Factors Influencing the Size Structure of Brook Trout and Brown Trout in Southeastern Wyoming Mountain Streams

JOSEPH G. LARSCHEID AND WAYNE A. HUBERT

U.S. Fish and Wildlife Service
Wyoming Cooperative Fish and Wildlife Research Unit
University of Wyoming, Laramie, Wyoming 82071, USA

Abstract.—We used discriminant models to identify relations among size structures of stocks of brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* and features of their habitats in small mountain streams (2,377–2,975 m above mean sea level) in the Medicine Bow National Forest, Wyoming. Size structure was predicted from position of the study reach in the watershed, from channel gradient, and from composition of the salmonid community. Brook trout were predominantly small in high-elevation, moderate-gradient, forested reaches with allopatric populations; they were larger in mid-elevation, low-gradient, meadow reaches that contained some brown trout. Brown trout were mostly small in mid-elevation, moderate-gradient, forested reaches; however, more large brown trout occurred lower in the watersheds, in meadow or rangeland stream reaches that had low gradients and that supported allopatric populations.

Biologists have directed considerable effort toward developing models to predict the standing stock of fish in streams from habitat characteristics (Fausch et al. 1988). Such models are useful because they help pinpoint the habitat variables that may limit the standing stock of fish in streams. However, models that predict standing stock do not elucidate the size structure—the abundance of fish of different lengths—of the stock, even though the quality of sport fisheries depends heavily on size structure (Anderson and Weithman 1978). For example, some populations of brook trout *Salvelinus fontinalis* may have high standing stocks, but the fish may be stunted and include few large individuals (Johnson 1989). Currently there is little knowledge of the factors governing size structure of salmonid populations in mountain streams.

In some models, life history stages or age-classes of fish have been considered in assessments of habitat quality. For instance, Gosse and Helm (1981), Bovee (1982), and Heggies (1988) found life stages (young of year, juvenile, adult) to be vital subdivisions in defining microhabitat needs of brown trout *Salmo trutta*. Raleigh (1982) and Raleigh et al. (1984) recognized the need to address separately the habitat requirements of different life stages of brook trout and brown trout, and Wesche (1980) developed separate cover ratings for small (total length, <15.2 cm) and large (≥15.2 cm) trout.

Recently, Johnson (1989) developed multiple-regression models that predict size structure of brook trout in beaver ponds from habitat variables. Except for these models, we know of none that predict size structure of salmonid populations from physical habitat measurements. Our objective was to ascertain whether size structures of brook trout and brown trout stocks were related to features of their habitats in small streams in the Medicine Bow National Forest, southeastern Wyoming.

Methods

This work was conducted in Medicine Bow National Forest in southeastern Wyoming. All study reaches were south of Wyoming highway 130 on the Snowy Range and east of the Continental Divide on the Sierra Madre. Fifteen watersheds that had been subjected to minimal logging, mining, overgrazing, or road construction were selected. No water diversions or water storage structures that would alter the natural hydrography were upstream from the study reaches. The hydrograph was typical of Rocky Mountain streams: flows peaked in spring and were low in fall and winter (Wesche 1982). Study reaches ranged from 2,377 to 2,975 m above mean sea level. Vegetation in the study area was primarily spruce *Picea* spp. and fir *Abies* spp. in subalpine areas, and lodgepole pine *Pinus contorta* in mountain areas. Willows *Salix* spp., sedges *Carex* spp., and various grasses dominated mountain meadows; sagebrush *Artemisia* spp., willows, and grasses dominated foothill areas.

1 The Unit is jointly supported by the University of Wyoming, the Wyoming Game and Fish Department, and the U.S. Fish and Wildlife Service.
Potential study reaches were selected from U.S. Forest Service records and U.S. Geological Survey topographic maps. They consisted of 200-m reaches of similar habitat and gradient in drainages with no record of clear-cutting, mining, or extensive livestock grazing. Specific sampling sites were selected to represent the range of drainage basin areas (0.7–100 km$^2$) and elevations in the study area. Selected study reaches and the upstream watershed were examined to confirm the lack of human effects. Channel gradients were assessed with a surveyor's level before field sampling.

The transect method was used to measure stream habitat features over 200-m reaches (Platts et al. 1983). Riffles marked the upper and lower ends of study reaches. In 1985, transects were spaced 2 m apart and point measurements were made at 0.3-m intervals. In 1986, transects were spaced 4 m apart and point measurements were made at seven equally spaced locations, plus at each bank. Water depth was measured at each point and at the bank, but the bank measurements were excluded from calculations of mean depth. Cover, dominant substrate, embeddedness, and microhabitat were visually classified at each point across a transect. Cover was classified into three categories: aquatic vegetation, woody debris, and boulder. Substrate was classified into six categories (after Platts et al. 1983; diameter in parentheses): small sediment (=0.8 mm), large sediment (0.9–4.7 mm), gravel (4.8–76.0 mm), cobble (77–304 mm), small boulder (305–609 mm), and large boulder (≥610 mm). Embeddedness (amount of fine sediment surrounding the underlying substrate particles) was rated from zero to 100% (Platts et al. 1983). Habitat types were classified according to Bisson et al. (1982). Water depth at the shore, presence of overhanging bank (as defined by Wesche et al. 1987), and extent of overhanging vegetation were determined at each bank. Bank angle was determined with a clinometer (Platts et al. 1983).

The length of each pool and riffle was measured and the physical structures associated with the formation of the pool—such as geologic formations (bedrock, boulders) or woody debris (log dams, natural log deflectors, debris jams)—were noted. The percentages of pool habitat created by geologic formations and woody debris were computed. Although most woody debris probably overlaid geologic formations, woody debris was the only physical structure noted for locations where it appeared to govern pool formation.

Discharge was measured at the lower end of each study reach with a current meter according to the procedure of Buchanan and Somers (1969). A water sample was taken for determination of conductivity and alkalinity. All sampling was conducted after spring high water between July and early October 1985 and 1986.

The removal method of DeLury (1951) was used to estimate trout standing stock in each study reach. Small-mesh seines (<3-mm-diameter openings) were used to block the upper and lower sections of each reach, and three depletion passes were made with a backpack electroshocker. Fish were weighed to the nearest 1 g and measured to the nearest 0.1 cm; all fish lengths are given as total lengths. Only fish longer than 10.0 cm were considered fully recruited into the fishery and were used in the population estimates and in the evaluations of size structure. Model M(bh) of the program CAPTURE (White et al. 1982) was used to estimate standing stock, because it allows for the variability that the first capture attempt causes in fish behavior.

Summary statistics for 60 habitat variables measured through the field techniques described by us were reported by Kozel (1987). These statistics were used to assess the influence of the habitat variables on size structure of brook trout and brown trout.

We defined quality length as greater than 20 cm for brook trout and greater than 25 cm for brown trout, based on the range of size structures of salmonid stocks observed among the study streams in Medicine Bow National Forest. Pearson correlation coefficients were computed between the proportion of quality-length fish of each trout species and the habitat variables. We also determined the standing stock of each species.

Discriminant analysis was used to identify differences between reaches with less than 5% quality-length brook trout (group 1) and reaches with a larger proportion of quality-length brook trout (group 2). Similarly, reaches with less than 20% quality-length brown trout (group 1) were separated from reaches with higher proportions of quality-length brown trout (group 2). These proportions were based on our knowledge that few brook trout exceed 20 cm, whereas many brown trout are larger than 25 cm. Reaches without the target species were also identified (group 3). All groups were given equal weight (i.e., equal prior probabilities) in the final classification. Nearly unbiased error rates were estimated with the leaving-one-out (i.e., jackknife) method of Lachenbruch (1975). Variables were selected for inclusion into
Table 1.—Brook trout and brown trout standing stocks in 48 study reaches in 15 streams of southeastern Wyoming.

| Reach                | Elevation (m) | Discharge (m³/s) | Gradient (%) | Standing stock (kg/hectare) |
|----------------------|---------------|------------------|--------------|-----------------------------|
|                      |               |                  |              | Brook trout | Brown trout |
| Fall Creek           |               |                  |              |             |             |
|                      | 2.975         | 0.05             | 1.6          | 188         | 0           |
|                      | 2.963         | 0.08             | 0.2          | 197         | 0           |
|                      | 2.952         | 0.08             | 0.5          | 204         | 0           |
|                      | 2.938         | 0.09             | 2.9          | 148         | 0           |
|                      | 2.931         | 0.09             | 2.1          | 132         | 0           |
| Cottonwood Creek     |               |                  |              |             |             |
|                      | 2.887         | 0.02             | 1.5          | 259         | 0           |
|                      | 2.758         | 0.12             | 1.6          | 90          | 0           |
|                      | 2.746         | 0.11             | 1.3          | 180         | 0           |
|                      | 2.682         | 0.20             | 4.3          | 137         | 16          |
| Savage Run           |               |                  |              |             |             |
|                      | 2.844         | 0.01             | 1.8          | 186         | 0           |
|                      | 2.813         | 0.04             | 3.9          | 123         | 0           |
|                      | 2.798         | 0.15             | 4.7          | 101         | 0           |
|                      | 2.762         | 0.15             | 4.2          | 51          | 0           |
|                      | 2.701         | 0.16             | 4.6          | 104         | 0           |
| Coon Creek           |               |                  |              |             |             |
|                      | 2.813         | 0.05             | 1.8          | 42          | 37          |
|                      | 2.792         | 0.16             | 2.8          | 45          | 7           |
|                      | 2.716         | 0.25             | 0.5          | 39          | 28          |
|                      | 2.704         | 0.24             | 2.9          | 24          | 37          |
| Park Run             |               |                  |              |             |             |
|                      | 2.755         | 0.03             | 0.2          | 235         | 0           |
|                      | 2.746         | 0.04             | 1.2          | 234         | 0           |
|                      | 2.732         | 0.09             | 0.5          | 230         | 94          |
| Encampment River, East Fork | | | | | |
|                      | 2.752         | 0.07             | 4.3          | 101         | 0           |
|                      | 2.713         | 0.13             | 2.8          | 86          | 29          |
|                      | 2.701         | 0.13             | 3.9          | 50          | 49          |
|                      | 2.688         | 0.14             | 3.4          | 44          | 43          |
| Illinois Creek       |               |                  |              |             |             |
|                      | 2.752         | 0.05             | 2.6          | 405         | 0           |
|                      | 2.739         | 0.06             | 1.3          | 472         | 0           |
| Pelton Creek, North Fork | | | | | |
|                      | 2.694         | 0.08             | 4.6          | 121         | 0           |
|                      | 2.673         | 0.09             | 7.1          | 119         | 0           |
| Badger Creek         |               |                  |              |             |             |
|                      | 2.670         | 0.08             | 3.2          | 168         | 0           |
|                      | 2.618         | 0.08             | 2.0          | 61          | 43          |
| North Spring Creek   |               |                  |              |             |             |
|                      | 2.661         | 0.23             | 1.0          | 27          | 37          |
|                      | 2.657         | 0.23             | 0.7          | 14          | 50          |
|                      | 2.652         | 0.23             | 1.7          | 14          | 36          |
|                      | 2.623         | 0.24             | 1.0          | 23          | 65          |
| McClain Creek        |               |                  |              |             |             |
|                      | 2.548         | 0.03             | 0.7          | 485         | 127         |
|                      | 2.542         | 0.04             | 0.6          | 316         | 190         |
|                      | 2.534         | 0.04             | 0.7          | 310         | 132         |
| Big Creek, South Fork |               |                  |              |             |             |
|                      | 2.463         | 0.88             | 1.2          | 0           | 46          |
|                      | 2.457         | 0.82             | 1.8          | 0           | 71          |

Table 1.—Continued.

| Reach                | Elevation (m) | Discharge (m³/s) | Gradient (%) | Standing stock (kg/hectare) |
|----------------------|---------------|------------------|--------------|-----------------------------|
|                      |               |                  |              | Brook trout | Brown trout |
| Big Creek, Middle Fork |               |                  |              |             |             |
|                      | 2.423         | 0.50             | 1.3          | 2           | 136         |
|                      | 2.418         | 0.47             | 0.8          | 1           | 86          |
| Big Creek, North Fork |               |                  |              |             |             |
|                      | 2.423         | 1.04             | 1.3          | 0           | 74          |
|                      | 2.422         | 0.96             | 0.3          | 0           | 36          |
| Fox Creek            |               |                  |              |             |             |
|                      | 2.377         | 0.62             | 2.2          | 1           | 108         |

We assessed 48 stream reaches. We found allopatric populations of brook trout in stream reaches that were 2,670-2,975 m above sea level, and we found allopatric brown trout populations at stream elevations of 2,419-2,463 m. Sympatric stocks of brook trout and brown trout were found at elevations of 2,377-2,813 m (Table 1). No other salmonid species were found in the study reaches.

Correlation analysis and discriminant function analysis identified 19 habitat variables that were related to the proportion of quality-size brook trout or brown trout (Table 2); 8 variables were significantly correlated with the proportion of quality-size brook trout (Table 3). High proportions of quality-size brook trout were associated with high standing stocks of brown trout; this combination of the discriminant functions based on a priori expectations and their univariate significances (as determined from comparisons by analysis of variance). Multicolinearity was reduced by excluding highly correlated (r ≥ 0.80) variables.

Canonical discriminant analysis was used to interpret the relations between habitat features and the size structures of trout. We used structure coefficients to interpret the importance of each variable to the discriminant process (Williams 1983). We used the Statistical Package for the Social Sciences (SPSS\textsuperscript{*}, version 3.1) to compute the correlations and to interpret the discriminant results (SPSS 1986), and Biomedical Programs (BMDP; Dixon et al. 1986) to derive the jackknifed classification results. All tests were determined significant at $P < 0.05$.

Results

We assessed 48 stream reaches. We found allopatric populations of brook trout in stream reaches that were 2,670-2,975 m above sea level, and we found allopatric brown trout populations at stream elevations of 2,419-2,463 m. Sympatric stocks of brook trout and brown trout were found at elevations of 2,377-2,813 m (Table 1). No other salmonid species were found in the study reaches.

Correlation analysis and discriminant function analysis identified 19 habitat variables that were related to the proportion of quality-size brook trout or brown trout (Table 2); 8 variables were significantly correlated with the proportion of quality-size brook trout (Table 3). High proportions of quality-size brook trout were associated with high standing stocks of brown trout; this combination...
Table 2.—Habitat variables that were found to be related to the proportion of either quality-size brook trout or quality-size brown trout in streams of the Medicine Bow National Forest.

| Variable                          | Measurement and unit                                      |
|----------------------------------|----------------------------------------------------------|
| Water depth                      | Mean water depth (cm)                                     |
| Shore depth                      | Mean depth of water along banks (cm)                     |
| Maximum pool depth               | Maximum water depth measured in a pool (cm)              |
| Discharge                        | Discharge in late summer or early fall (m$^3$/s)         |
| Elevation                        | Elevation above mean sea level (m)                       |
| Conductivity                     | ($\mu$/cm)                                               |
| Alkalinity                       | As CaCO$_3$ (mg/L)                                       |
| Deep water                       | Percentage of surface area with a water depth $\geq$ 45 cm|
| Deep pools                       | Percentage of surface area in pool habitat with water depth $\geq$ 15 cm |
| Secondary channel pools          | Percentage of surface area with secondary channel pools  |
| Pools with wood cover            | Percentage of surface area with pool habitat and wood cover |
| Boulder cover                    | Percentage of surface area with boulder cover            |
| Overhead cover                   | Percentage of surface area with overhead cover           |
| Deep shoreline                   | Percentage of streambanks with adjacent water depth $\geq$ 15 cm |
| Overhanging vegetation           | Percentage of streambanks with vegetation overhanging water |
| Bank angle $<90^\circ$           | Percentage of streambanks with a bank angle $<90^\circ$  |
| Undercut banks                   | Percentage of streambanks with an overhang of $\geq$ 15 cm |
| Overhanging vegetation with deep water | Percentage of streambanks with vegetation overhanging water and water depth $\geq$ 15 cm |
| Log dams                         | Number of log dams/100 m of stream                       |

was found in reaches with substantial amounts of overhead cover (indicated by large values for shore depth, overhead cover, bank angle $<90^\circ$, undercut bank, and deep shoreline). High proportions of quality-size brook trout were also positively associated with conductivity and alkalinity, which tended to be highest in larger streams at low elevations. Five variables were correlated with the proportion of quality-size brown trout (Table 3). Abundant quality-size brown trout were associated with high standing stocks of brown trout, as well as with two chemical features indicative of high biological productivity—conductivity and alkalinity—as was the case with brook trout. The proportion of quality-size brown trout was negatively correlated with overhanging vegetation.

The best discriminant models classified reaches into the three groups—reaches with few quality-size fish, those with abundant quality-size fish, or those without the species of interest—on the basis of seven or eight variables (Tables 4, 5). Multicollinearity was not a problem because there were no high univariate correlations among these variables (all $r \leq 0.70$). All discriminant functions were significant ($P < 0.05$), based on the amount of residual discrimination (Wilks' lambda). The first functions accounted for the most variance (95% for brook trout, 86% for brown trout) and were most related to the groups (canonical correlations were 94% for brook trout and 85% for brown trout) for each model being assessed. Though significant, the second functions did not explain as much variation (5% for brook trout, 14% for brown trout) and were not as related to the groups (canonical correlations were 62% for brook trout, 54% for brown trout).

The first dimension of the discriminant function (position in watershed) for brook trout separated reaches dominated by brook trout from reaches dominated by brown trout (Figure 1). Allopatric brook trout stocks were in relatively small streams at high elevations (Table 5), whereas sympatric stocks were in larger streams at lower elevations. Comparison of group centroids determined that reaches with brook trout were significantly different from reaches with allopatric brown trout stocks in terms of their relative positions in the watershed. The second dimension (gradient) separated

Table 3.—Statistically significant ($P \leq 0.05$) Pearson correlations between the proportion of quality-size brook trout or brown trout in the study reaches ($N = 48$) and measured features of the habitat. See Table 2 for a description of the variables.

| Variable                      | Brook trout | Brown trout |
|-------------------------------|-------------|-------------|
| Brown trout standing stock    | 0.60        | 0.52        |
| Shore depth                   | 0.62        |             |
| Conductivity                  | 0.74        | 0.37        |
| Alkalinity                    | 0.73        | 0.34        |
| Overhead cover                | 0.66        |             |
| Overhanging vegetation        |             | -0.36       |
| Bank angle $<90^\circ$        | 0.62        |             |
| Undercut bank                 | 0.55        |             |
| Overhanging vegetation        |             |             |
| with deep water               |             | -0.47       |
| Deep shoreline                | 0.54        |             |
Table 4.—Structure coefficients and unstandardized coefficients for the discriminant models for brook trout and brown trout. Structure coefficients are based on pooled within-group correlations between the habitat variables and the derived canonical discriminant functions. Variables are ordered by the magnitude of their loadings on each function. Asterisks denote principal loadings on each function. See Table 2 for a description of the variables.

| Variable or constant          | Structure coefficients | Unstandardized coefficients |
|------------------------------|------------------------|-----------------------------|
|                              | First function         | Second function             |
|                              | First function         | Second function             |
| Discharge                    | 0.79*                  | -0.14                       | -8.6002                     | 3.9439                     |
| Elevation                    | -0.40*                 | -0.21                       | -0.0045                     | -0.1127                     |
| Deep water                   | 0.21*                  | 0.10                        | -0.0468                     | -0.0849                     |
| Maximum pool depth           | 0.16                   | 0.52*                       | -0.0355                     | 0.0597                      |
| Log dams                     | 0.16                   | -0.48*                      | -0.1858                     | -0.5651                     |
| Water depth                  | 0.31                   | 0.36*                       | 0.1114                      | 0.0198                      |
| Overhanging vegetation       | -0.16                  | -0.25*                      | -0.0143                     | -0.0052                     |
| Constant                     |                        |                             | 10.8797                     | 5.6768                      |

Brook trout

| Variable or constant          | Structure coefficients | Unstandardized coefficients |
|------------------------------|------------------------|-----------------------------|
|                              | First function         | Second function             |
| Elevation                    | -0.64*                 | -0.06                       | -0.0077                     | -0.0012                     |
| Deep pools                   | 0.61*                  | -0.03                       | 0.0553                      | -0.0422                     |
| Maximum pool depth           | 0.53*                  | -0.11                       | 0.0281                      | 0.0284                      |
| Discharge                    | 0.44*                  | -0.23                       | 2.2751                      | 0.5282                      |
| Secondary channel pools      | 0.01                   | -0.60*                      | -0.0038                     | -0.8688                     |
| Deep shoreline               | 0.08                   | 0.37*                       | -0.0184                     | 0.0435                      |
| Boulder cover                | -0.03                  | -0.37*                      | 0.0086                      | -0.4228                     |
| Pools with wood cover        | -0.13                  | -0.31*                      | 0.0033                      | -0.0333                     |
| Constant                     |                        |                             | 16.3362                     | 4.4432                      |

Brown trout

reaches by size structure of the brook trout stocks (Figure 1). Brook trout stocks dominated by small fish (group 1) were in reaches with relatively shallow water and abundant woody debris, whereas those stocks with abundant quality-size fish (group 2) were found in reaches with deeper water and less woody debris (Table 5). As gradient increased, the proportion of quality-size brook trout decreased \( r = -0.3992, P = 0.002 \). Comparison of the group centroids indicated that reaches with abundant quality-size brook trout differed significantly from those with predominantly small brook trout.

The first dimension of the discriminant function (position in watershed) for brown trout separated reaches with brown trout stocks from reaches with

Table 5.—Means of habitat variables in each stream reach group. Group 1 = few quality-size fish; group 2 = abundant quality-size fish; group 3 = no species of interest. See Table 2 for a description of the variables.

| Variable                  | Group 1 | SD | Group 2 | SD | Group 3 | SD |
|---------------------------|---------|----|---------|----|---------|----|
| Water depth (cm)          | 13.2    | 3.6| 16.4    | 4.0| 24.2    | 5.2|
| Deep water (%)            | 1.0     | 1.8| 2.4     | 3.0| 9.5     | 9.9|
| Maximum pool depth (cm)   | 52.2    | 17.1| 68.3    | 16.3| 77.1    | 16.4|
| Log dams (number/100 m)   | 2.0     | 1.6| 0.8     | 0.9| 0.1     | 0.2|
| Overhanging vegetation (%)| 43.2    | 23.8| 32.6    | 21.9| 14.3    | 5.7|
| Discharge (m³/s)          | 0.1     | 0.1| 0.1     | 0.1| 0.8     | 0.2|
| Elevation (m)             | 2.761.0 | 98.4| 2.703.0 | 135.5| 2,426.0 | 23.2|

Brown trout

| Variable                  | Group 1 | SD | Group 2 | SD | Group 3 | SD |
|---------------------------|---------|----|---------|----|---------|----|
| Deep shoreline (%)        | 19.3    | 9.8| 30.2    | 17.5| 22.1    | 15.8|
| Maximum pool depth (cm)   | 73.2    | 21.3| 75.7    | 14.7| 49.4    | 12.0|
| Deep pools (%)            | 76.5    | 12.8| 81.5    | 11.0| 53.0    | 15.4|
| Secondary channel pools (%)| 1.3    | 1.5| 0.2     | 0.5| 0.6     | 0.8|
| Pools with wood cover (%) | 7.5     | 7.3| 3.7     | 4.4| 7.5     | 5.7|
| Boulder cover (%)         | 1.0     | 1.3| 0.2     | 0.5| 0.7     | 1.3|
| Discharge (m³/s)          | 0.4     | 0.4| 0.4     | 0.3| 0.1     | 0.1|
| Elevation (m)             | 2,591.0 | 125.2| 2,528.0 | 130.8| 2,786.0 | 107.6|
allopatic brook trout stocks (Figure 2). Brown trout stocks with abundant quality-size fish were most common at relatively low elevations (Table 5). Comparison of the group centroids indicated that reaches with allopatic brook trout stocks differed significantly from reaches with brown trout stocks in terms of their relative positions in the watershed. The second dimension (gradient) separated brown trout stocks according to size structure (Figure 2). Brown trout stocks with many quality-size fish (group 2) were in low-gradient reaches within the foothills, whereas those stocks with few quality-size fish (group 1) were in higher gradients in reaches at greater elevations within the forest (Table 5). As gradient increased, the proportion of quality-size brown trout decreased ($r = 0.40$, $P = 0.002$). By comparing the group centroids, we found that reaches with few quality-size brown trout were significantly different from reaches with abundant quality-size brown trout, in terms of gradient and riparian features.

The overall classification accuracy was 81% for brook trout and 75% for brown trout. Most of the errors in classification were between groups 1 and 2—few or many quality-size fish (Table 6). Our classification results were nearly unbiased—that is, we would expect a similar level of classification accuracy for reaches with unknown trout size structure.

**Discussion**

Our results indicated that two interacting physical features influence the size structures of brook trout and brown trout stocks in small streams in southeast Wyoming mountains. The first is elevation of the stream reach, which influences species composition (e.g., allopatic brook trout stocks at high elevations, sympatric brook trout and brown trout stocks at mid-elevations, and allopatic brown trout stocks at low elevations); the second feature is a composite of channel gradient and related riparian features. For both brook trout and brown trout, stocks with the highest proportion of quality-size fish were in low-gradient stream reaches that meander to form deep trench pools with abundant overhanging banks.

One factor that limits brown trout stocks at higher elevations seems to be related to temperature (Vincent and Miller 1969), because brown trout fare better in water warmer than is optimum for brook trout (Piper et al. 1982). Another habitat feature that may limit brown trout abundance at high elevations is the amount of suitable pool habitat (Kozel 1987; Kozel and Hubert 1989).

Brook trout stocks with many quality-size fish were found in low-gradient reaches with deep pools, overhead cover, and abundant brown trout. It seemed that the habitat dimension was separating
the brook trout stocks of various size structures on the basis of differences in gradient and riparian features, but interspecific interactions and elevation (water temperature) may also influence the size structure of brook trout stocks. Brown trout feed on small trout (Alexander 1977; Gosse and Helm 1981; Bachman 1984), so selective predation on small brook trout by larger brown trout may have increased the average size of brook trout in mid-elevation reaches.

Fausch and White (1981) suggested that brown trout can competitively exclude brook trout from streams. It seems plausible that large brook trout can compete with brown trout but that small brook trout can be excluded from areas of optimal habitat. This conclusion was supported by Bachman (1984), who observed that only large brown trout were able to exclude smaller trout from optimal areas. Thus, competition with brown trout may lead to an enhanced size structure of brook trout in mid-elevation reaches but exclude brook trout at low elevations.

Brook trout and brown trout stocks with predominantly small fish were found in high-gradient reaches that had abundant boulders and pools formed by woody debris. Undercut banks, aquatic vegetation, and deep pools (mostly trench pools) were more abundant in low-gradient reaches than in moderate-gradient reaches (Kozel et al. 1989). Such habitat provides refuges near invertebrate drift lanes (Fausch 1984) and areas of low light intensity (Gosse and Helm 1981). Wesche (1980) found that undercut banks were critical habitat for brown trout. Large brown trout are more cover-oriented than small brown trout (Bachman 1984) and need large and deep pools with cover to overwinter (Cunjak and Power 1986). The needs of large brown trout seem to be met more fully by the cover features common to low-gradient reaches in meadows and rangelands than by the features common in higher-gradient forested reaches.

Table 6.—Nearly unbiased classification results (leaving-one-out method) of the derived canonical discriminant functions. Group 1 = few quality-size fish; group 2 = abundant quality-size fish; group 3 = species of interest absent.

| Species size-group | N | Classified into group | Percent correct |
|--------------------|---|-----------------------|-----------------|
| Brook trout        |   |                       |                 |
| 1                  | 26| 20 6 0                | 77              |
| 2                  | 12| 3 9 0                 | 75              |
| 3                  | 10| 0 0 10                | 100             |
| Brook trout        |   |                       |                 |
| 1                  | 11| 6 2 3                 | 55              |
| 2                  | 12| 2 8 2                 | 67              |
| 3                  | 25| 1 2 22                | 88              |

Figure 2.—Plot of individual reaches with allopatric and sympatric brown trout stocks, as well as allopatric brook trout stocks, in canonical space: group 1 (triangles) = brown trout stocks with less than 20% of the fish longer than 25 cm; group 2 (circles) = brown trout stocks with more than 20% of the fish longer than 25 cm; and group 3 (squares) = allopatric brook trout stocks. The darkened markers represent the centroids of these groups. Territorial boundaries (dashed lines) indicate the possible areas each group can occupy in canonical space.
Kozel and Hubert (1987) found that brook trout collected from two streams (elevation, ≥2,750 m above mean sea level) within our study area of Medicine Bow National Forest were significantly older when aged with otoliths than when aged with scales. Maximum age of brook trout that were aged with otoliths was 9 years, but the maximum was only 5 years for those aged with scales. The mean total length of 4-year-old brook trout aged with otoliths was 18.9 cm. The observations of Kozel and Hubert (1987) suggest that quality-size brook trout (20 cm) of streams in Medicine Bow National Forest are at least 5 years old. Similar information on brown trout aged with otoliths is not available.

Our models allow fisheries managers to assess the potential of streams to support quality-size brook trout or brown trout fisheries in southeast Wyoming mountains. The models can assist managers in identifying stream reaches where (1) habitat improvement could yield significant fisheries values, (2) stocking brown trout could enhance fisheries quality, or (3) more-restrictive harvests (i.e., size restrictions) could increase the abundance of quality-size fish. The models have not been tested with an independent data set, so their applicability to streams outside Medicine Bow National Forest is unknown. We encourage others to develop similar models elsewhere based on the same variables.

Acknowledgments
We thank Steven J. Kozel for the detailed data gathered during his graduate research; A. Bauer, A. Collotzi, L. Frary, M. Parsons, R. Schmal, and M. Wilcox of the U.S. Forest Service for their assistance; G. Anderson, M. Bock, A. Harris, J. Hart, D. Kane, J. Lessard, T. Mathison, S. Olsen, J. Peterson, and R. Sanchez for field assistance; and P. Eschmeyer, B. Esmoil, D. Harris, D. O'Shea, N. Schmal, and M. Young for their editorial comments. Support for the project was provided by the U.S. Forest Service.

References
Alexander, G. R. 1977. Consumption of trout by large predatory brown trout in the north branch of the Au Sable River. Michigan Department of Natural Resources, Fisheries Research Report 1855. Ann Arbor.
Anderson, R. O., and A. S. Weithman. 1978. The concept of balance for coolwater fish populations. American Fisheries Society Special Publication 11. Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream.

Transactions of the American Fisheries Society 113: 1–32.
Bisson, P. A., J. L. Nielsen, R. A. Palmerton, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low stream flow. Pages 62–73 in N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat. American Fisheries Society, Western Division. Bethesda, Maryland.
Bovee, K. D. 1982. A guide to stream habitat analysis using the in-stream flow incremental methodology. U.S. Fish and Wildlife Service FWS-OBS-82/26.
Buchanan, T. J., and W. P. Somers. 1969. Techniques of water-resources investigations of the United States Geological Survey. U.S. Government Printing Office, 2401-0498, Washington, D.C.
Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta). Canadian Journal of Fisheries and Aquatic Sciences 43:1970–1981.
Delury, D. B. 1951. On the planning of experiments for estimation of fish populations. Journal of the Fisheries Research Board of Canada 8:281–307.
Dixon, W. J., and six coauthors. 1986. BMDP statistical software manual. University of California Press, Berkeley.
Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.
Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. U.S. Forest Service General Technical Report PNLO-GTR-213.
Fausch, K. D., and R. J. White. 1981. Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220–1227.
Gosse, J. C., and W. T. Helm. 1981. A method for measuring microhabitat components for lotic fishes and its application with regard to brown trout. Pages 138–149 in N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.
Heggenes, J. 1988. Effects of short-term flow fluctuations on displacement of habitat use by brown trout in a small stream. Transactions of the American Fisheries Society 117:336–344.
Johnson, S. 1989. Factors influencing the size structure of brook trout populations in beaver ponds in southeastern Wyoming: management applications. Master's thesis. University of Wyoming, Laramie.
Kozel, S. J. 1987. Trends in habitat features and trout abundance among unaltered stream reaches on the Medicine Bow National Forest. Master's thesis. University of Wyoming, Laramie.
Kozel, S. J., and W. A. Hubert. 1987. Age estimates of brook trout from high-elevation Rocky Mountain streams using scales and otoliths. Northwest Science 62:216–219.
Kozel, S. J., and W. A. Hubert. 1989. Factors influencing the abundance of brook trout (Salvelinus fontinalis) in forested mountain streams. Journal of Freshwater Ecology 5:113–121.

Kozel, S. J., W. A. Hubert, and M. G. Parsons. 1989. Habitat features and trout abundance relative to gradient in some Wyoming streams. Northwest Science 4:175–182.

Lachenbruch, P. A. 1975. Discriminant analysis. Hafner Press, New York.

Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. Fish hatchery management. U.S. Fish and Wildlife Service, Washington, D.C.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service General Technical Report INT-221.

Raleigh, R. F. 1982. Habitat suitability index models: brook trout. U.S. Fish and Wildlife Service FWS/ OBS-82/10.24.

Raleigh, R. F., L. D. Zuckerman, and P. C. Nelson. 1984. Habitat suitability index models and instream flow suitability curves: brown trout. U.S. Fish and Wildlife Service FWS/OBS-82/10.71.

SPSS. 1986. SPSS® users guide, 2nd edition. SPSS, Chicago.

Vincent, R. E., and W. H. Miller. 1969. Altitudinal distribution of brown trout and other fishes in a tributary of the South Platte River, Colorado. Ecology 50:464–466.

Wescie, T. A. 1980. The WRRI trout cover rating method, development and application. University of Wyoming, Water Resources Research Institute, Water Resources Series 78, Laramie.

Wescie, T. A. 1982. The Snowy Range Observatory: an update and review. University of Wyoming, Wyoming Water Research Center, Water Resources Series 81, Laramie.

Wescie, T. A., C. M. Goertler, and C. B. Frye. 1987. Contribution of riparian vegetation to trout cover in small streams. North American Journal of Fisheries Management 7:151–153.

White, G. C., D. R. Anderson, K. P. Bornham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.

Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283–1291.