Bank vegetation cover, stream width, and bank angle were all significantly different between transect types (***: $P < 0.0001$).

recruitment functions, it is important to understand the processes responsible for these different curves.

The stock-recruitment literature for salmonids suggests that while anadromous populations typically show a dome-shaped stock-recruitment curve for age-0 fish (e.g., Allen 1969, Elliot 1984*a*, Everest et al. 1987), stream-resident salmonids typically show a linear stock-recruitment curve (Beard and Carline 1991, Bozek and Rahel 1991*a*, Delacoste et al. 1993, Elliot 1987, Magee et al. 1996, this study). We suggest, as did Elliot (1987, 1994), that these differences are the result of the much higher densities of age-0 fish found in anadromous populations (often exceeding 5/m^2: e.g., Egglishaw and Shackley 1977, Elliot 1984*b*) than in stream-resident populations (rarely exceeding 1/m^2: e.g., Newman and Waters 1989, Bozek and Rahel 1991*a*, Beard and Carline 1991, this study). Our linear or near-linear stock-recruitment relationship for age-0 golden trout and the similar relationships developed by others for stream-resident salmonids (Elliot 1987, Beard and Carline 1991, Bozek and Rahel 1991*a*, Delacoste et al. 1993) suggest that the density of age-0 fish in stream-resident populations may only rarely be high enough to cause density-dependent mortality.

The positive correlation we found between the density of age-0 golden trout and redd density may have little consequence for the adult population if age-1 and older trout experience density-dependent mortality strong enough to produce a dome-shaped stock-recruitment curve. Under this scenario, increases in the production of age-0 trout would only increase recruitment into older age classes up to a certain point, after which further increases in the production of age-0 trout would produce smaller subsequent age classes. In contrast, if the stock-recruitment curve for age-1 and older trout is asymptotic (as described by the Beverton-Holt model) or linear, increases in the production of age-0 trout would always produce increased recruitment.

Studies of age-1 and older salmonids have repeatedly shown that the number of fish in a particular cohort in one year is positively and linearly correlated with the number of fish in the same cohort in the following year (i.e., mortality of age-1 and older fish is density independent; Mortensen 1977, Mills 1989, Elliot 1994); we predicted that this would also be true for golden trout. In our study, the relationship between the density of age-0 trout in one year and the density of age-1 trout the following year was best described by an asymptotic curve. The relationship between the density of age-1 trout in one year and the density of age-2 trout the following year was best described by an asymptotic curve or a slightly dome-shaped curve. The shape of both of these curves suggests that mortality in age-1 and age-2 golden trout is at least weakly density dependent. Unfortunately, our sample sizes were insufficient to characterize the exact shape of these functions for age-1 and age-2 golden trout, and both functions were strongly influenced by single data points. Additional electrofishing surveys of the golden trout study population will be necessary to determine whether these points are part of the stock-recruitment curve or are ‘‘outliers.’’

More important than the actual shape of these curves, however, is the fact that over most of the range of

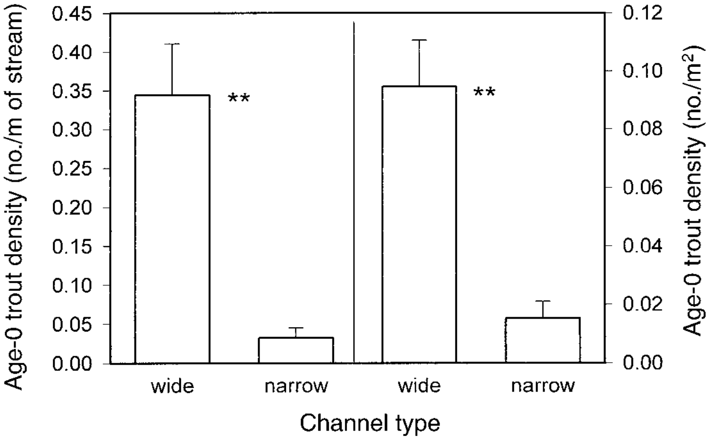

FIG. 8. Comparison of the density of age-0 golden trout (number/m of stream, number/m^2) for wide vs. narrow reaches in Mulkey Creek. Bars represent means, and error bars show 1 SE. Wide reaches contained significantly higher age-0 trout densities than did narrow reaches (**: $P < 0.005$).

observed fish densities, all significant stock-recruitment models had positive slopes. This suggests that regardless of whether mortality is density independent or density dependent, over most fish densities the size of an age-1 or age-2 cohort in one year will be positively influenced by the size of that cohort during the previous year. Therefore, the relative size of a particular cohort will generally be maintained between the age-0 stage and the adult population (~50% of age-2 golden trout are sexually mature: Knapp and Vredenburg 1996; R. A. Knapp, *unpublished data*), and increases in the production of age-0 golden trout will eventually lead to increases in the density of the adult population.

Our findings support the hypothesis that the availability of spawning habitat limits the density of golden trout in our study population. Based on the large amount of spawning habitat available in the wide stream reaches used in the present study (>10% of the stream bottom) and the predominance of wide reaches in Mulkey Creek (R. A. Knapp, *personal observation*), we would predict that golden trout densities in Mulkey Creek should be very high. In fact, golden trout populations in Mulkey Creek are among the densest ever recorded for stream-resident salmonids in the western U.S., and are an order of magnitude denser than the average for salmonid populations in this region (Platts and McHenry 1988, Knapp and Matthews 1996).

Although our golden trout study population was limited by spawning habitat and is characterized by high densities of age-0 fish, Magee et al. (1996) used high densities of age-0 cutthroat trout (*O. clarki*) as evidence that spawning habitat was not limiting their populations. However, a high density of age-0 fish alone is not sufficient evidence to conclude that spawning habitat is not limiting. In order to demonstrate that spawning habitat is not limiting, it would need to be demonstrated that the production of even more age-0 fish would not result in a further increase in population size (Caley et al. 1996). The results of our study clearly show that the density of age-0 trout is an increasing function of redd density, and that the density of a particular cohort is generally positively correlated between years for age-0, age-1, and age-2 trout. Therefore, an increase in the availability of spawning habitat would likely result in increase in the size of the golden trout population.

Given the importance of spawning habitat in limiting the density of golden trout, an understanding of the factors influencing spawning habitat availability would allow prediction of how habitat changes might influence recruitment dynamics. Our results suggest that vegetation plays a critical role in controlling the availability of spawning habitat by its influence on channel morphology. This is supported by the significantly lower bank vegetation cover for transects containing spawning habitat than for transects without spawning habitat, and by the strong negative correlations between bank vegetation cover (primarily sedges, *Carex* sp.) and both stream width and bank angle. Our assertion

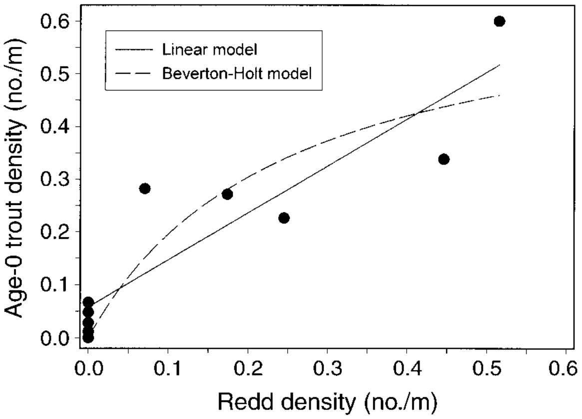

FIG. 9. Relationship between the density of age-0 golden trout (number/m of stream) and redd density (number/m of stream) in Mulkey Creek. The five data points near the origin represent results from the narrow stream reaches. Redd density was a significant predictor of age-0 trout density, and linear, Beverton-Holt, and Ricker models all provided similar fits to the data (Table 2A). Only linear and Beverton-Holt curves are shown, since Beverton-Holt and Ricker curves were nearly identical.

TABLE 2. Regression equations, R^2 values, and P values for the relationship between (A) the number of redds constructed in a stream reach and the number of age-0 trout produced, (B) the number of age-0 trout in year t and the number of age-1 trout in year $t + 1$, and (C) the number of age-1 trout in year t and the number of age-2 trout in year $t + 1$.

Model	Equation	R^2	P
A) Redds vs. age-0 ($N = 10$)			
Linear	$y = 0.89x + 0.06$	0.82	0.0003
Beverton-Holt	$y = 2.75x/(1 + 4.04x)$	0.84	0.0002
Ricker	$y = 1.66x^{-1.09x}$	0.83	0.0002
B) Age-0 vs. age-1 ($N = 9$)			
Linear	$y = 0.53x + 0.36$	0.54	0.023
Beverton-Holt	$y = 4.87x/(1 + 4.45x)$	0.47	0.040
Ricker	$y = 1.98x^{-0.70x}$	0.58	0.016
C) Age-1 vs. age 2 ($N = 9$)			
Linear	$y = 0.32x + 0.51$	0.24	0.184
Beverton-Holt	$y = 4.02x/(1 + 3.76x)$	0.38	0.076
Ricker	$y = 2.44x^{-1.05x}$	0.50	0.034

that bank vegetation influences channel morphology is further supported by the stream classification system of Rosgen (1994), in which streams with substrates dominated by sand and gravel and lacking erosion resistant cobbles and boulders (such as streams in the South Fork Kern River watershed; Knapp and Matthews 1996) have their channel morphologies controlled largely by vegetation. The critical role of riparian sedges in influencing channel morphology is also suggested by research showing that these plant species have exceptionally high root densities (Manning et al. 1989), positive effects on the unconfined compressive strength of soil (Kleinfelder et al. 1992), and strong erosion reducing capabilities (Dunaway et al. 1994).

The abundance of streamside vegetation can be altered by land management practices such as livestock grazing. Previous research on the effects of livestock grazing on streams in the Golden Trout Wilderness showed that grazed streams have less riparian vegetation than streams protected from grazing, and as a result, grazed streams are wider and shallower than ungrazed streams (Sarr 1995, Knapp and Matthews 1996). Similar findings have been reported in numerous other studies (e.g., Kauffman et al. 1983, Kauffman and Krueger 1984, Platts 1991, Armour et al. 1994, Trimble and Mendel 1995). Therefore, by reducing streamside vegetation and increasing stream widths, livestock grazing has likely increased the availability of golden trout spawning habitat, and this in turn may have increased age-0 trout production, recruitment, and adult density. The possibility that livestock grazing has affected golden trout population structure by changing stream channel morphology is supported by our results showing that the density of golden trout redds was much higher outside the Upper Ramshaw Meadow livestock exclosure than inside the exclosure. These two stream reaches were apparently quite similar at the time of exclosure construction (Knapp and Matthews 1996; T. Dudley and R. Knapp, *unpublished data*), but the stream reach inside the exclosure is now substantially deeper and narrower than the stream reach outside the exclosure (Knapp and Matthews 1996). Similar effects of channel alteration on trout production were also reported in a study by Chapman and Knudsen (1980); their results showed that the biomass of age-0 trout was often significantly higher in streams modified by livestock grazing and channelization than in relatively unaltered control streams.

One paradoxical result of the present study is the absence of redds from the ‘‘narrow’’ study reaches. If livestock grazing has converted meadow streams in the Golden Trout Wilderness from narrow and deep to shallow and wide (as suggested by Odion et al. 1988, Knapp and Matthews 1996), where did golden trout spawn under historical (pre-grazing) conditions? Although it is possible that spawning habitat was absent from meadow reaches, we think it more likely that the lack of redds from our narrow stream reaches was a consequence of the spatial scale of our study. Our study reaches were relatively short and were selected for their uniformly narrow or wide morphology to allow comparisons between these distinct channel types. If we had used longer reaches, narrow reaches would have included short stretches of wide channel containing spawning habitat. Under historical conditions, we suspect that meadow streams in the South Fork Kern River watershed were dominated by narrow reaches, but that localized areas of instability (e.g., caused by natural bank failure) would have produced some wide sections with spawning habitat.

Although livestock grazing has likely increased golden trout spawning habitat and recruitment, these results should not be construed to mean that the effects of livestock grazing are entirely beneficial to golden trout populations. For example, golden trout in Mulkey Meadow grow very slowly and reach a maximum size of only 200 mm (Knapp and Dudley 1990, Knapp and Vredenburg 1996; R. A. Knapp, *unpublished data*). Because growth rates in salmonids are typically density

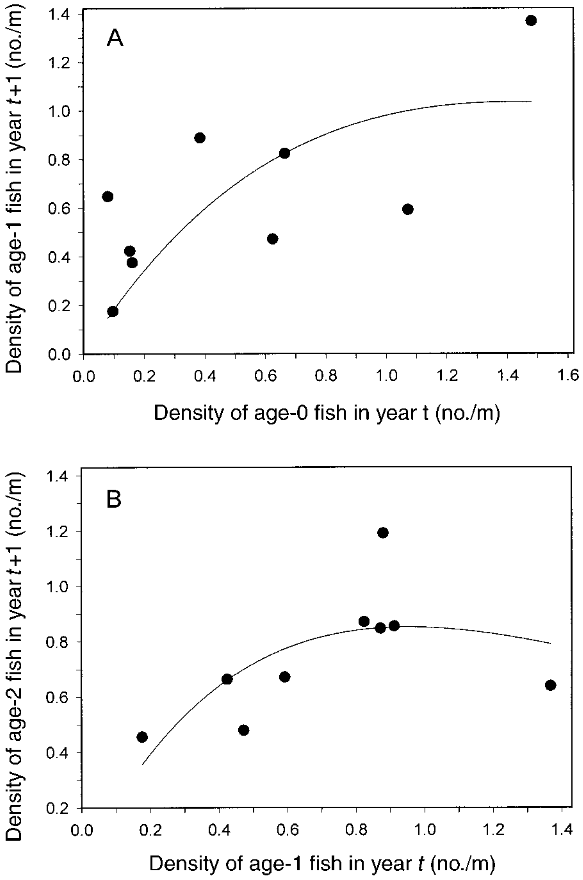

FIG. 10. (A) Relationship between the density of age-0 golden trout (number/m) in one year and the density of age-1 golden trout the following year (number/m) in Mulkey Creek. Age-0 trout density is a significant predictor of age-1 trout density and was best described by the Ricker model (Table 2B). (B) Relationship between the density of age-1 golden trout (number/m) in one year and the density of age-2 golden trout the following year (number/m) in Mulkey Creek. Age-1 trout density is a significant predictor of age-2 trout density and was best described by the Ricker model (Table 2C). Comparisons of cohort size were made for 1993 vs. 1994, 1994 vs. 1995, and 1995 vs. 1996 based on data from three electrofishing sections (n = [3 yr × 3 sections] = 9). Curves for both relationships were fit using the SigmaPlot V. 4.0 curve fitter.

dependent (Egglishaw and Shackley 1977, Mortensen 1977, Crisp 1993, Bohlin et al. 1994), the slow growth of golden trout may be a consequence of high fish densities (Knapp and Dudley 1990). This is supported by data collected after the elimination of all golden trout from the upper South Fork Kern River in 1977 and their subsequent reintroduction in 1982. In 1984, the California Department of Fish and Game estimated that there were ~75 golden trout/km of stream (excluding age-0 fish) in Templeton Meadow (2 km downstream of Ramshaw Meadow). Fish >250 mm made up ~13% of the population. In 1995, we estimated that there were 6400 golden trout/km of stream (excluding age-0 fish) in Templeton Meadow, and despite capturing 1185 fish, we did not capture any fish >215 mm (R. A. Knapp and K. R. Matthews, *unpublished data*). Fish >200 mm made up <0.2% of the population. Therefore, although livestock grazing has likely increased trout densities, our data on the density-dependent nature of growth rates suggests that growth rates have been reduced as a result.

In conclusion, our results suggest that golden trout (and perhaps other stream-resident salmonids) do not fit the paradigm that salmonid populations are regulated by strong density-dependent mortality at the age-0 stage. Our golden trout study population was instead limited by spawning habitat, a result that has important implications for land management practices that might affect spawning habitat availability. In light of these findings, we suggest that it is only by gaining an understanding of how processes operate that we will be able to reliably predict the effects of habitat alteration on populations.

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