Are trout populations affected by reach-scale stream slope?

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Abstract: Reach-scale stream slope and the structure of associated physical habitats are thought to affect trout populations, yet previous studies confound the effect of stream slope with other factors that influence trout populations. We isolated the effect of stream slope on trout populations by sampling reaches immediately upstream and downstream of 23 marked changes in stream slope on 18 streams across Wyoming and Idaho. No effect of stream slope on areal trout density was observed, but when trout density was expressed volumetrically to control for differences in channel cross sections among reaches in different slope classes, the highest densities of trout occurred in medium-slope reaches, intermediate densities occurred in high-slope reaches, and the lowest densities occurred in low-slope reaches. The relative abundance of large trout was reciprocal to the pattern in volumetric trout density. Trout biomass and species composition were not affected by stream slope. Our results suggest that an assumption made by many fish-habitat models, that populations are affected by the structure of physical habitats, is at times untenable for trout populations in Rocky Mountain streams and is contingent upon the spatial scale of investigation and the population metric(s) used to describe populations.

Résumé : On pense que la pente des cours d'eau à l'échelle des tronçons et la structure des habitats physiques associés influent sur les populations de truites, mais des études antérieures ont confondu l'effet de la pente avec d'autres facteurs qui influent sur ces populations. Nous avons isolé l'effet de la pente sur les populations de truites en prélevant des échantillons immédiatement en amont et en aval de 23 changements marqués de la pente dans 18 cours d'eau du Wyoming et de l'Idaho. On n'a observé aucun effet de la pente sur la densité des truites par unité de superficie, mais, quand la densité des truites était exprimée par unité de volume pour tenir compte des différences entre les sections transversales des chenaux des tronçons de différentes classes de pente, les plus fortes densités de truites se trouvaient dans les tronçons de pente moyenne, les densités intermédiaires dans les tronçons à forte pente et les plus faibles densités dans les tronçons à faible pente. L'abondance relative des truites de grande taille suivait le profil des densités volumétriques de truites. La pente n'avait pas d'effet sur la biomasse de truites et la composition par espèces. Nos résultats laissent penser que l'hypothèse introduite dans de nombreux modèles d'habitat du poisson suivant laquelle les populations sont affectées par la structure des habitats physiques est dans certains cas non valides pour les populations de truites des cours d'eau des Rocheuses, et qu'on doit prendre en considération dans l'application de cette hypothèse les paramètres utilisés pour décrire les populations.

[Traduit par la Rédaction]

Introduction

A stream reach is a 10 to several hundred metre length of stream that exhibits consistent slope (Frissell et al. 1986). Reach-scale stream slope and the energy that it helps to generate exert a dominant influence on the structure of physical habitat in streams (Hubert and Kozel 1993), and reaches of specific slopes contain characteristic assortments of smaller-scale habitats (i.e., channel units, subunits, substrate particles; Kershner et al. 1992). If fish populations are influenced by the structure of physical habitat, as many models assume (Fausch et al. 1988), change in reach-scale stream slope should elicit change in fish populations.

Researchers working with trout have collected data that seem to support the preceding logic, and most work has focused on four population metrics: biomass, species composition, density, and length structure. Several investigators have described a negative relationship between trout biomass and stream slope (Fig. 1*a*) (MacPhee 1966; Chisholm and Hubert 1986; Kozel et al. 1989), with the explanation often being a habitat-based hypothesis that asserts that optimal living conditions are associated with the undercut banks, overhanging vegetation, and the amount of pool habitat found in reaches with low stream slopes. Alternatively, Wilzbach and Hall (1985) have formulated a food-based hypothesis that suggests that macroinvertebrates preferred by trout will be more abundant and easier to obtain due to higher light levels in low-slope reaches that often occur with open canopy riparian zones dominated by willows (*Salix* spp.), alders (*Alnus* spp.), or sedges (*Carex* spp.) It has also been common for researchers to document changes in species composition as a function of stream slope (Moore et al. 1985; Fausch 1989; Bozek and Hubert 1991). Proposed mecha-

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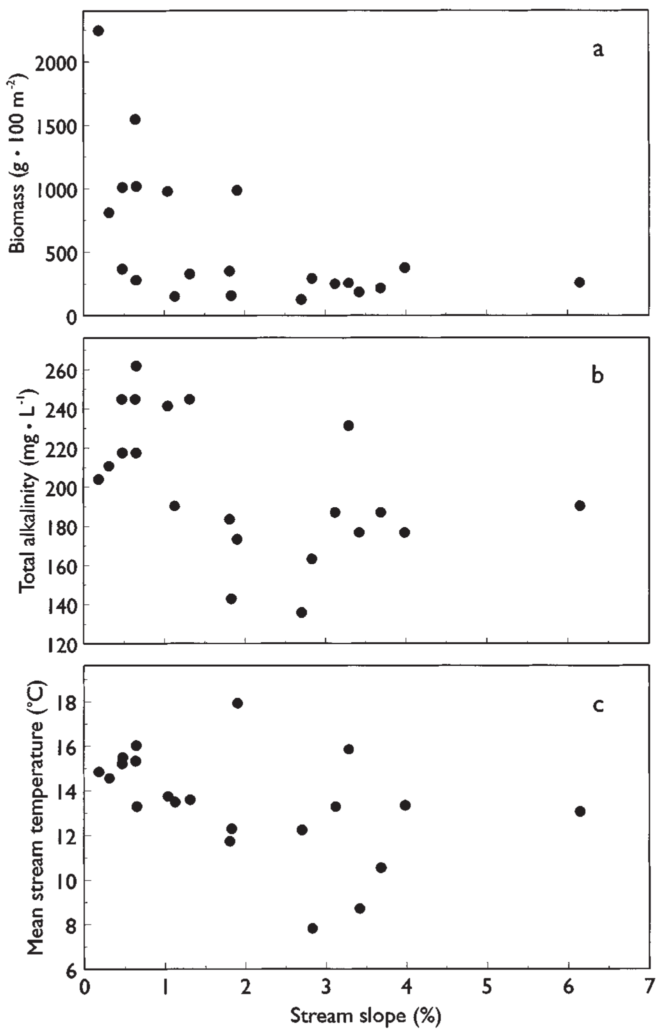
Fig. 1. Correlations among stream habitat variables and trout biomass. (*a*) Inverse relationship often reported between trout biomass and stream slope and concurrent relationships between stream slope and either (*b*) total alkalinity or (*c*) temperature. Data are from our own unpublished surveys and were collected using a longitudinal sampling design on five streams draining two physiographically similar mountain ranges in southeastern Idaho.



nisms are either that one trout species is competitively excluding another from optimal habitats or that individual trout species prefer the types of physical habitats associated with particular stream slopes.

The relationship between reach-scale stream slope and trout density has not been clearly defined. Hermansen and Krog (1984) described a positive relationship between stream slope and the density of hatchery trout longer than 15 cm but gave no explanation for their findings. Conversely, Kennedy and Strange (1982) and Moore and Gregory (1989) documented negative relationships between stream slope and densities of age-1 and older (age-1+) trout. These researchers concluded that changes in trout densities resulted from the preference of age-1+ trout for the deeper water habitats that occurred at low stream slopes. Less work has described the influence of stream slope on population length structure, but a study by Larscheid and Hubert (1992) indicated that larger trout composed a greater proportion of populations at lower stream slopes. Proposed mechanisms included competitive exclusion of smaller trout by larger trout and a habitat-based hypothesis suggesting that conditions for growth and survival of larger fish were better in reaches with low stream slopes.

Despite the existing body of evidence, we contend that a causal link has yet to be established between reach-scale stream slope and trout populations. All studies addressing this issue have used sampling designs wherein data were collected either in a longitudinal upstream progression or from stream reaches distributed across space and time. Both sampling designs make it impossible to separate the effect of stream slope from other factors that affect trout populations. Causal inference from longitudinal sampling designs is negated by intercorrelations among many habitat variables that result from the concavity of stream slope profiles and environmental gradients that occur over the length of streams (Figs. 1*b* and 1*c*). Distributed sampling designs are limited by similar problems due to the universal concavity of stream slope profiles and similarities among streams draining a physiographic region. However, inference from distributed sampling designs is further weakened by inclusion of interstream differences and temporal variation in trout populations if samples are collected over extended periods of time.

For the above reasons, we believe that much of the thought regarding how reach-scale stream slope and associated physical habitats affect trout populations has been poorly substantiated. Our goal was to determine whether stream slope had a causal effect on any of several trout population metrics by conducting a study that isolated the effect of stream slope. To accomplish this goal, we eliminated the effects of confounding variables by sampling trout populations immediately upstream and downstream of marked, reach-scale changes in stream slope and describe the responses that we observed in trout biomass, density, species composition, and length structure. We also linked the observed changes in trout populations to changes in physical habitat characteristics and discuss how patterns manifest in trout populations at the reach scale may be affected by mechanisms operating at other spatial scales.

Materials and methods

Sample sites

Potential sample sites were initially identified as marked changes in stream slope on 1:24 000 scale U.S. Geological Survey topographic maps. Sites were then located in the field to ensure that a large change in stream slope existed (as inferred from the amount of supercritical flow, channel patterns, array of channel units, and substrate types) and that reaches at least 100 m long with consistent slope occurred both upstream and downstream of the marked change in stream slope. Sites with beaver (*Castor canadensis*) dam complexes, severe habitat degradation, angler harvest, or recent stocking were avoided. Forty-six reaches at 23 sites on 18 streams met these selection criteria and were sampled on U.S. Forest Service land. Stream slopes of the two reaches at each site were measured with an Abney level following procedures described in Isaak et al. (1999) and differed on average by 2.4%. Steeper-sloped reaches were located upstream from lower-sloped reaches 70% of the time. Reaches averaged 183 m in length and

Table 1. Summary of study reach attributes by stream slope class.

Stream slope class	Reaches	Stream slope range (%)	Wetted width range (m)	Channel unit composition (%)[a]	Substrate composition (%)[b]	Channel pattern	Riparian vegetation
Low	17	0.2–1.8	1.9–7.0	28:5:0:41:25:0:0:1	1:2:39:49:4:5	Sinuous	Willows and sedges
Medium	18	1.8–4.3	1.6–7.2	19:34:2:32:6:3:3:1	5:8:61:22:2:2	Straight	Mixed conifers
High	11	4.0–7.2	1.7–7.0	16:34:14:16:1:8:6:5	15:12:50:20:2:1	Straight	Mixed conifers

[a]Channel unit types are ordered as follows: riffle, rapid, cascade, run, lateral scour pool, trench pool, plunge pool, dam pool.
[b]Substrate types are ordered as follows: large boulder, small boulder, cobble, gravel, large fines, small fines.

were of three general types corresponding to Rosgen (1994), A, B, and C channels, that, for clarity, we hereafter term high slope, medium slope, and low slope, respectively. Additional attributes of the study reaches are given in Table 1.

The majority of sites (17 of 23) were sampled during late-summer baseflow conditions in 1996 and 1997 on streams draining the Caribou and Webster ranges in southeastern Idaho and streams draining the Salt River Range in western Wyoming. Allopatric cutthroat trout (*Oncorhynchus clarki*) populations existed at most sites, but brook trout (*Salvelinus fontinalis*) were sympatric with cutthroat trout at one site, and another site contained allopatric brown trout (*Salmo trutta*). The only nonsalmonid fish species occasionally present was Paiute sculpin (*Cottus beldingi*). Additional data were collected from streams draining the Medicine Bow Mountains in southeastern Wyoming and consisted of two sites that we sampled during late summer in 1998 and four sites sampled in late summer by Kozel (1987) that met our site selection criteria and used similar fish sampling methods. Species composition at sites in the Medicine Bow Mountains consisted of allopatric populations of brown trout or brook trout or mixtures of these species. Hydrographs of all study streams were typical for the Rocky Mountain region, with peak discharges driven by snowmelt in May or June, followed by baseflows from July to February.

Data collection

Trout populations in the reaches downstream from abrupt changes in stream slope were sampled first at the sample sites and trout populations in upstream reaches were sampled within 2 days on average. Trout populations were sampled by deploying a block net at the downstream end of a reach and then collecting trout using a backpack electrofisher (model 15-C, Smith-Root,[3] Vancouver, Wash.) and multiple removal efforts within the stream reach (Zippin 1958). Each removal effort consisted of a single electrofishing pass through a reach in an upstream direction. An effort was made to capture 35 age-1+ trout during the initial pass through a reach (average total number of age-1+ trout collected per reach was 119), but this was not always possible when trout densities were low. In these cases, we stopped sampling once stream slope began to change or 300–400 m of stream had been sampled. When trout were abundant, at least 100 m of stream were sampled so that habitat could later be characterized accurately. Because the endpoint of a reach was not predetermined, the second block net was not set until a criterion for stopping was met. Electrofishing was then conducted up to a natural barrier or the block net was set a short distance upstream and the remainder of the reach electrofished. Trout captured during a pass were identified to species and measured to the nearest millimetre total length (TL) before being released downstream of the reach. Trout weights were later estimated from species-specific length–weight regressions that had r^2 values ranging from 0.96 to 0.99 and were developed from trout sampled within the study areas.

Additional electrofishing passes (one to four) were made until the width of the confidence interval (CI) associated with the population estimate for trout longer than 135 mm TL was less than 30% of the size of the population estimate (average widths of CIs were 16% of the population estimate). Only trout longer than 135 mm were considered when calculating the approximate precision of population estimates in the field because these fish composed the majority of fish biomass in a reach, and, for reasons described below, separate population estimates were calculated for trout shorter and longer than 135 mm. Population estimate precision was estimated after the second and subsequent electrofishing passes using a graph from MicroFish 3.0 (Van Deventer and Platts 1989) in conjunction with rough estimates of population size and electrofishing efficiency derived from the following equations:

(1) $$S = x_1/(1 - (x_2/x_1))$$

(2) $$E = (x_1 - x_2)/x_1$$

where S is population size, E is electrofishing efficiency, x_1 is the number of trout longer than 135 mm captured during the first removal effort, and x_2 is the number of trout longer than 135 mm captured during the second removal effort.

Electrofishing effort was standardized by thoroughly searching all habitat during each pass and having the same person, accompanied by one netter, run the electrofisher. We minimized electrofishing- and temperature-related changes in fish behavior that would violate the assumption of constant catchability employed by closed-population removal estimators (Zippin 1958) by leaving reaches undisturbed for 1 h between electrofishing passes and electrofishing only when water temperatures exceeded 7°C.

After completion of electrofishing activities, habitat variables were measured using a transect methodology. Transects were spaced every 10 m and wetted width was measured to the nearest centimetre along each transect. Water depths were recorded to the nearest centimetre at one quarter, one half, and three quarters of the wetted width. A water velocity index was estimated from the height of water displacement (estimated to the nearest centimetre) on the upstream side of the depth staff at each depth measurement. Mean depths and water velocities were calculated for each transect as the sum of these measurements divided by 4 before the calculation of reach averages. Dominant substrate was visually estimated for a 0.3-m^2 area surrounding each point where water depth was measured using substrate categories defined in Platts et al. (1983). Unobstructed sun-arc was measured at the stream's surface at the midpoint of every third transect using a clinometer and procedures described in Platts et al. (1983). Trout cover as defined by Wesche (1980) was measured within an area extending 1 m upstream and 1 m downstream from each transect and was converted to a percentage of reach surface area. The longitudinal lengths of channel units were measured with a tape, and channel units were visually classified as trench pools, plunge pools, dam pools, lateral scour pools, runs, riffles, rapids, or cascades following definitions in Bisson et al. (1982). Additional criteria used to identify fast-water habitats such as amount of supercritical flow, presence–absence of

[3]Mention of trade names does not imply endorsement by the University of Wyoming.

transverse bars, and stream slope were obtained from Grant et al. (1990).

Data processing and analysis

Population estimates for age-1+ trout were calculated using the maximum likelihood estimator in MicroFish 3.0 (Van Deventer and Platts 1989). Age-0 trout were removed from consideration based on the timing of appearance in study streams and breaks in length–frequency histograms. Based on our own empirical observations and work by Anderson (1995), we calculated separate population estimates for trout shorter and longer than 135 mm in an effort to reduce length-related differences in catchability that would otherwise decrease the accuracy of population estimates. Areal and volumetric density estimates for a reach were obtained by adding population estimates for both length categories and dividing the total by either the surface area or the volume of the reach. Biomass estimates were calculated by multiplying the population estimate for a length category by the mean weight of trout in that length category, adding biomass estimates for both length categories, and dividing the total by either the surface area or the volume of the reach.

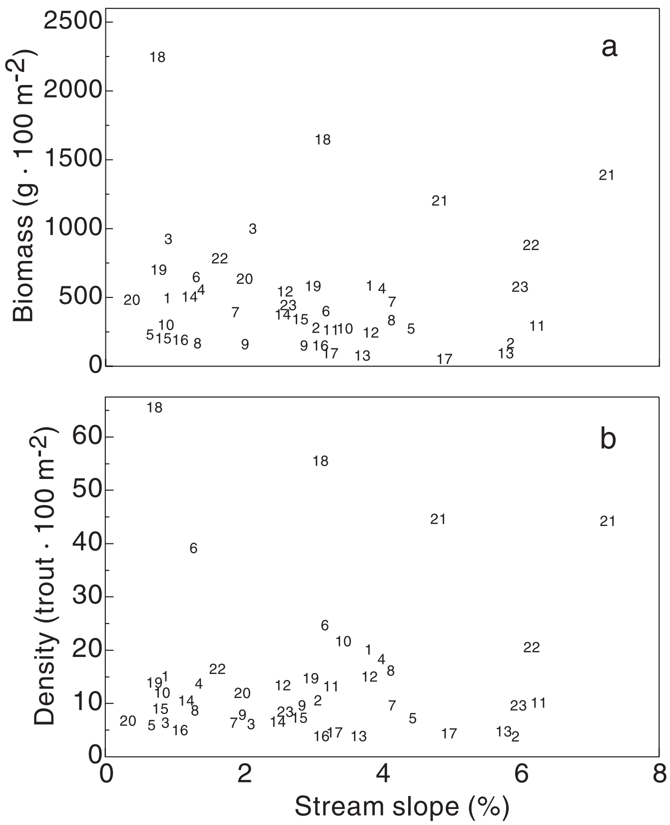
Population length structure for age-1+ trout was summarized by calculating the proportion of trout from each reach that were shorter or longer than the respective mean trout length at a site (one pair of reaches). Length structure was also summarized using the length of the shortest trout in the group of largest trout (those comprising 50% of the biomass) sampled from a site to delineate length categories. For sites with sympatric trout populations, species composition was enumerated by number and weight for age-1+ trout.

The effect of stream slope on population metrics or habitat attributes was assessed by testing whether the change in a variable between the reaches at a site differed from zero. Each site provided one sample and the variance among these samples was used to calculate 95% CI around the average amount of change in a variable. If zero was excluded from or occurred in the extremity of a CI, it was concluded that stream slope affected the variable. When sample sizes permitted, CIs for continuous variables such as density, biomass, or habitat attributes were constructed using bootstrapping techniques and were corrected for bias after Dixon (1993). Confidence intervals were constructed using standard normal theory techniques when sample sizes limited the utility of bootstrapping techniques ($N < 5$). Confidence intervals for population length structure were constructed using a technique suitable for categorical data (DerSimonian and Laird 1986), and Cochran's Q statistic was used to test for homogeneity among changes in length structure across sites. Small numbers of sites with sympatric trout populations precluded a similar approach to statistical testing, so chi square tests were used to assess changes in species composition by number at each sympatric site.

Results

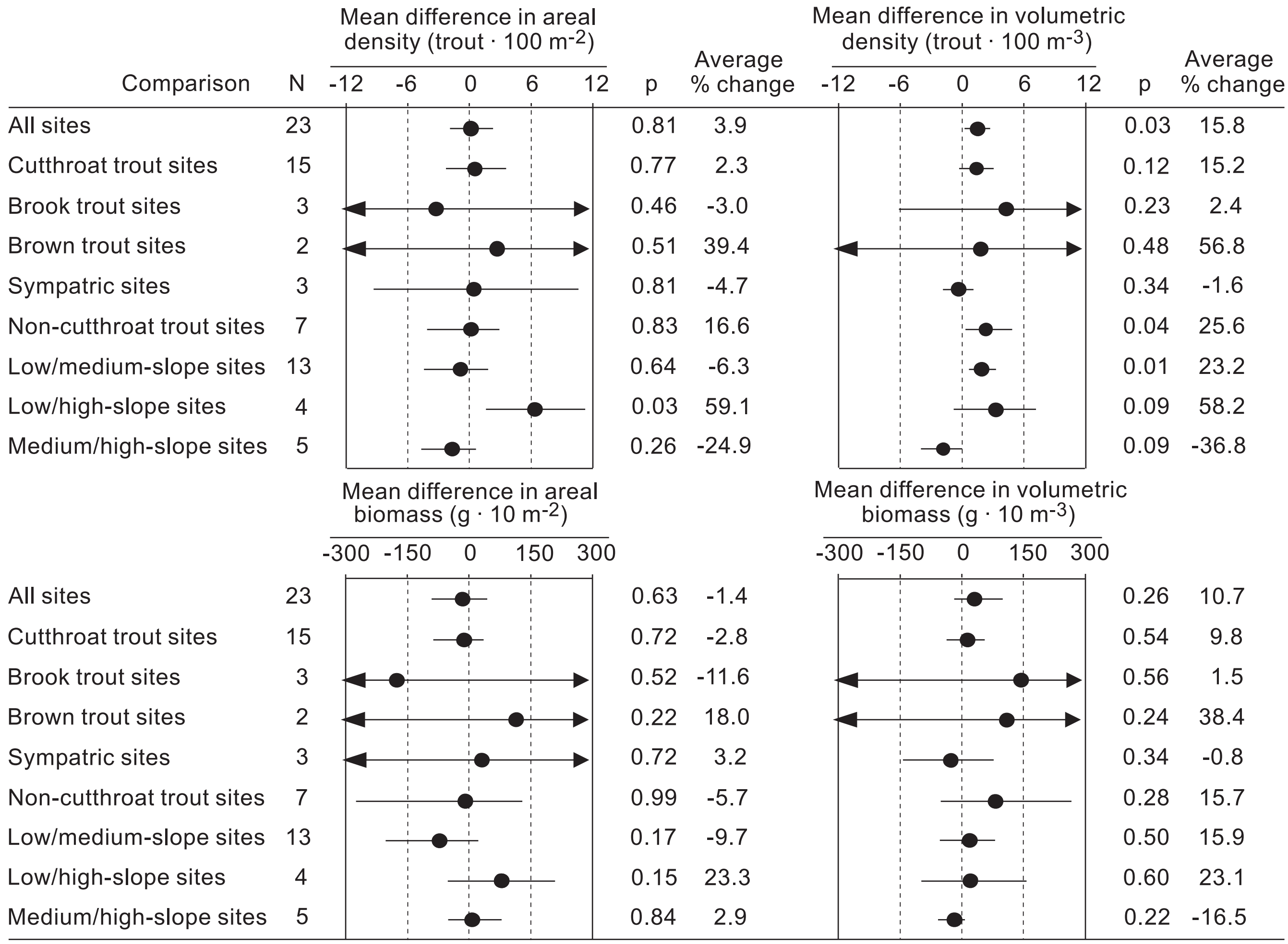
In contrast with the negative relationship often reported between trout biomass and stream slope, scatter plots of our trout biomass and density estimates obtained using a paired-reach sampling design gave no indication that increased stream slope negatively affected trout populations (Fig. 2). Additionally, some of the data collected with the paired-reach design were obtained from streams where, using a longitudinal sampling design, we had observed a negative relationship between stream slope and biomass (Fig. 1*a*). These results suggest that the previously documented negative relationship between trout biomass and stream slope was largely an artifact of sampling design.

Fig. 2. Scatter plots of stream slope versus the areal trout (*a*) biomass and (*b*) density data sets used in this study. Data were obtained using a paired-reach sampling design at 23 sites on 18 streams draining four mountain ranges in Idaho and Wyoming. Data points with the same number represent the two reaches sampled at a site.



Statistical tests based on the paired data structure indicated that stream slope did not affect areal trout density across the 23 sample sites (average change = 3.9%; $p = 0.81$, $N = 23$). This result was consistent for areal densities across most of the comparisons based on subsets of the 23 sites that had similar trout species or stream slope classes (Fig. 3). The only exception was the greater trout densities that occurred in high-slope reaches relative to low-slope reaches (average change = 59.1%; $p = 0.03$, $N = 4$). Statistically improbable patterns were common, however, when changes in channel cross sections among reaches in different slope classes were corrected for by expressing trout density volumetrically. Volumetric trout density across the 23 sample sites increased as stream slope increased (average change = 15.8%; $p = 0.03$, $N = 23$) as did volumetric densities in the majority of more specific comparisons based on trout species (Fig. 3). Sites with cutthroat trout comprised the majority of the data set, but changes in volumetric density at non-cutthroat trout sites (average change = 25.6%; $p = 0.04$, $N = 7$) were similar to changes observed at cutthroat trout sites (average change = 15.2%; $p = 0.12$, $N = 15$). In comparisons based on stream slope classes, volumetric densities increased from low-slope reaches to either medium- (average change = 23.2%; $p = 0.01$; $N = 13$) or high-slope reaches (average change = 58.2%; $p = 0.09$, $N = 4$) but decreased from

Fig. 3. Effect of reach-scale stream slope on trout density and biomass. Error bars are 95% CIs that encompass the average difference in a population metric among sites. One site was eliminated from comparisons based on stream slope classes because both reaches were in the high-slope category.



medium- to high-slope reaches (average change = –36.8%; p = 0.09, N = 5).

Results of statistical tests involving areal and volumetric expressions of trout biomass were similar. Increases in stream slope did not affect either areal (average change = –1.4%; p = 0.63, N = 23) or volumetric (average change = 10.7%; p = 0.26, N = 23) trout biomass across the 23 sample sites, and a similar trend held for more specific comparisons based on subsets of the 23 sites with similar trout species or stream slope classes (Fig. 3). The width of CIs associated with some comparisons suggested that statistical power was occasionally low, but changes in biomass were not observed even when precise estimates were obtained (e.g., average change in volumetric biomasses at cutthroat trout sites or medium/high-slope sites).

No patterns in population length structure relative to stream slope class were apparent when mean trout length at a site was used to delineate length categories (Fig. 4). Length structure changed less than 6.3% for two of three comparisons, and Cochran's Q statistic indicated that the amount of change in length structure between reaches at a site was often heterogeneous among sites. Patterns in length structure were discerned, however, when length categories were delineated based on the shortest trout length in the group of largest trout (those comprising 50% of the biomass) sampled at a site (Fig. 4). Changes in length structure were reciprocal to changes in volumetric trout densities among stream slope classes, and disproportionately small numbers of the largest trout occurred in medium- (average change = –14.1%; N = 13) and high-slope reaches (average change = –25.0%; N = 4) relative to low-slope reaches and greater numbers of large trout occurred in high-slope reaches relative to medium-slope reaches (average change = 14.4%; N = 5).

Stream slope had no effect on species composition (Fig. 5). At one site with brook trout and cutthroat trout, the numerical abundance of brook trout decreased by 7.2% as stream slope increased, but this change was not statistically improbable (χ^2 = 1.27, p = 0.26, N = 139). A similar trend was observed when change in species composition was calculated by weight and brook trout abundance decreased by 4.3%. The change in stream slope between the two reaches at this site was small (1.0–2.4%) but involved a marked change in channel characteristics from a low-slope reach with a sinuous channel pattern and channel units composed of lateral scour pools, riffles, and runs to a medium-slope reach with a straight channel pattern and riffles, rapids, and

Fig. 4. Effect of reach-scale stream slope on population length structure. Error bars are 95% CIs that encompass the average difference in a population metric among sites. One site was eliminated from comparisons based on stream slope classes because both reaches were in the high-slope category.

Length categories	Comparison	N	Cochran's Q	p
Mean length	Low/medium-slope sites	13	90.06	< 0.01
	Low/high-slope sites	4	2.49	0.48
	Medium/high-slope sites	5	30.26	< 0.01
Largest trout	Low/medium-slope sites	13	38.99	< 0.01
	Low/high-slope sites	4	8.49	0.04
	Medium/high-slope sites	5	7.93	0.09

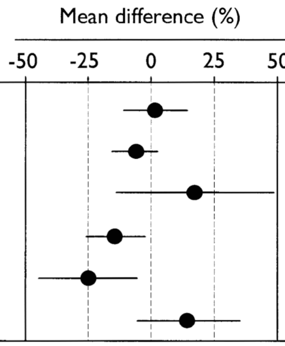
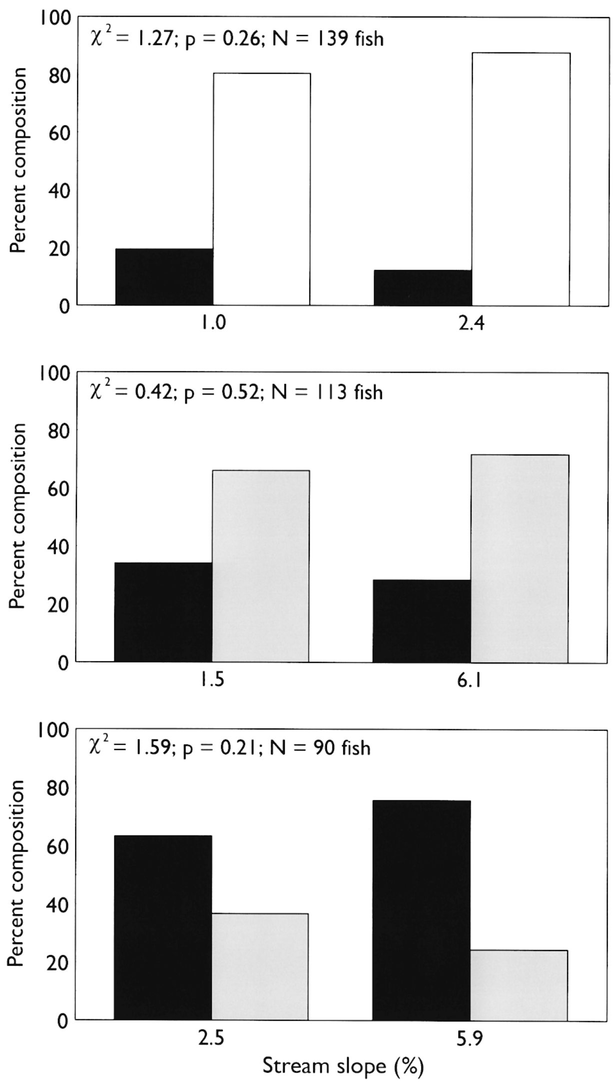


Fig. 5. Effect of reach-scale stream slope on species composition by number for sites with sympatric trout populations. Cutthroat trout are represented by open bars, brook trout by solid bars, and brown trout by shaded bars. Patterns in species composition by weight were similar and are not shown.



trench pools. At two sites with brook trout and brown trout, changes in species composition were inconsistent. Numerical brook trout abundance decreased by 5.7% at site 1 (χ^2 = 0.42, p = 0.52, N = 113) but increased by 12.3% at site 2 (χ^2 = 1.59, p = 0.21, N = 90) as stream slope increased. Changes in species composition by weight mirrored changes in number, and brook trout abundance by weight decreased by 6.6% at site 1 and increased by 10.5% at site 2.

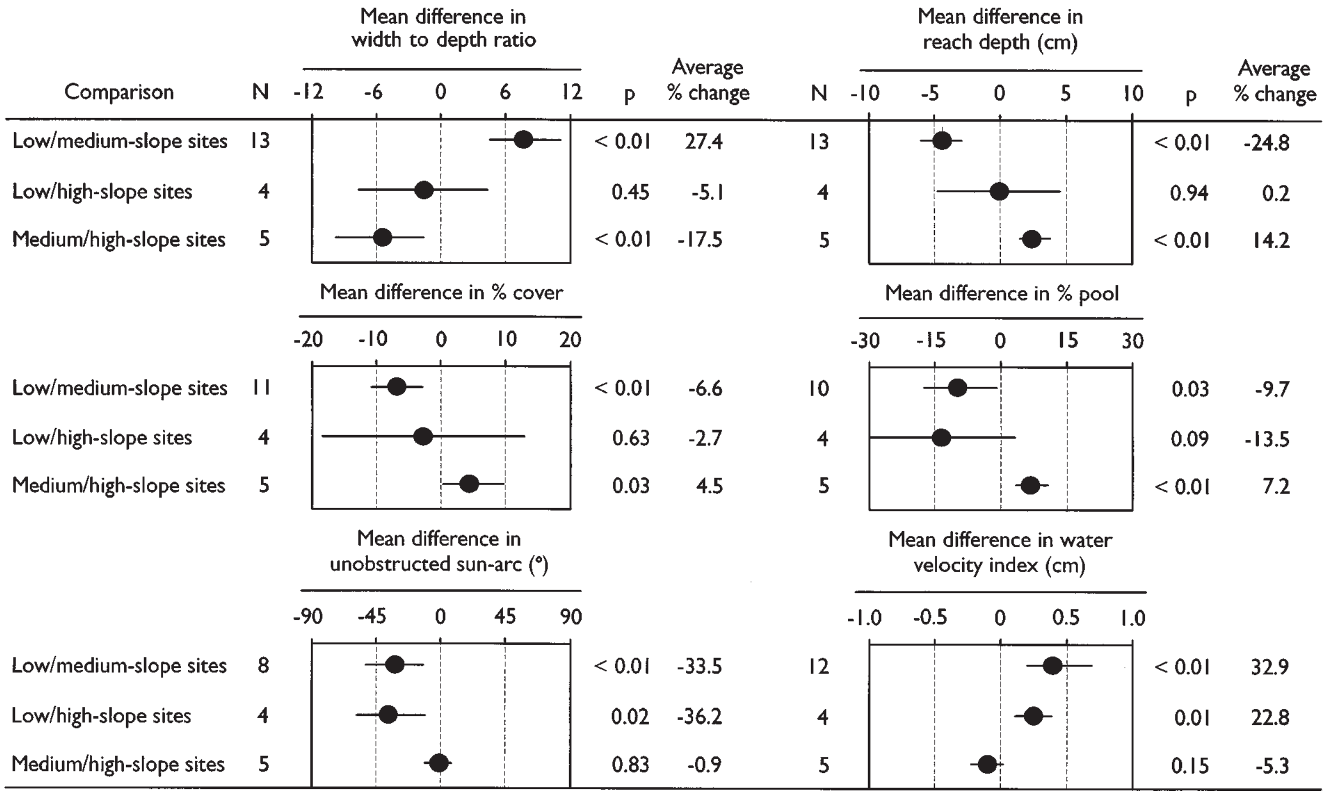
Most habitat attributes differed among the three stream slope classes (Fig. 6). Medium-slope reaches had the greatest width to depth ratios, some of the fastest water velocities, and the smallest amounts of trout cover and pool habitat. Low-slope reaches had the greatest amount of pool habitat, the most open canopies, and the slowest water velocities. High- and low-slope reaches had similar width to depth ratios (average change = –5.1%; p = 0.45, N = 4), mean depths (average change = 0.2%; p = 0.94, N = 4), and amount of trout cover (average change = –2.7%; p = 0.63, N = 4).

Discussion

Patterns in trout populations

Numerous studies have suggested that trout biomass is negatively related to stream slope (e.g., MacPhee 1966; Chisholm and Hubert 1986; Kozel et al. 1989), but these studies used data sets in which many factors were confounded with stream slope. After sampling in a manner that eliminated the effects of confounding factors, we observed no effect of stream slope on trout biomass. Our results were unexpected, given differences in the amount of pool habitat among stream slope classes and the well-documented preference of trout for pools. However, Riley and Fausch (1995) have indicated that pools serve to concentrate trout from adjacent areas. If this "concentration effect" affected trout more strongly in habitats adjacent to pools than in distant habitats, trout distributions would be more patchy in reaches with more pool habitat and these reaches would not necessarily support greater trout biomass. Our results were also unexpected, given that changes in trout biomass did not track available cover, despite the documented relationship between trout biomass and cover (Wesche et al. 1987; Kozel and Hubert 1989). However, many systems for rating trout habitat (e.g., Binns and Eiserman 1979; Platts et al. 1983), including the one that we used (Wesche 1980), comprise

Fig. 6. Effect of reach-scale stream slope on habitat attributes among stream slope classes. Error bars are 95% CIs that encompass the average difference in a habitat attribute among sites. Sample sizes vary among comparisons because all habitat attributes were not measured at each site.



several cover types of which overhead cover and deepwater cover are major constituents. Many habitat rating systems may therefore be predisposed towards providing better ratings in downstream areas where streams are deeper and the sinuous channel patterns associated with low-slope reaches generate overhead bank and vegetative cover. As such, better cover ratings will coincide with factors not related to the structure of physical habitat (e.g., water temperature, macroinvertebrate abundance) but that favor the production of trout in downstream areas. This hypothesis may explain why the physical habitat in low-slope reaches is often erroneously perceived as optimal trout habitat.

A pattern in population length structure was detected when we focused on the largest trout sampled from our sites. Large trout were most abundant in low-slope reaches, of intermediate abundance in high-slope reaches, and least abundant in medium-slope reaches. This ordering concurred with the availability of deepwater habitats (as inferred from channel cross sections and pool abundance) across slope classes and, when combined with the reciprocal changes in trout density that we observed, suggested that a competitive mechanism may have been at work whereby large trout were excluding smaller trout from certain habitats. Reciprocity between density and large trout abundance was likely enhanced by the preference of smaller fish for shallow-water habitats (Kennedy and Strange 1982; Moore and Gregory 1988) that were most available in medium-slope reaches. Reciprocal patterns in density and large fish abundance also explain how biomass remained constant across stream slope classes despite changes in large fish abundance.

Our results regarding the effect of reach-scale stream slope on species composition do not agree with the findings of previous investigators. In the most comprehensive treatment of the subject, Fausch (1989) concluded that stream slope was an important determinant of species composition in sympatric cutthroat trout and brook trout populations, and similar conclusions have been reached for different combinations of trout species (Moore et al. 1985; Bozek and Hubert 1991). However, the changes in species composition that we observed at sympatric sites were small and not statistically improbable. The direction of these changes at sites with brook trout and brown trout was also inconsistent, despite studies that suggest that brown trout outcompete brook trout (Fausch and White 1981; Waters 1983) and should, therefore, have always been most abundant in reaches with low slopes. Similar competitive mechanisms or the perceived preference of cutthroat trout for higher slopes (e.g., Griffith 1988) could be invoked to argue that the small decrease in cutthroat trout relative to brook trout in the low-slope reach where these species were sympatric supported previous understanding, but this change was so small (7.2% by number, 4.3% by weight) that it likely had little biological relevance. Unfortunately, our data set contained few sites with sympatric trout populations, which precluded us from making stronger inferences regarding specific combinations of trout species or stream slope classes. Despite this limitation, our results, in combination with the nature of previous sampling designs that precluded drawing strong causal inference, call into question the belief that stream slope affects trout species composition.

Spatial scale considerations

The scale at which studies are conducted influences the patterns that are discerned and the mechanisms responsible for effecting these patterns (Levin 1992). Our study is a case in point, as our data suggest that the strong patterns in species composition (Griffith 1972; Fausch and White 1981) and trout biomass (Saffel and Scarnecchia 1995; Herger et al. 1996) that have been observed at channel unit and smaller scales do not translate to patterns at the reach scale. In the case of trout biomass, this implies that stream-scale gradients in the quality and quantity of materials moving through a reach (e.g., allocthonous materials, water temperature, discharge, macroinvertebrate drift) may ultimately determine the amount of trout biomass that occurs within a reach. Similarly, a stream-scale gradient in water temperature seems the most logical variable capable of effecting change in species composition at larger scales based on mechanisms related to the physiology of individual fish species. Once stream-scale gradients have set biomass levels and species composition within a reach, mechanisms intrinsic to trout (i.e., competitive tendencies or affinities for particular habitats) further structure trout populations and lead to the patterns observed at channel unit and subunit scales.

In contrast with species composition and biomass, trout density and length structure were affected by reach-scale stream slope. Because it is likely that many of the mechanisms operating at stream and subreach scales that we implicated above also influence density and length structure, these population metrics are influenced by mechanisms operating at a minimum of three spatial scales. When all possible interactions among scales are considered, the issue of how density and length structure are regulated becomes complex and makes it difficult to speculate about the various roles played by stream system components to regulate these population metrics. However, we view formulation and empirical testing of such hypotheses as challenging avenues for future research.

Regional differences

The paired-reach sampling design that we used eliminated the effects of most confounding variables, but it was impossible to control for differences in riparian vegetation and the amount of solar insolation among stream slope classes. Low-slope reaches occurred in wider, alluviated valleys, where streams had riparian canopies composed of sedges and willows that provided less shade than the mixed conifer stands adjacent to steeper-sloped reaches. The food-based hypothesis proposed by Wilzbach and Hall (1985) suggests that open canopies will facilitate increased primary productivity, which ultimately translates to greater macroinvertebrate and trout abundance. Paired-reach studies conducted in the Pacific Northwest have supported this hypothesis by describing increases in trout abundance associated with canopy removal (Murphy and Hall 1981; Hawkins et al. 1983). If the food-based hypothesis held true in our study streams, the greatest trout densities and biomass should have occurred in low-slope reaches. Instead, low-slope reaches had the lowest trout densities, and biomass levels were similar to those in steeper-sloped reaches, possibly suggesting that differences in macroinvertebrate abundance among our stream slope classes were minor.

Support for the explanation that macroinvertebrate differences among stream slope classes were minor can be inferred from the decreased density of timbered stream canopies in the Rocky Mountain region relative to the Pacific Northwest region (Johnson et al. 1986; Platts and Nelson 1989). Decreased tree shading, in combination with the greater shading that our low-slope reaches received relative to the clearcut streams studied in the Pacific Northwest (Hawkins et al. 1983), should have decreased differences in insolation and macroinvertebrate abundance between low- and steeper-sloped reaches. Alternatively, trout populations in Rocky Mountain streams may not be strongly regulated by macroinvertebrate abundance. Average trout biomasses that are nearly four times greater than biomasses in Pacific Northwest streams (Platts and McHenry 1988) and studies demonstrating strong food limitations (Warren et al. 1964; Mason 1976) in streams of the Pacific Northwest suggest that this may be the case. Without additional data, both explanations appear plausible.

In conclusion, our study took a detailed and synthetic look at how stream slope affected several trout population metrics and stream habitat by focusing on marked, reach-scale changes in stream slope. Some of our results call into question or contravene existing thought and suggest that patterns between stream slope and trout population metrics observed in previous research were correlative in nature and arose from the effects of many stream habitat variables acting simultaneously rather than a causal effect of stream slope. Contrary to previous research, our study suggests that trout biomass and species composition are unaffected by reach-scale stream slope. Trout density and population length structure, however, are affected by stream slope, and these metrics appear to change in reciprocal fashion such that available biomass is structured to make efficient use of the habitat within a reach. Our results have implications for fish habitat modeling because many models have been developed predicated on the assumption of a causal link between the structure of instream physical habitats and the characteristics of fish populations. Previously, however, this supposition had not been rigorously tested. It now appears that this assumption is at times untenable for trout populations in Rocky Mountain streams and is dependent on the population metric(s) used to describe populations and the spatial scale(s) at which studies are conducted. This leads us to believe that full understanding of the factors regulating trout populations will only be gained once studies are conducted that address the multimetric response of trout populations across multiple scales of inquiry.

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