TROUT MORTALITY, MOVEMENTS, AND HABITAT SELECTION DURING WINTER IN SOUTH WILLOW CREEK, MONTANA

by

William Cecil Schrader

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APPROVAL

of a thesis submitted by

William Cecil Schrader

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

June 9, 1989 — Date

Robert G. White — Chairperson, Graduate Committee

Approved for the Major Department

Date

Head, Major Department

Approved for the College of Graduate Studies

Date

Graduate Dean

STATEMENT OF PERMISSION TO USE

VITA

William Cecil Schrader, son of William Lee and Carolee Mae Schrader, was born in Boulder, Colorado, on October 27, 1956. He attended Mustang High School, Mustang, Oklahoma, and Salida High School, Salida, Colorado; he received a General Education Diploma in 1975. He entered Colorado Mountain College, Leadville, in 1976 and received an Associate of Applied Science degree in Environmental Protection Technology in 1979. After enrolling at Montana State University in 1981, he received a Bachelor of Science degree in Biological Sciences in 1984. In the autumn of that year, he began graduate studies and research toward a Master of Science degree in Fish and Wildlife Management at Montana State University. He is married to Lynn Helen Kalberer of Hazelton, North Dakota, and they have one son, William Conrad Schrader.

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ABSTRACT

Few studies have assessed impacts of small hydropower development or provided information to recommend winter minimum instream flows. I examined trout populations, movements, and habitats selected during winter in three South Willow Creek study sections before small hydropower development. Streamflows were lowest during winter (November-March) both years of the study (1984-86). Overwinter decreases in rainbow trout (>75 mm) densities averaged 32% (range 18 to 45%) over both years and all sections; standing crops decreased 30% (range 11 to 36%). Changes in brook trout populations were less. During winter 1985-86, net distances moved by radio-tagged rainbow trout (>225 mm) ranged from 3 to 261 m. They selected high-quality pools with overhead cover, especially overhanging rock and surface turbulence, and avoided areas without cover. Selected depths were >45 cm and selected velocities were <30 cm/s; they avoided depths <15 cm and velocities >45 cm/s. Substrate selection was variable, but large substrate (>256 mm) was used for cover. Instream flows that provide maximum quantities of these selected habitats are recommended to sustain rainbow trout populations during winter.

INTRODUCTION

Recent federal and state economic incentives have stimulated development of renewable electrical energy and have led to increased interest in small hydropower (less than 5 megawatts) production. For example, since passage of the Public Utility Regulatory Policies Act in 1978 and the National Energy Security Act in 1980, the Federal Energy Regulatory Commission (FERC) has received over 6,100 hydropower applications; less than 3,000 applications had been submitted in the preceding 60 years (O'Connor 1985). In Montana, nearly 90 applications for small hydropower were filed with FERC in 1981 and 1982 (Leathe and Enk 1985). Although most of this interest has proved to be speculative, several projects in Montana have been licensed or exempted from licensing and are now operational.

Small hydropower development in Montana and elsewhere has resource management agencies, developers, and the public concerned about potential impacts to stream fisheries. This concern led to a symposium on small hydropower and fisheries in Colorado in 1985 (Olson et al. 1985). Graham (1985) noted that the potential for adverse impacts is partly dependent on the type of project, its mode of operation, and the status of the stream fishery.

Projects of primary concern in the Rocky Mountains are high-head diversions on small, high-gradient streams inhabited by salmonids (Graham 1985). This kind of project would impound and then divert water around a section of stream (often a kilometer or more) to create hydraulic head and run electrical turbines. Although streamflows in the section would be reduced throughout the year, relatively severe dewatering could occur during winter when power demand is largest and streamflows are smallest. Salmonid abundance may decrease with winter dewatering if winter habitat is limiting or if fish are already stressed by snow and ice, low water temperatures, or other harsh conditions.

Besides reduced streamflows, other potential impacts include (Rochester et al. 1984; Graham 1985; Leathe and Enk 1985):

1. Direct mortality from turbines.
2. Barriers to migration.
3. Increased fine sediment deposition.
4. Altered flow and temperature regimes.
5. Excessive streambed scouring by ice.
6. Gas supersaturation.

These concerns are compounded by lack of information (Sale 1985). Little research has been published describing the individual or cumulative impacts of small hydropower development. This is especially true with regard to winter dewatering. Resource agencies are responsible for recommending minimum instream flows to protect stream fisheries, and they often rely on information about habitats selected by fish (e.g., Instream Flow Incremental Methodology-Bovee and Cochnauer 1977; Bovee and Milhous 1978; Bovee 1982, 1986). Yet habitat selection information for salmonids, though generally known for summer and fall (Bovee 1978; Raleigh et al. 1984), is lacking for winter (Wesche and Rechard 1980). This lack of information may be particularly significant if salmonid habitat requirements change seasonally (Campbell and Neuner 1985; Cunjak and Power 1986).

Lotic ecosystem response to modified flow regimes is complex and not well understood for any season (Sale 1985). Flow alterations can result in changes not only in physical habitat availability but also in water chemistry and temperatures, nutrient cycling, biomass and energy relationships, and fish population and community dynamics.

This study was conducted at South Willow Creek, Montana, during 1984-86. My objectives were to (1) provide baseline information on stream physical conditions and trout population parameters, especially winter mortality and movements, before small hydropower development; and (2) quantify winter habitats selected by adult rainbow trout. "Winter" is defined as that period when water temperatures were less than 4C (November through March).

STUDY AREA

The study area was in South Willow Creek, Montana (Figure 1), at and around a site where a small hydropower project began operating in 1986. Starting at a diversion dam immediately below the confluence of Potosi Creek (Figure 2), water from the mainstem is piped 700 m downstream, run through a turbine, and returned to the stream channel. Montana Department of Fish, Wildlife, and Parks (MDFWP) recommends that a minimum flow of 0.28 m^3/s remain in the bypassed channel throughout the year (Fred Nelson, MDFWP, personal communication).

South Willow Creek is a drainage of the Tobacco Root Mountains in southwestern Montana (Figure 1). The stream originates at the confluence of its north headwater fork, which flows from Granite Lake (elevation 2719 m), with its south fork, which flows from Bell Lake (2682 m). From its headwaters, South Willow Creek flows 22 km northeast, joins North Willow Creek, and forms a braided inlet to Harrison (Willow Creek) Reservoir. Willow Creek drains into the Jefferson River at the town of Willow Creek, Gallatin County, Montana.

The South Willow Creek drainage basin is about 90 km^2 and ranges in elevation from 1609 to 3228 m. Average stream

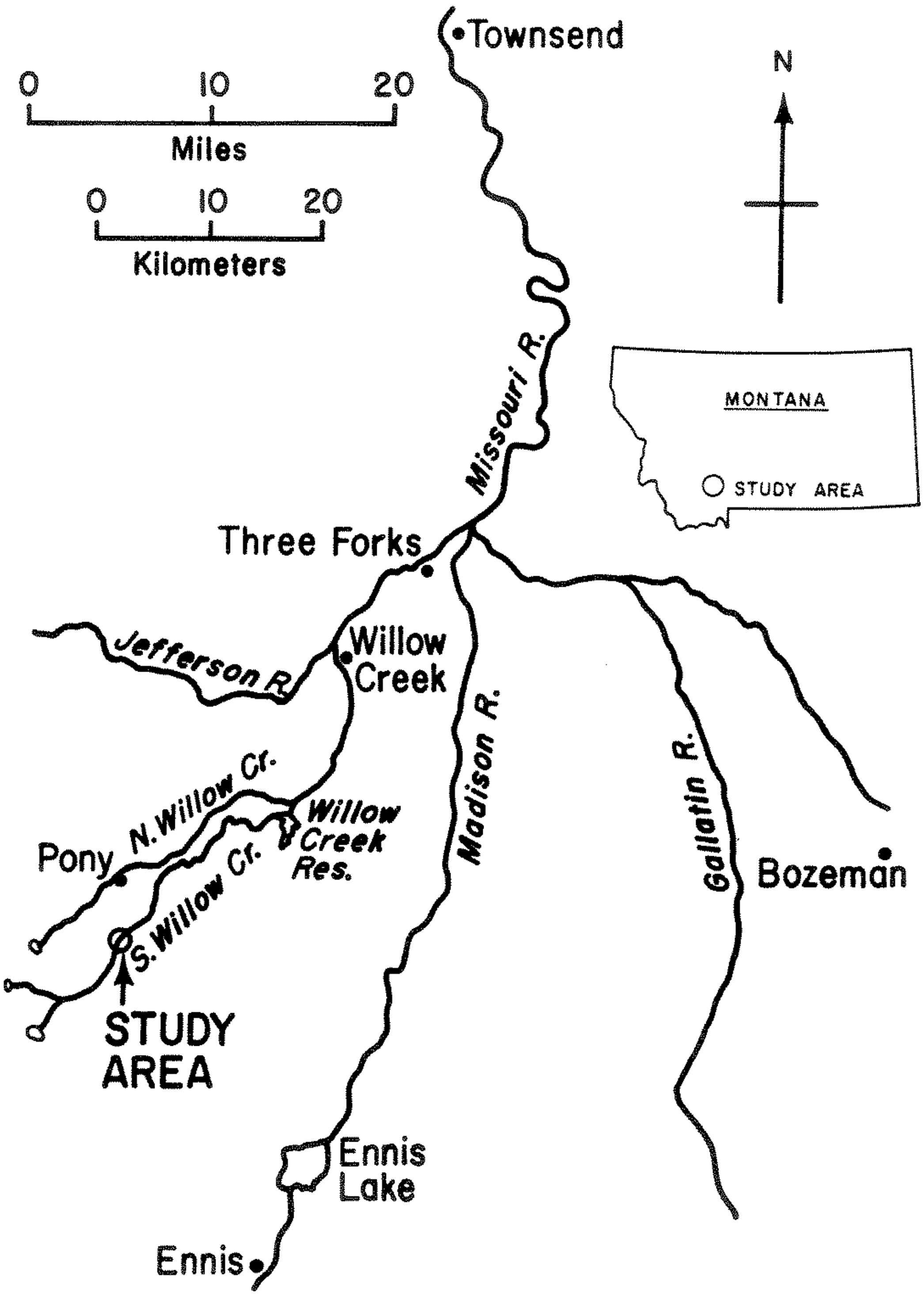

Figure 1. Location of the study area, South Willow Creek, Montana.

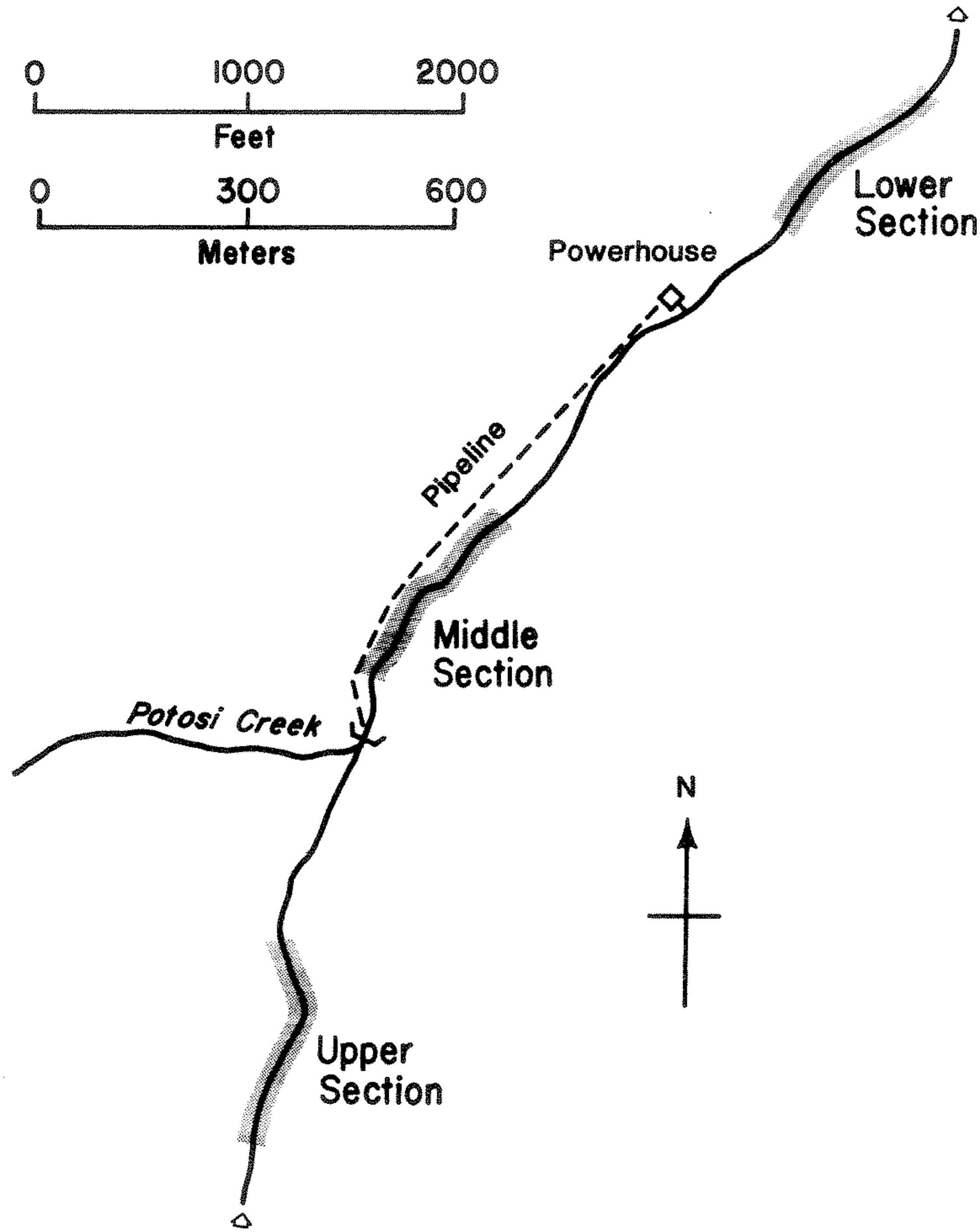

Figure 2. Location of the study sections in relation to the small hydropower project, South Willow Creek, Montana.

gradient above the study area is about 4%. Major tributaries to the mainstem are Rock, Camp, and Potosi Creeks; the last is influenced by thermal hot springs. No flow or temperature records exist for the mainstem or any of its tributaries. Some manipulation of flows for irrigation occurs at the Bell Lake outlet during summer.

The study area is about 14 km downstream from the headwater lakes (7 km below the joining of the forks) and 6 km south of Pony, Madison County, Montana, in Section 6, T3S, R2W (Figure 1). At 1829 m elevation, South Willow Creek is a third order stream at the site. MDFWP considers the study area to be representative of small, high-gradient mountain streams being developed for small hydropower production in Montana.

Three study sections (Figure 2) were chosen in fall, 1984, and surveyed and mapped in spring, 1985. The upper and lower sections are controls and are upstream and downstream of the partially dewatered middle section. Sections were chosen based on within-section habitat diversity, between-section habitat similarity, and ease of accessibility.

The lower and middle sections have similar habitats and represent typical high-gradient areas (>4%) chosen for small hydropower development (Table 1). These sections are characterized by rapids and cascades with backwater and pocketwater pools. In contrast, the upper section is of

Table 1. General characteristics of the three study sections, South Willow Creek, Montana. Measurements were made shortly after ice-out, April 13 and 14, 1985, following procedures of Orth (1983).

	Upper	Middle	Lower
Slope (%)	1.2	4.3	4.0
Channel center length (m)	294	307	300
Mean wetted width (m)	6.9	6.6	6.9
Surface area (ha)[a]	0.204	0.203	0.206
Mean water depth (cm)	19	29	22
Mean water velocity (cm/s)[b]	37	51	45
Streamflow (m^3/s)	0.680	0.850	0.708

[a]Product of channel center length and mean wetted width.
[b]Taken at 0.6 depth.

lower gradient (1.2%) and mostly riffle with some pools. Streambed substrate is primarily boulders (>256 mm) in the lower and middle sections and cobble (65 to 256 mm) in the upper section. Riparian vegetation bordering all sections is predominately willow (*Salix* spp.) and alder (*Alnus* spp.) associated with lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*). Riparian areas were not grazed by livestock during the study.

Logging, mining, livestock grazing, and recreation are the primary land uses above the study area. Camping and fishing are the major recreational activities. The Beaverhead National Forest maintains a campground 3 km upstream from the study area, and fishing pressure there in 1975-76 was estimated to be 55 angler-days per 10 km annually (George Holton, MDFWP, personal communication). Though the upper 60% of the stream lies within the National Forest, much of the adjacent riparian land (including the upper and middle study sections) is privately owned. Few fishermen were observed in the study area during summer, and the stream was closed to fishing from November to May.

South Willow Creek has been managed for wild trout since 1973 when the last hatchery plant occurred; catchable rainbow trout (Oncorhynchus mykiss, formerly Salmo gairdneri) were stocked in the lower part of the stream in the summer of that year (George Holton, MDFWP, personal communication). Fingerling brook trout (Salvelinus fontinalis) were last planted at unknown locations on the stream in 1951, and cutthroat trout (Oncorhynchus clarki, formerly Salmo clarki) were last planted in 1936. In addition to these species, brown trout (Salmo trutta) and mottled sculpins (Cottus bairdi) are present. Hybrid rainbow x cutthroat trout are common, so much so that the likely hybrid is referred to as "rainbow trout" in this writing and cutthroat trout are ignored.

METHODS

Stream Physical Conditions

Stream discharge and temperature were monitored at the study area before small hydropower development. General ice conditions were noted and photographed but were not measured.

Discharge was monitored using a staff gage placed immediately above the middle section but below the confluence of thermally-influenced Potosi Creek. I placed the gage below the confluence to reduce the probability of icing during cold weather; ice dislodged gages that had been installed in the other sections. Water stage was recorded about once each week beginning in December, 1984. To calibrate the gage, a range of streamflows was measured using standard United States Geological Survey techniques (Buchanan and Sommers 1969; Platts et al. 1983) and then regressed against water stage using a logarithmic least-squares procedure (Nelson 1984; Herschey 1985). I estimated discharge from weekly stage readings using the fitted regression equation (Figure 3).

Water temperature was monitored in the upper section and immediately above the middle section using submersed continuous-recording Peabody Ryan thermographs, accurate to

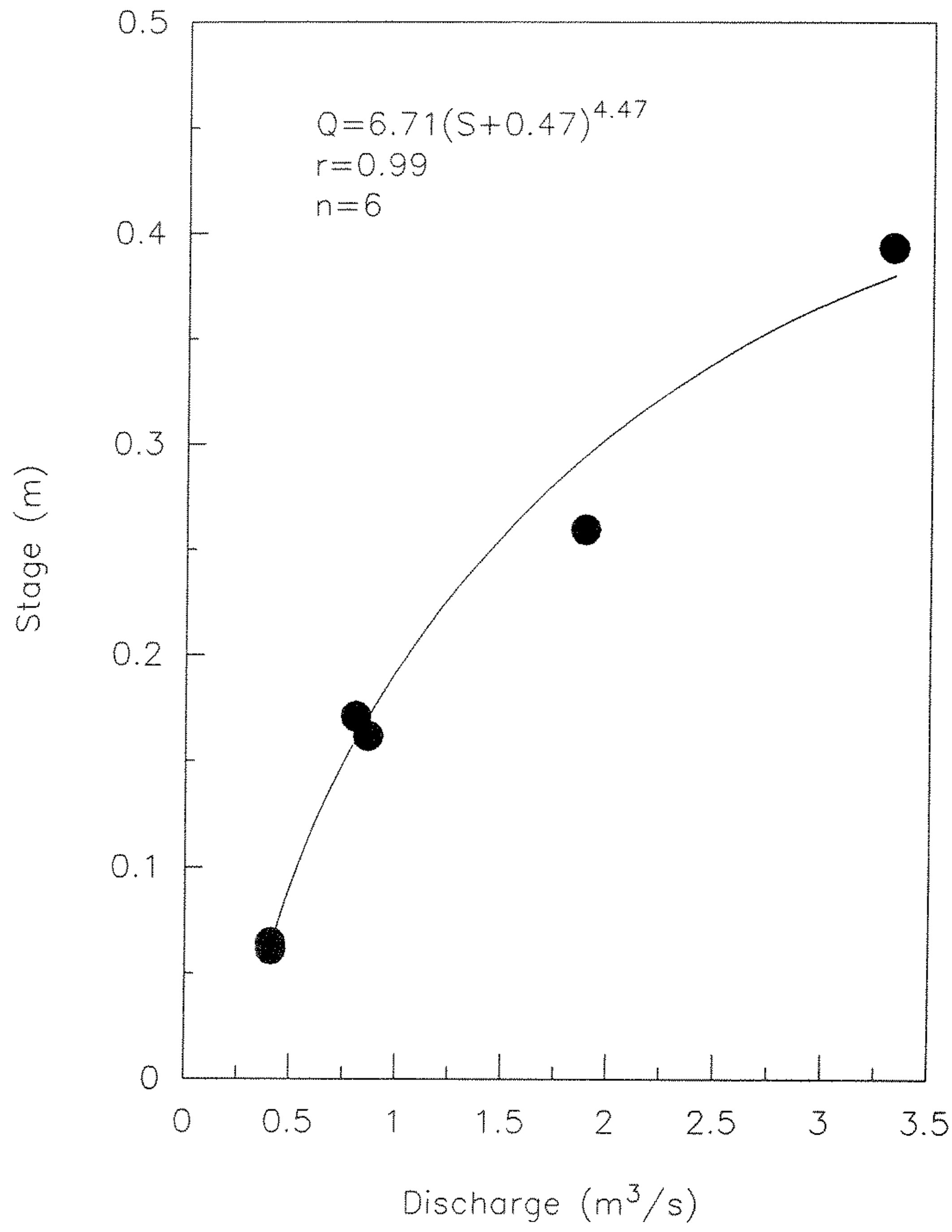

Figure 3. Stage-discharge rating curve for the staff gage near the middle section, South Willow Creek, Montana. Q = predicted discharge and S = stage in the fitted regression equation.

$\pm$ 0.6 C and 3 min/d. Thermographs were calibrated and installed in September, 1984, and were frequently checked for accuracy using a hand-held thermometer. I did not place a thermograph in the lower section due to the probability of icing. Air temperature data were obtained from the national weather station at nearby Pony, Montana (elevation 1700 m).

Trout Populations

I collected baseline information on trout populations by electrofishing each study section during early October, 1984, late April and late September, 1985, and late March, 1986. Fish were captured using streambank direct-current electrofishing equipment. Though sections were not blocked at each end, I assumed fish would not move beyond natural habitat boundaries. I allowed 7 d or more for fish to redistribute themselves between marking and recapture runs.

After capture, trout were anesthetized with tricaine methane-sulfonate (MS-222), identified, weighed to the nearest 5 g, and measured to the nearest millimeter (total length). Rainbow and brook trout were fin-clipped for population estimates. Color-coded, numbered Floy fingerling tags were attached to the anterior base of the dorsal fin of rainbow and brook trout >100 mm during spring and fall, 1985, to evaluate movement.

Several parameters were used to describe trout populations over time and space. As unbiased population estimates could not always be made for brook and brown trout, I estimated relative abundance of each trout species using proportions of all trout captured. Size structures were estimated using length frequency distributions of unmarked trout captured. Chapman's modification of Peterson's mark-recapture formula was used to estimate abundance (Ricker 1975):

$$N = \left[\frac{(M + 1)\ (C + 1)}{(R + 1)} \right] - 1$$

where N = estimated number; M = number of fish marked on the first run; C = total number of fish captured on the second run; and R = number of marked fish recaptured on the second run. Seber's formula was used to estimate the variance (Seber 1973):

$$s^2 = \frac{(M + 1)\ (C + 1)\ (M - R)\ (C - R)}{(R + 1)^2\ (R + 2)}$$

where s^2 = estimated variance, and other variables are as above. A Fulton-type condition factor was calculated for individual fish using the formula (Anderson and Gutreuter 1983):

$$K = \frac{W}{L^3} \times 10^5$$

where K = condition factor; W = weight in g; and L = total length in mm. Condition factors of fish >125 mm were then averaged.

I assumed that fish in each study section were a distinct population, and that each population during each sampling period was geographically and demographically closed (Otis et al. 1978; White et al. 1982). I further assumed that no marks were lost during the sampling period, that all marks were recognized and recorded correctly, and that marked and unmarked fish mixed at random.

Estimates of abundance, biomass, and average condition factor were calculated using a computer program described by Vincent (1971, 1974). Estimates of density were derived from abundance estimates, as was standing crop from biomass estimates, using water surface areas of each section.

Winter Movements and Habitat Selection

Radiotelemetry

During winter, 1985-86, I used radiotelemetry to monitor adult rainbow trout movements and their use of habitats. Fish >225 mm were collected in each study section with a Coffelt BP-2 backpack electrofishing unit, anesthetized in a 0.004% MS-222 solution, weighed, and measured. The radio transmitter was surgically implanted using standard procedures reported for fish of similar size (Hart and Summerfelt 1975; Wichers 1978; Winter 1983;

Chisholm 1985). I practiced my techniques using cutthroat trout at the U.S. Fish and Wildlife Service Fish Technology Center, Bozeman, Montana.

The procedure involved inverting fish in a V-shaped trough with the head and gills submerged in anesthetic. A 30 mm incision was made through the ventral abdominal wall immediately anterior to the pelvic girdle. After inserting the transmitter into the body cavity, the incision was closed with four or five stitches using a 1/2-curved cutting needle and non-absorbable chromic 4-0 collagen suture. Water was kept out of the incision, and instruments were kept clean but not sterile. Antiseptic was not used. Time in surgery was generally less than 10 min. Opercular movement was monitored and anesthetic strength adjusted accordingly.

Immediately after surgery, radio-tagged trout were fin-clipped, placed in holding cages in the stream, and given 24 h for recovery. All fish regained their equilibrium within 15 min and appeared active when released a day later.

Sixteen adult rainbow trout (6 males and 10 females) were radio-tagged on November 16 and 17, 1985. Five trout were released in the upper section, five in the middle section, and six in the lower section. One fish released in the lower section had originally been captured in the upper section.

Radiotelemetry equipment was manufactured by Custom Telemetry and Consulting, Athens, Georgia. The beeswax-coated transmitters had an expected life of 90 d, magnetic on-off reed switches, and enclosed loop antennas. Individual frequencies were unique and ranged from 30.046 to 30.246 MHz; pulse rates ranged from 26 to 40 pulses per min (Table 2). The transmitters were capsule-shaped and approximately 26 mm long by 15 mm in diameter. Weights in air ranged from 4.57 to 4.94 g and from 1.6 to 3.3% of the fish's body weight.

The receiver operated on the 30 MHz band with 12 operating channels and a frequency range of 30.000 to 30.250 MHz. A hand-held bi-directional loop antenna (19.0 by 19.7 cm) was connected to the receiver with 4.88 m of coaxial cable. Headphones were used with the receiver when tracking fish.

All equipment was checked and calibrated before being used for data collection. Accuracy and precision of transmitter locations were determined for a single transmitter located on the ground and in water with and without ice cover. Transmitters had an effective detection range of about 100 m and appeared unaffected by snow and ice. All transmitters were operated for 48 h before being implanted.

Table 2. Characteristics of radio transmitters used to evaluate adult rainbow trout winter habitat use in South Willow Creek, Montana.

Number	Frequency (MHz)	Pulse rate (ppm)	Length (mm)	Diameter (mm)	Weight (g)	Percent fish weight	Operating time (d)
1	30.046	27	25	14	4.90	2.6	--[a]
2	30.059	36	27	15	4.73	2.3	58
3	30.067	36	25	15	4.72	3.1	87
4	30.169	40	25	15	4.67	2.1	100
5	30.171	37	26	15	4.73	2.9	86
6	30.179	37	27	16	4.88	2.0	64
7	30.189	36	27	14	4.60	2.6	78
8	30.196	34	26	13	4.73	2.6	87
9	30.209	39	27	15	4.94	3.3	65
10	30.216	35	28	14	4.81	2.3	85
11	30.218	40	27	14	4.57	2.0	100
12	30.227	26	26	15	4.76	3.1	87
13	30.230	39	26	15	4.75	2.5	100
14	30.238	34	26	15	4.72	1.6	80
15	30.239	36	26	15	4.83	3.2	80
16	30.246	26	26	14	4.59	2.6	106

[a] Transmitter frequency dropped below range of receiver detection.

<u>Movements and Habitat Use</u>

I attempted to locate all radio-tagged trout at least once a week after releasing them. About half of the locations were made during the day (1000 to 1430 h); the other half were made during evening (1430 to 2400 h). I held the antenna over the surface of the ice or water and used the point of maximum signal strength to define a fish's location. To minimize frightening the fish, I attached the antenna to the end of a 4 m pole and searched areas while wading upstream. I often saw the fish whose signal was being received.

Fish locations were marked with a weighted buoy and later plotted on a detailed map of each study section. Maps were constructed using on-shore baselines parallel to the stream channel. In addition, 30 transects, 10 per study section, were established 27.4 m apart and perpendicular to the channel. After surveying baselines and transects, general habitat features were used to help construct the maps.

Habitat variables were measured within 24 h after marking fish locations and included:

(1) Primary habitat type within a 30 cm radius of the fish's location. Five categories were used (Bisson et al. 1981): rapid, riffle, glide, pocket water, and pool. Pools were rated according to Platts et al. (1983) and ranged from one (low quality) to five (high quality).

(2) Total depth of the water column. Depths were measured to the nearest 3 cm with a top-setting rod and grouped into 15 cm categories. Herein, "depth" refers to total depth.

(3) Average water velocity (at 0.6 depth). They were measured to the nearest 3 cm/s with a Marsh/McBirney current meter and grouped into 15 cm/s categories. Herein, "velocity" refers to average water velocity.

(4) Major overhead cover type within a 30 cm radius of the fish's location. Seven categories were used (Bisson et

al. 1981): organic debris (rootwads and small and large debris); overhanging vegetation (live or dead plant material within 1 m of the water surface); undercut bank; moss (*Fontinalis* spp.); turbulence (assigned if the bottom of the top-setting rod could not be seen due to the presence of air bubbles in the water column); overhanging rock; and no cover. In cases where two or more cover types were present, I chose the one I thought to be most important to the fish.

(5) Predominant substrate type within a 30 cm radius of the fish's location. Four categories were used (Platts et al. 1983; Bovee 1986): sand/silt (< 2 mm); gravel (2 to 64 mm); cobble (65 to 256 mm); and boulder (> 256 mm).

Habitat Availability

Habitat availability was estimated in each section during late winter, 1986-87, immediately after ice-out. Streamflows were lowest of the year and were similar to those during which habitat use data were collected. I assumed structural and hydraulic characteristics of the stream channel had not changed between years.

To quantify available habitat, I used a random-point, non-mapping technique described by Marcum and Loftsgaarden (1980). Stream areas used by radio-tagged fish were divided into a grid with points one pace apart (about 60 cm). A separate grid encompassed each study section. Points within each grid were then randomly sampled to evaluate habitat variables (as described above).

Although this technique is useful in evaluating highly complex areas where habitat variables are difficult or impossible to map (e.g. depth and velocity), it does not provide absolute measurements for those variables. Thus, point estimates and their simultaneous confidence intervals were made according to Neu et al. (1974) as modified by Byers et al. (1984). Habitat use data were analyzed similarly. I concluded fish were selecting or avoiding certain habitats when the two intervals did not overlap. Other statistical analyses were performed according to Zar (1974) using MSUSTAT (Lund 1985).

RESULTS

Stream Physical Conditions

Discharge

Estimated discharge in the middle section (Figure 4) was lowest during November to March and highest during May and June. After peak snowmelt and rainfall in the spring, flows gradually declined through late summer and fall. Flows ranged from 0.37 to 4.43 m^3/s in 1985 and from 0.37 to 10.68 m^3/s in 1986.

Measured discharge was similar in the three sections (within 0.20 m^3/s) during winter, early spring, and late summer (Table 3). Discharge was always greatest, however, in the middle section, followed by the lower and upper sections. Flows in Potosi Creek were estimated to be from 0.03 to 0.20 m^3/s during winter, early spring, and late summer and provided the added discharge to the middle and lower sections.

Temperature

Average monthly maximum and minimum water temperatures in the upper and middle sections (Figure 5) were lowest during November to March and highest during July and August. Average maximum temperatures ranged from 2 C in December to

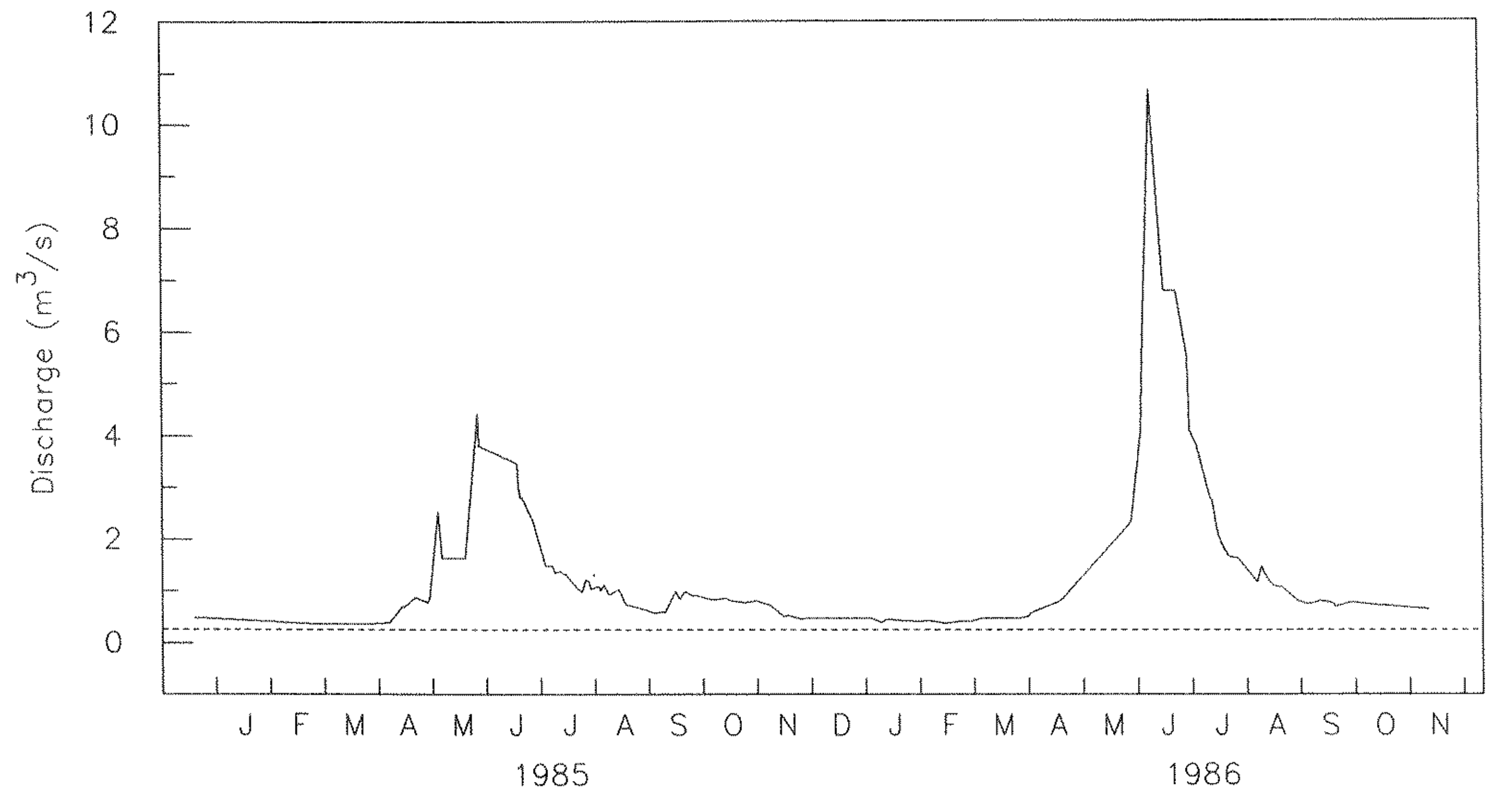

Figure 4. Point estimates of discharge and interpolations over time in the middle section, South Willow Creek, Montana (n=118). Dashed line is MDFWP's minimum flow recommendation (0.28 m^3/s) as determined by the wetted perimeter method.

Table 3. Measured discharge (m^3/s) in the three study sections, South Willow Creek, Montana.

Date	Upper	Middle	Lower
1/27/85	0.35	0.40	----
2/2/85	----	0.41	----
4/14/85	0.66	0.86	0.68
5/18/85	1.46	1.88	----
6/16/85	2.92	3.31	----
8/6/85	0.66	0.80	0.71

13 C in August. Average minimum temperatures ranged from 1 C in December to 8 C in August.

Average monthly water temperatures and seasonal temperature patterns were similar between the upper and middle sections (Figure 5). Small differences between the two sections were attributed to sampling error; point temperatures measured with a hand-held thermometer did not differ between any section (including the lower one) on any day sampled.

Although water temperatures were similar in all three sections, ice conditions were different. Anchor ice was common during very cold weather (<-18 C) in the upper and lower sections, but was never observed in the middle section. Surface ice did form in the middle section, however, and was common in all sections from October to

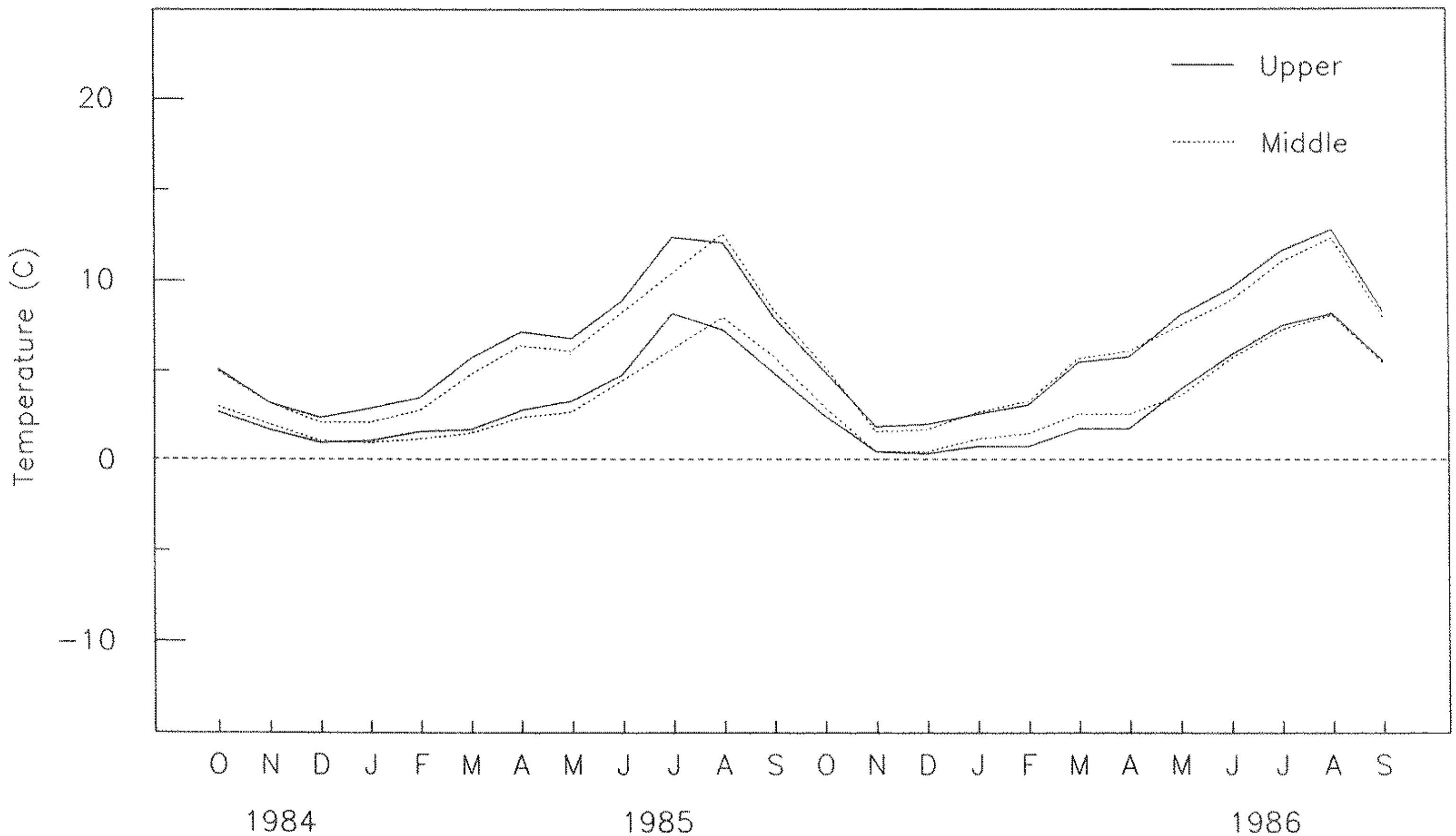

Figure 5. Average monthly maximum and minimum water temperatures and interpolations over time in the upper and middle sections, South Willow Creek, Montana.

April.

Patterns of average monthly maximum and minimum air temperatures were similar but more extreme than water temperatures (Figure 6). Air temperatures were lowest during November to March and highest during June to August. With the exception of an unusually cold November, temperatures during the winter of 1985-86 were warmer than the winter of 1984-85. Average minimum air temperatures <0 C occurred during 7 months of each year.

Trout Populations

Species Composition and Relative Abundance

Rainbow trout were the predominant species in the study area, followed by brook and brown trout (Figure 7). Overall, about 70% of the trout captured were rainbow, 27% were brook, and 3% were brown. There was no significant difference in these proportions over the study period ($p>0.5$, chi-square 4x3 contingency table).

Relative abundance of trout species differed between sections but, for any given section, remained similar throughout the study period (Figure 7). Proportions of rainbow to brook to brown trout captured were roughly 50:45:5 in the upper section, 75:23:2 in the middle section, and 85:13:2 in the lower section. Differences in relative abundance between sections were highly significant for any given season of sampling ($p<0.0001$, chi-square 3x3

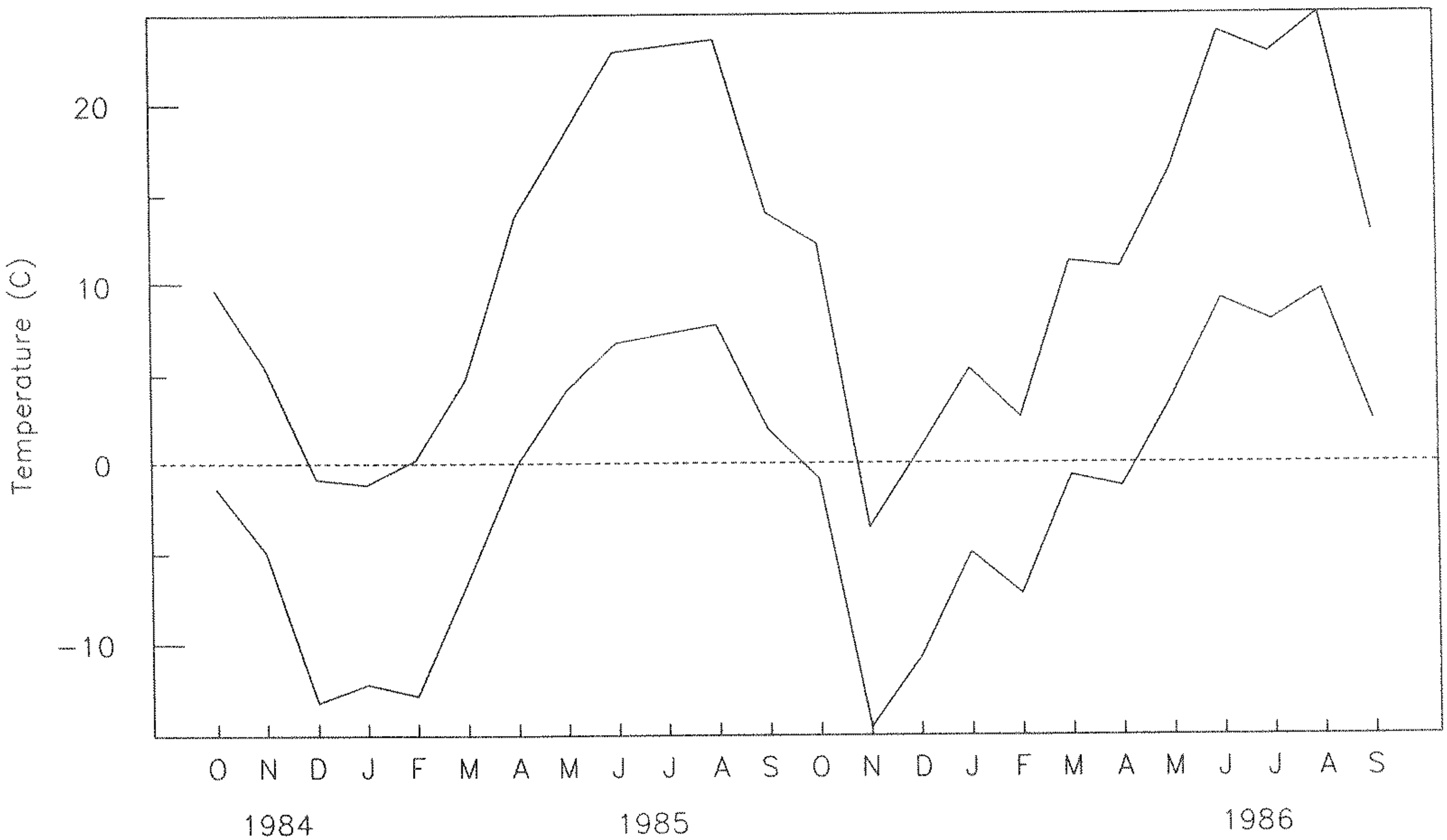

Figure 6. Average monthly maximum and minimum air temperatures and interpolations over time at Pony, Montana (NOAA, 1984-86).

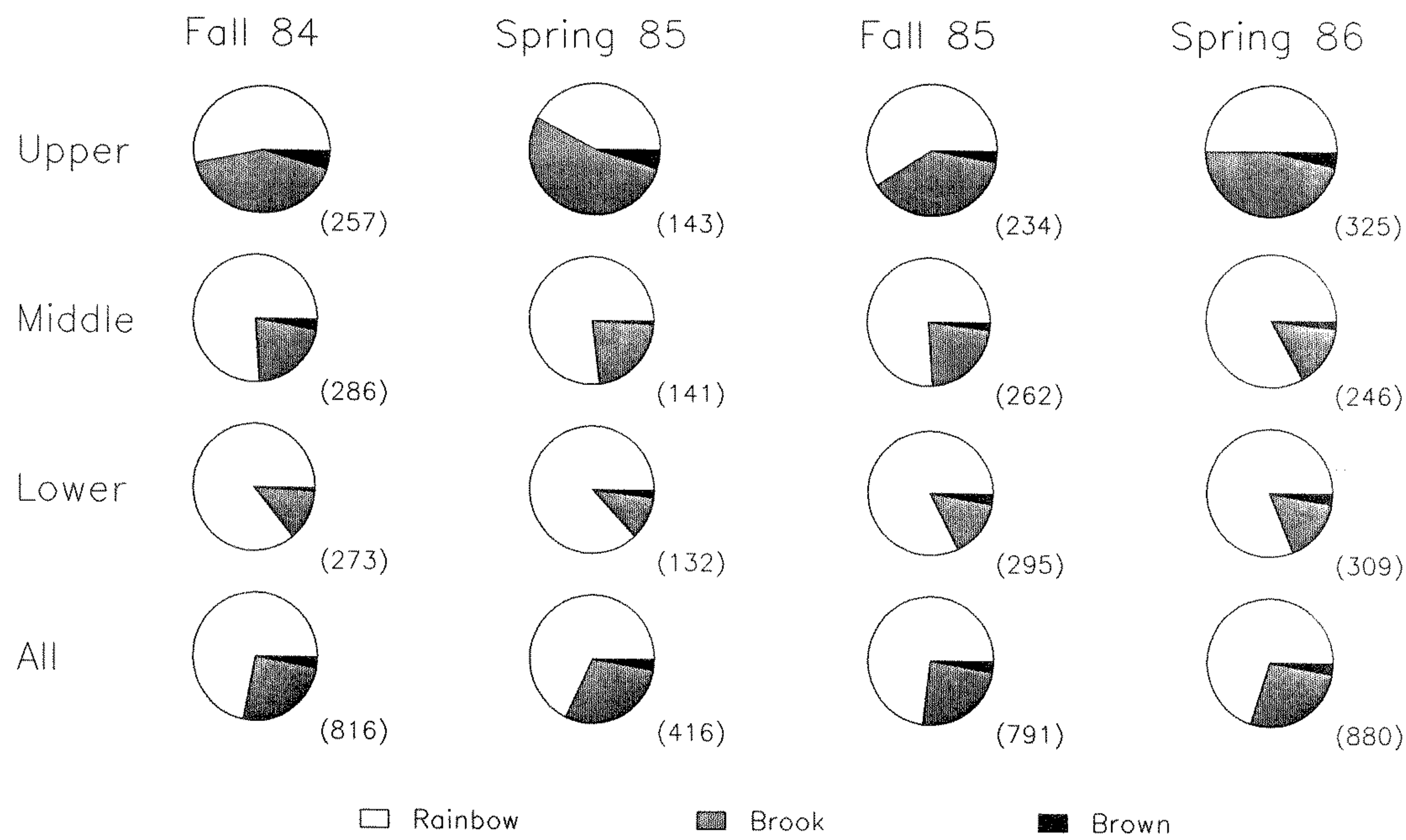

Figure 7. Relative abundance of trout species captured in the three study sections and all sections combined, South Willow Creek, Montana. Sample sizes are in parentheses.

contingency tables). For any given section, however, there was no significant difference over the study period ($p>0.05$, chi-square 4x3 contingency tables).

Size Structure

Because water temperatures were similar (Figure 5), and because rainbow trout lengths were distributed similarly between sections (Figures 20-22, Appendix A), all sections were combined to generate composite length frequency distributions by sampling period (Figure 8). Brook trout were also combined (Figure 9).

Although I did not age fish, modal peaks in these composite distributions may indicate average sizes-at-age. For rainbow trout captured in the fall, modal peaks of 55 mm might represent young-of-the-year (YOY) fish, 105 mm likely indicate age I fish, and 145 to 155 mm probably represent those age II and older (Figure 8). Modal peaks of 65, 115, and 165 mm in the spring might indicate average overwinter growth of these cohorts.

For brook trout captured in the fall, modal peaks of 65 mm might represent YOY fish, 115 mm likely indicate age I fish, and 145 to 155 mm probably represent those age II and older (Figure 9). Modal peaks of 75, 125 to 135, and 165 to 175 mm in the spring might indicate their average overwinter growth.

Captured rainbow trout ranged in size from 40 to >300

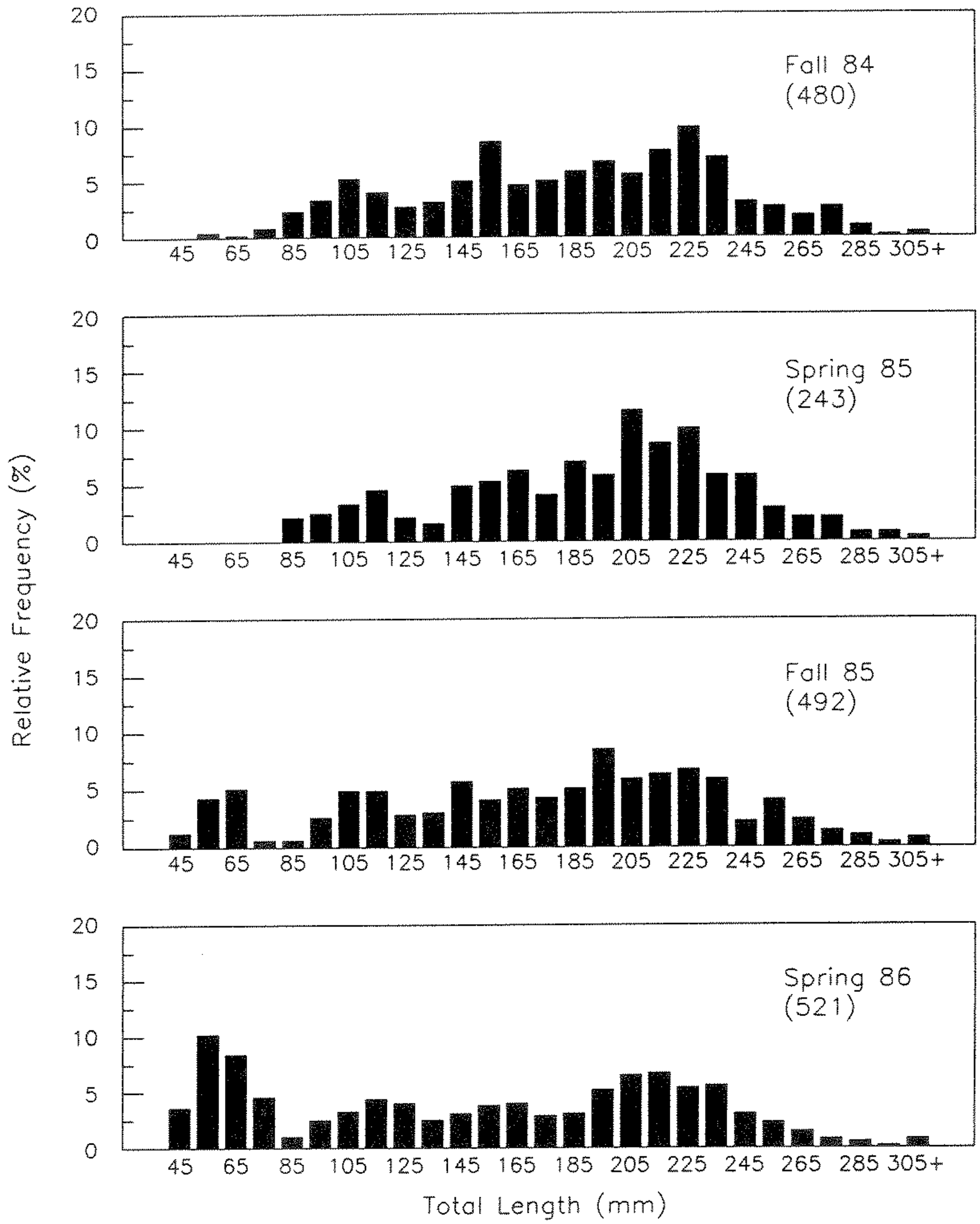

Figure 8. Length frequency distributions of rainbow trout captured in all sections combined, South Willow Creek, Montana. Sample sizes are in parentheses.

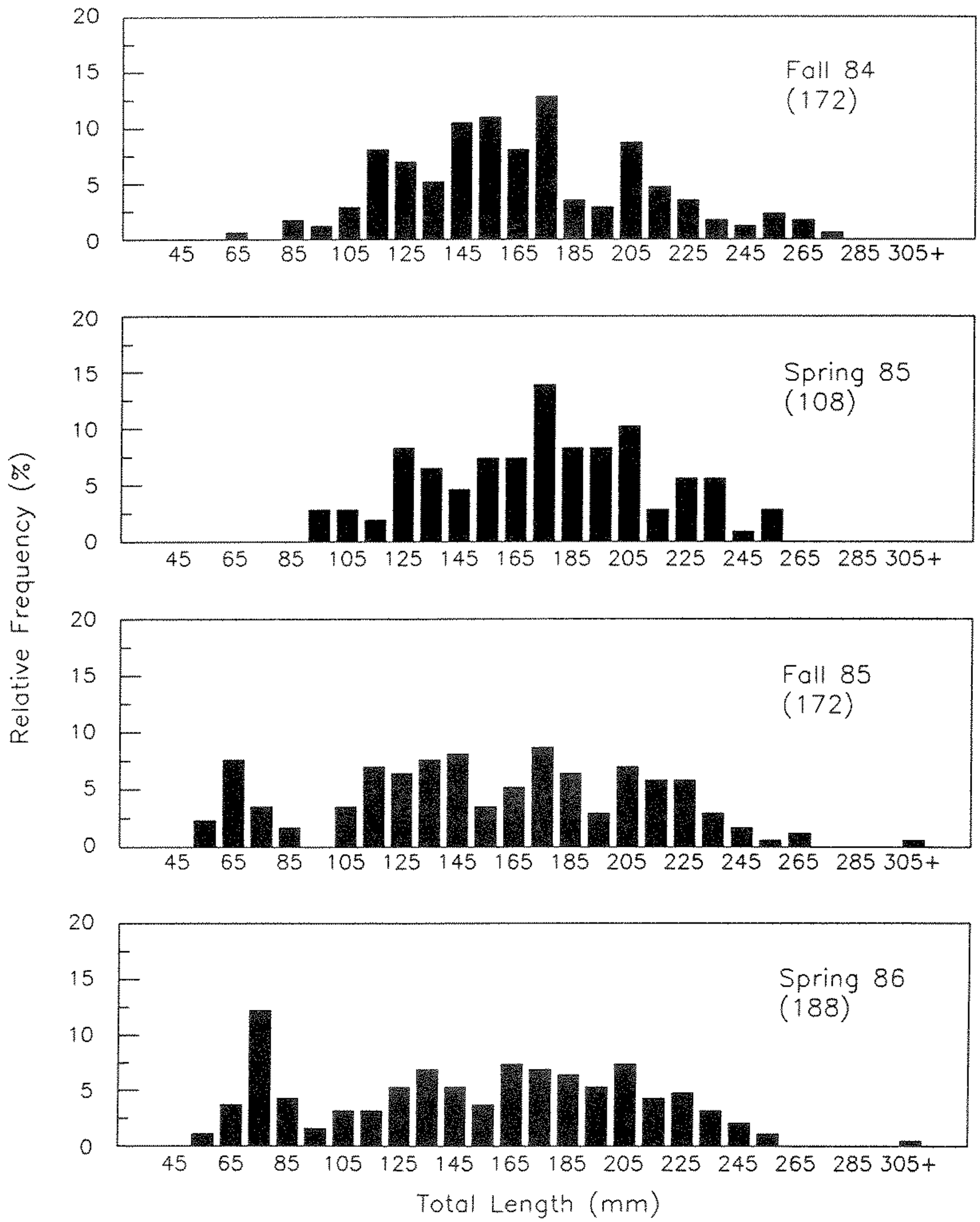

Figure 9. Length frequency distributions of brook trout captured in all sections combined, South Willow Creek, Montana. Sample sizes are in parentheses.

mm (Figure 8); brook trout ranged from 50 to >300 mm (Figure 9). Less than 2% of either species exceeded 300 mm. YOY rainbow (<80 mm) and brook (<90 mm) trout were poorly represented in fall, 1984, and spring, 1985. Less effort was expended to sample YOY fish during fall, 1984, and high discharge hampered sampling efforts during spring, 1985. Though brown trout were uncommon in the study area, they were often the largest fish found; some measured >400 mm total length.

Density and Standing Crop

Rainbow trout (>75 mm) densities were highest in the lower section, intermediate in the middle section, and lowest in the upper section during each season of the study (Figure 10). Over all seasons, densities ranged from about 980 to 2100 fish/ha in the lower section, 770 to 1350 fish/ha in the middle section, and 520 to 850 fish/ha in the upper section. Except for spring, 1985, when point estimates and sample sizes were small, confidence intervals (80%) rarely overlapped between sections.

Rainbow trout (>75 mm) standing crops were also highest in the lower section but were about equal in the middle and upper sections during each season of the study (Figure 11). Over all seasons, standing crops ranged from about 90 to 150 kg/ha in the lower section, 60 to 90 kg/ha in the middle section, and 50 to 90 kg/ha in the upper section.

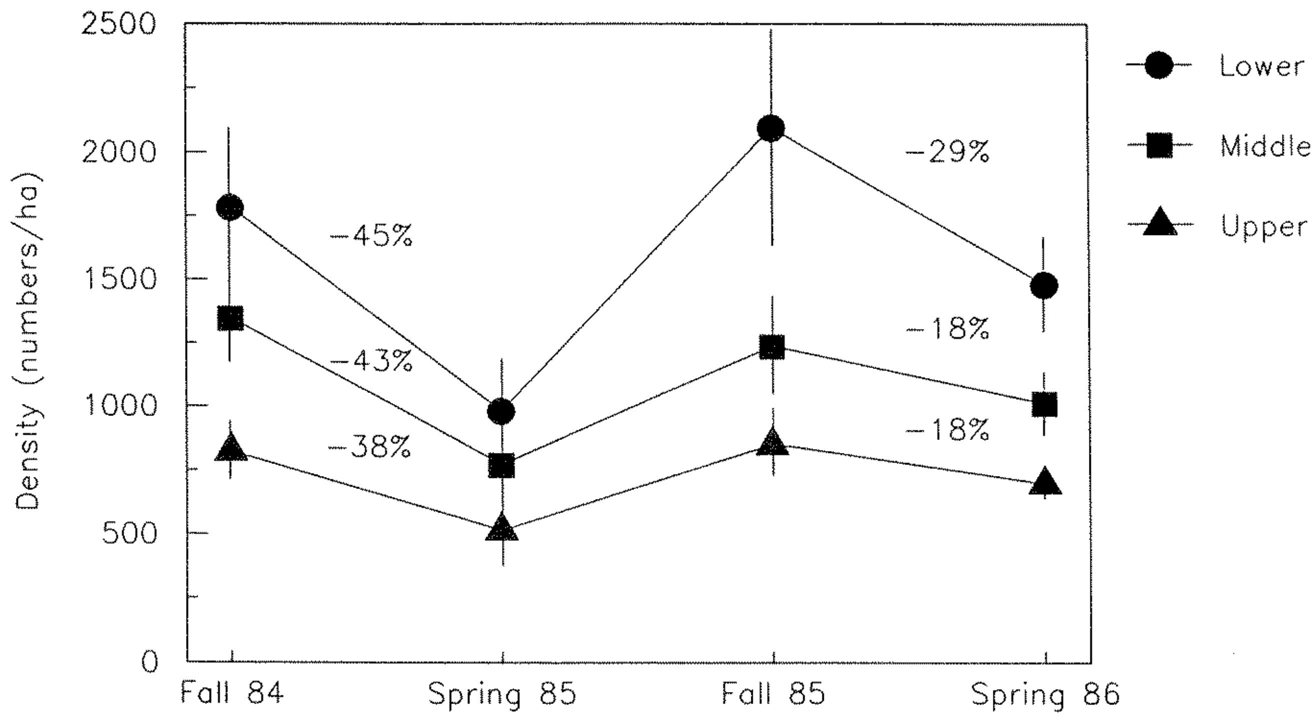

Figure 10. Point estimates and confidence intervals (80%) of rainbow trout (>75 mm) densities in the three study sections, South Willow Creek, Montana. Percentage figures are changes from fall to spring.

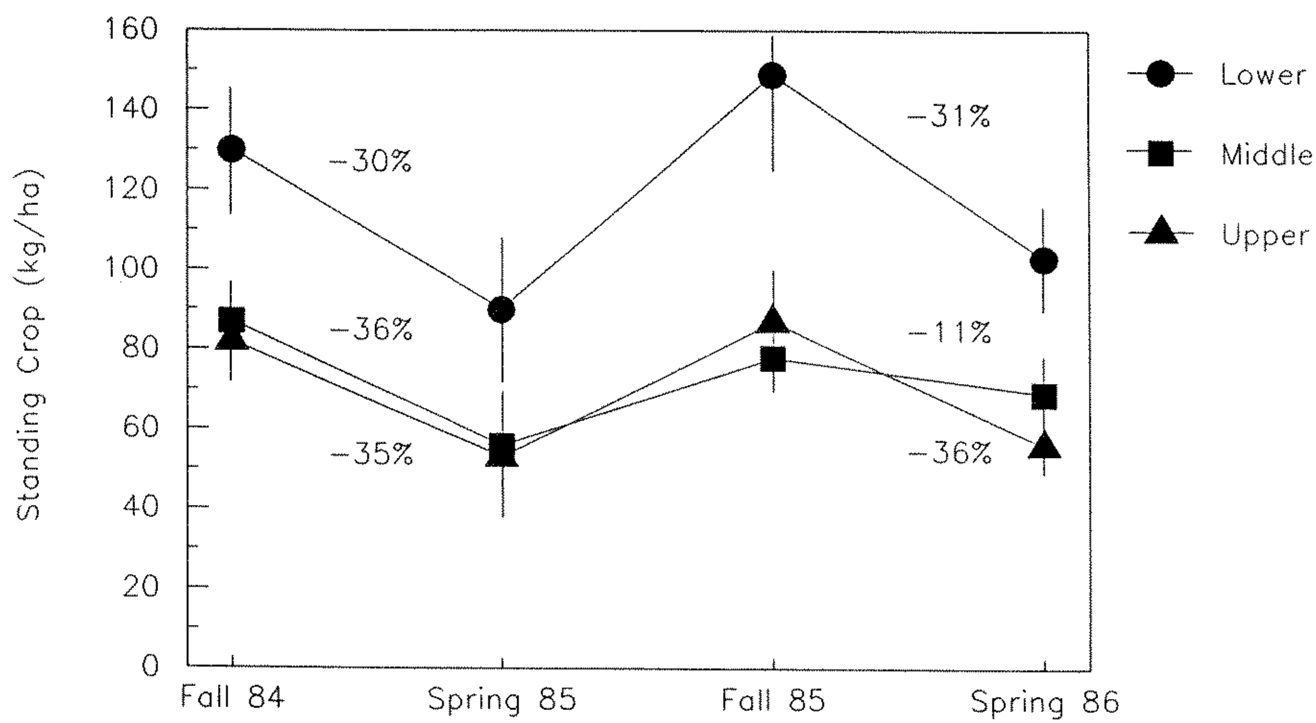

Figure 11. Point estimates and confidence intervals (80%) of rainbow trout (>75 mm) standing crops in the three study sections, South Willow Creek, Montana. Percentage figures are changes from fall to spring.

Confidence intervals (80%) did not overlap between the lower and middle sections, nor between the lower and upper sections, during any season of sampling. They always overlapped between the middle and upper sections.

Rainbow trout (>75 mm) densities (Figure 10) and standing crops (Figure 11) were highest in the fall and lowest in the spring in all sections during both years of the study. Although densities decreased an average 32% (range 18 to 45%) over both winters, and standing crops decreased an average 30% (range 11 to 36%), 80% confidence intervals sometimes overlapped between successive seasons. Both densities (Table 10, Appendix B) and standing crops (Table 11, Appendix B) increased during summer, 1985. In general, levels observed during fall, 1985, were similar to those of fall, 1984. Levels observed during the two spring periods were also similar.

Estimates of brook trout (>75 mm) densities in the upper section (Figure 12) ranged from about 650 to 880 fish/ha during the study; standing crops (Figure 13) ranged from about 40 to 50 kg/ha. Unbiased estimates could not be made in the middle and lower sections due to the small numbers of brook trout captured.

Brook trout (>75 mm) density in the upper section decreased during the first winter but increased during the second winter (Figure 12); standing crops decreased over both winters (Figure 13). Confidence intervals (80%) for

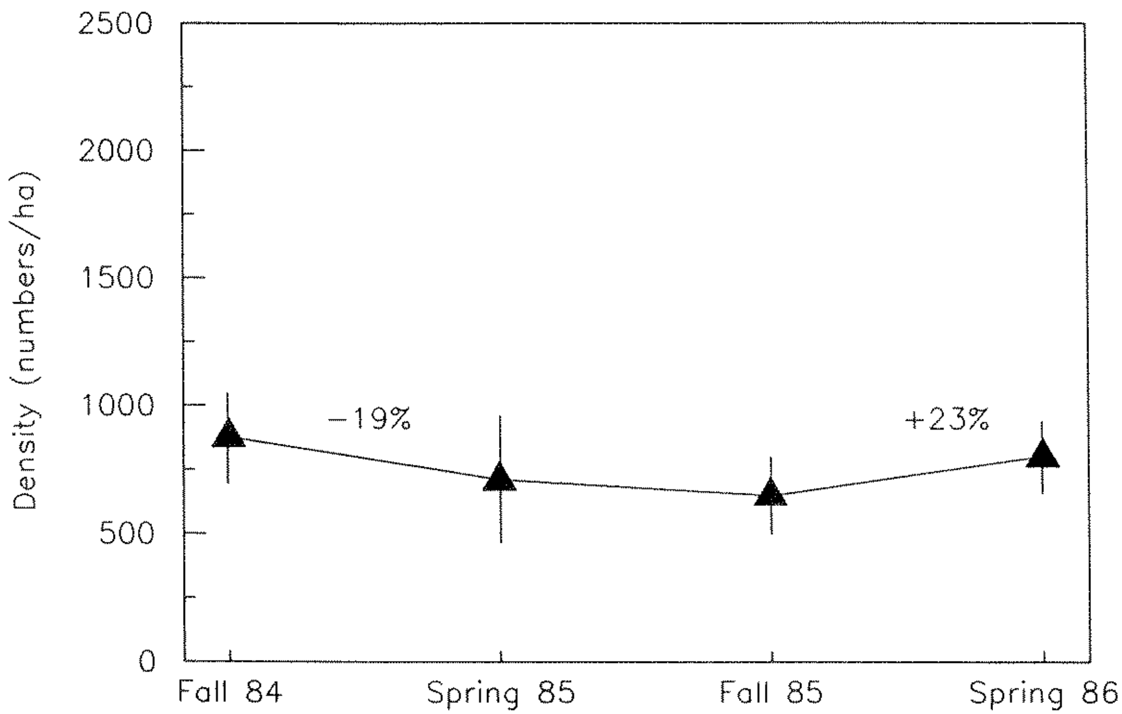

Figure 12. Point estimates and confidence intervals (80%) of brook trout (>75 mm) densities in the upper section, South Willow Creek, Montana. Percentage figures are changes from fall to spring.

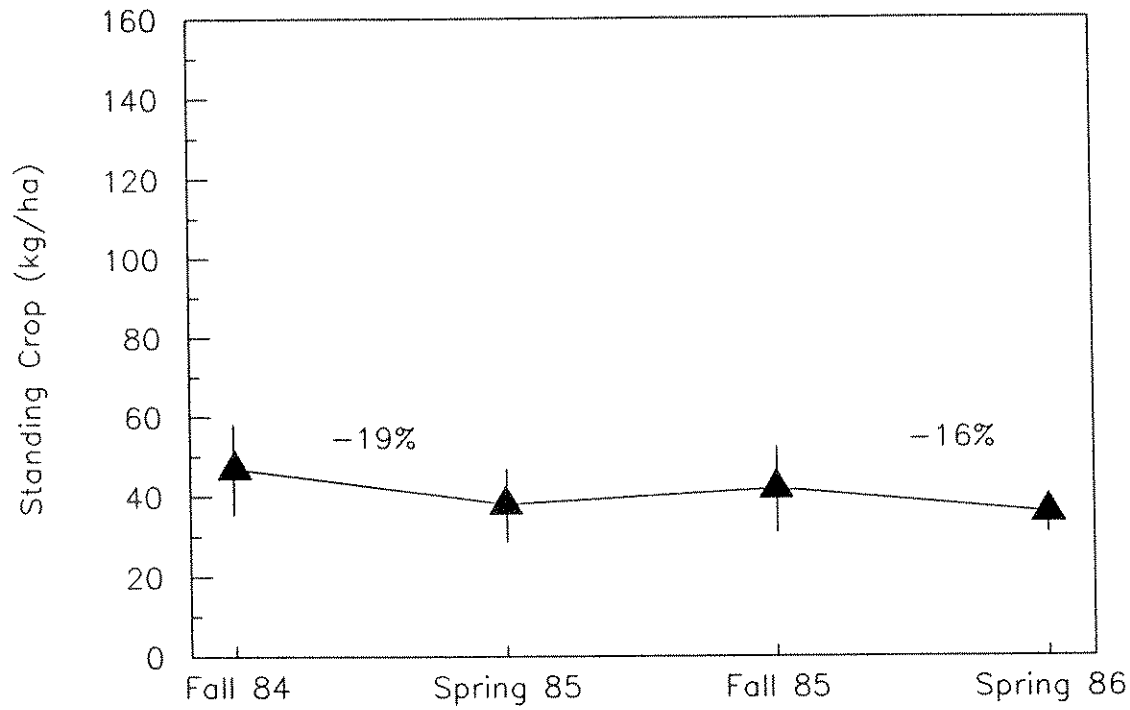

Figure 13. Point estimates and confidence intervals (80%) of brook trout (>75 mm) standing crops in the upper section, South Willow Creek, Montana. Percentage figures are changes from fall to spring.

both parameters always overlapped between successive seasons. Absolute and relative changes in densities (Table 10, Appendix B) and standing crops (Table 11, Appendix B) were generally less than for rainbow trout.

Average Condition Factor

Confidence intervals (80%) for rainbow and brook trout (>125 mm) average condition factors always overlapped between sections and seasons (Table 4). Average condition factors for rainbow trout ranged from 1.02 to 1.16, and averages ranged from 0.89 to 1.11 for brook trout. Averages for brook trout were always less than for rainbow trout for any given section or season. I did not measure the effect of reproduction on condition factors of mature fish.

Winter Movements

Radio-tagged rainbow trout (>225 mm) movements were small but variable when summed by individual fish over the winter, 1985-86 (Table 5). For all 15 radio-tagged fish, total distances moved averaged 114 m (range 3 to 423 m); net (adjusted for direction) distances moved averaged 65 m (range 3 to 261 m). Eleven of the 15 fish moved <100 m net distance. The maximum observed distance moved between periods of tracking (about 1 week) was 141 m. Each of the 15 fish remained in or near (<60 m) study sections where released, and 12 of the 15 were recovered in their

Table 4. Point estimates and confidence intervals (80%) of rainbow and brook trout (>125 mm) average condition factors (K) in the three study sections, South Willow Creek, Montana.

	Fall 1984		Spring 1985		Fall 1985		Spring 1986	
Species	K	80% CI[a]	K	80% CI	K	80% CI	K	80% CI
			Upper section					
Rainbow	1.11	0.94-1.27	1.08	0.91-1.25	1.11	0.91-1.27	1.11	0.97-1.25
Brook	1.02	0.83-1.22	0.97	0.80-1.13	1.05	0.91-1.19	0.94	0.80-1.11
			Middle section					
Rainbow	1.02	0.83-1.22	1.05	0.80-1.30	1.08	0.89-1.27	1.08	0.86 1.30
Brook	0.97	0.75-1.19	0.89	0.66-1.11	1.05	0.86-1.25	0.89	0.72-1.08
			Lower section					
Rainbow	1.11	0.94-1.30	1.16	0.94-1.38	1.13	0.97-1.27	1.05	0.89-1.19
Brook	1.00	0.78-1.19	1.11	0.83-1.41	1.05	0.83-1.27	0.89	0.75-1.05

[a]80% confidence intervals (CI) are approximated by point estimates ±1.28 SD.

respective sections during electrofishing the following spring.

On average, radio-tagged fish in the lower section moved less than did fish in the middle or upper sections (Table 5). They also moved in a net upstream direction, in contrast to about equal upstream and downstream movements in

Table 5. Total and net distances radio-tagged rainbow trout (>225 mm) moved (±3 m) between mid-November 1985, and late February 1986, in South Willow Creek, Montana. Maximum distance is the greatest distance measured between weekly tracking periods. Total and net distances moved were summed from N daytime (0700-1800) locations.

Fish number[a]	Total length (mm)	Weight (g)	N	Total distance moved (m)	Net distance (m) and direction (+ or -) moved[b]	Max distance (m) and direction (+ or -) moved
				Upper section		
5	249	165	11	57	21 -	21 -
8	251	180	12	423	105 +	93 +
11	277	225	14	195	141 -	141 -
15	237	150	8	135	72 +	75 +
Mean				202	85	83
				Middle section		
2	265	210	7	9	3 +	6 +
6	278	250	8	147	66 +	63 +
9	234	150	6	294	177 -	120 -
12	233	155	10	45	15 +	12 +
14	308	295	9	273	261 -	126 -
Mean				154	104	65
				Lower section		
3	225	150	8	39	39 +	39 +
4	271	225	13	9	3 +	3 +
7	250	175	10	3	3 +	3 +
10	251	205	10	3	3 +	3 +
13	256	190	11	60	60 +	39 +
16	261	175	13	12	6 +	6 +
Mean				21	19	16
Overall mean				114	65	50

[a]Fish number corresponds to transmitter number (Table 2).
[b]Upstream is +, downstream is -.

the other two sections. Of the six fish radio-tagged in the lower section, five (#4, 7, 10, 13, and 16) were released in a large pool (> 1.0 m deep) where they were originally captured; four remained throughout the winter and one (#13) moved upstream. Though fish in the other sections were also released in small pools (<0.5 m deep), only one remained throughout the winter (#2).

Most rainbow and brook trout Floy-tagged in spring or fall, 1985, and recaptured in fall, 1985, or spring, 1986, were recaptured in the sections in which they had been marked; less than 10% were recaptured in another section (Table 6). From the middle section, where both upstream and downstream movements might best be detected, 6 of 7 tagged fish that moved during the year had moved to the lower section. In all sections combined, 9 of 11 fish that moved were rainbow trout. The number of tagged fish that moved to areas outside the study sections, did not survive, or lost their tags is not known. No spawning migrations were observed.

Winter Habitat Selection

I combined the middle and lower sections to improve statistical analyses of habitat variables. As distributions of available habitat types (Figure 23, Appendix C), depths (Figure 24, Appendix C), velocities (Figure 25, Appendix C), overhead cover types (Figure 26, Appendix C), and

Table 6. Movement of rainbow and brook trout based on Floy fingerling tag returns, South Willow Creek, Montana. Tag returns include multiple returns (individuals recaptured more than once). Number moved includes over-summer and over-winter movements to other sections by both species.

Section	Number fish tagged	Number tag returns	Number multiple returns	Number moved	Direction moved	
					Up	Down
Upper	141	85	29	1	0	1
Middle	158	71	15	7	1	6
Lower	164	67	9	3	3	0
Combined	463	223	53	11	4	7

substrate types (Figure 27, Appendix C) were not significantly different between these two sections ($p>0.17$; Table 7), I combined them (Figures 14-18). Because differences between the upper and the middle, lower, and combined middle/lower sections were always significant ($p<0.05$; Table 7), I did not combine them.

Small sample sizes precluded a similar comparison of rated pools by study section. However, I combined the middle and lower sections (Figure 19) because simultaneous confidence intervals (95%) overlapped (Figure 28, Appendix C) and relative diversity indices were similar (Table 8). Diversity indices calculated for each of the other habitat variables were also similar between the middle and lower sections.

Radio-tagged rainbow trout (>225 mm) did not use

Table 7. Summary of statistical comparisons (X^2 tests of independence) between sections by habitat variable. Variables reflect availability during winter in South Willow Creek, Montana. $p<0.05$ = *, $p<0.01$ = **.

Habitat variable	Section			
	Upper x Middle	Middle x Lower	Upper x Lower	Upper x Middle/Lower
Habitat type:				
X^2	107.6	5.0	109.4	142.5
p	<0.01**	0.29	<0.01**	<0.01**
df	4	4	4	4
Depth:				
X^2	31.2	6.4	24.7	31.4
p	<0.01**	0.17	<0.01**	<0.01**
df	4	4	4	4
Velocity:				
X^2	12.7	3.9	20.3	19.8
p	0.03*	0.56	<0.01**	<0.01**
df	5	5	5	5
Overhead cover type:				
X^2	53.6	4.7	58.2	74.8
p	<0.01**	0.32	<0.01**	<0.01**
df	5	4	6	6
Substrate type:				
X^2	83.1	3.5	110.8	124.9
p	<0.01**	0.32	<0.01**	<0.01**
df	3	3	3	3

habitat types (Figure 14), depths (Figure 15), velocities (Figure 16), or overhead cover types (Figure 17) in proportion to their availability during winter, 1985-86. In all sections there were significant differences ($p<0.05$; Table 9) between observed frequency of use and "expected" use (based on availability). There were also significant

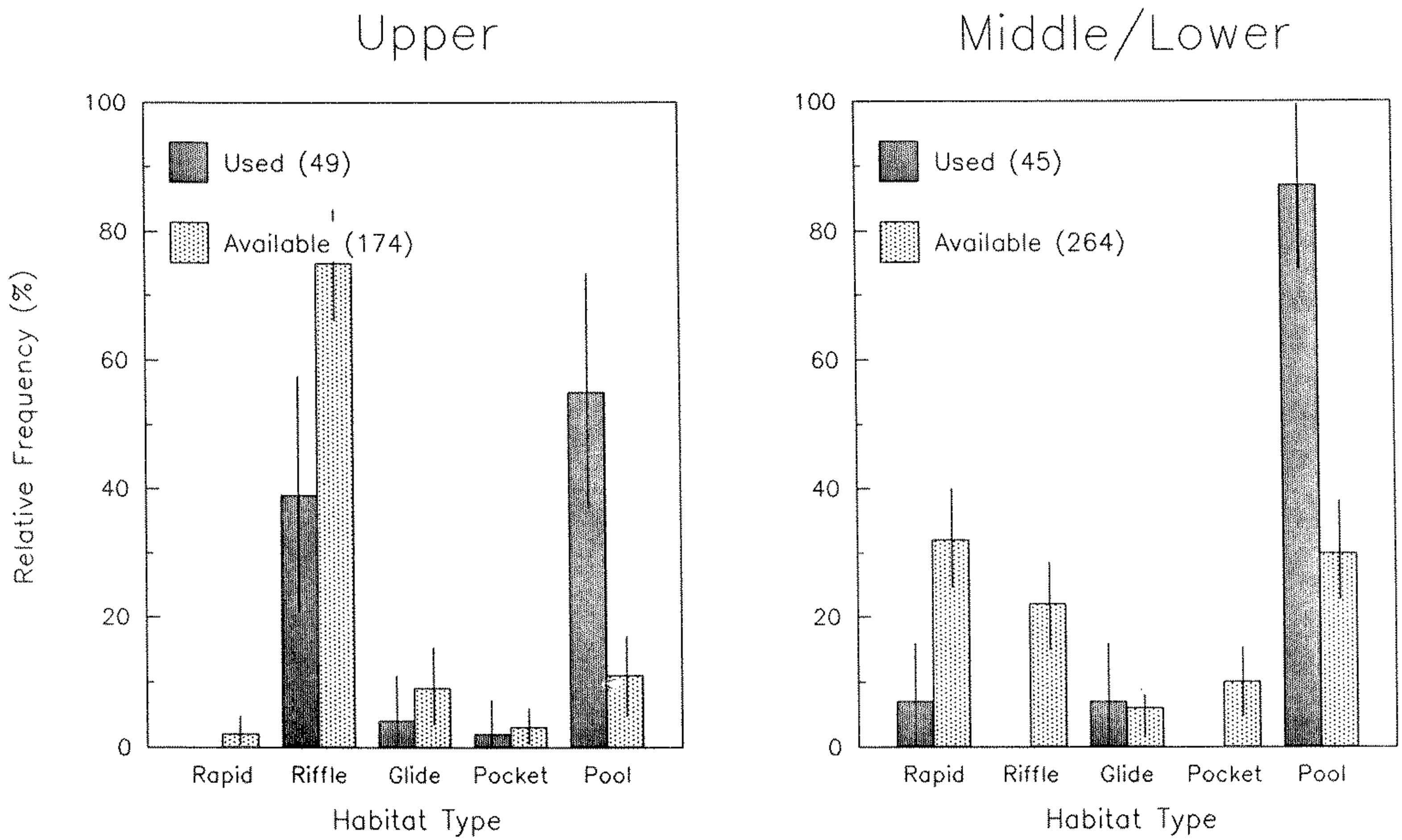

Figure 14. Point estimates and confidence intervals (95%) of winter habitat types used by radio-tagged rainbow trout (>225 mm) compared to available types in the upper and combined middle/lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

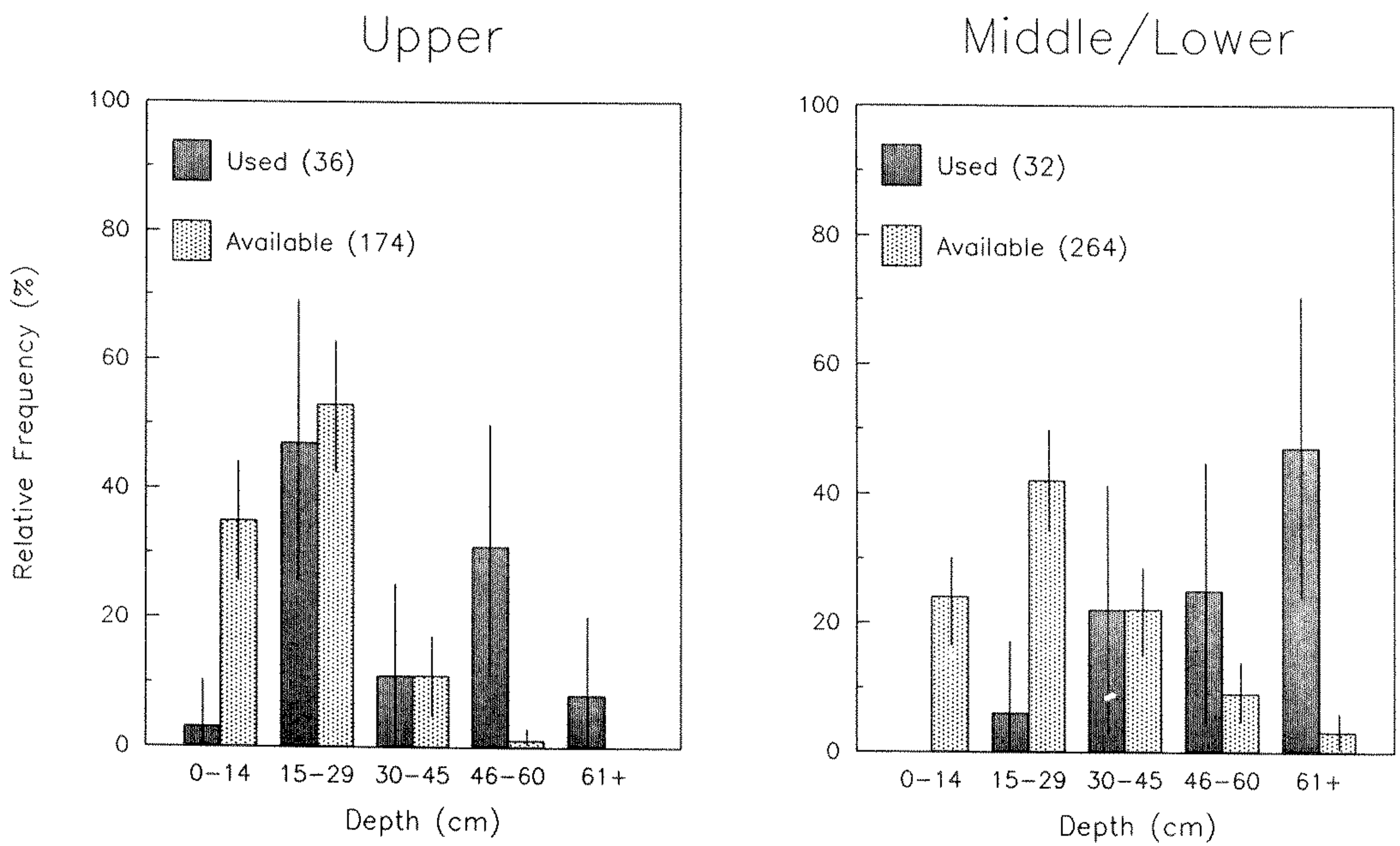

Figure 15. Point estimates and confidence intervals (95%) of winter depths used by radio-tagged rainbow trout (>225 mm) compared to available depths in the upper and combined middle/lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

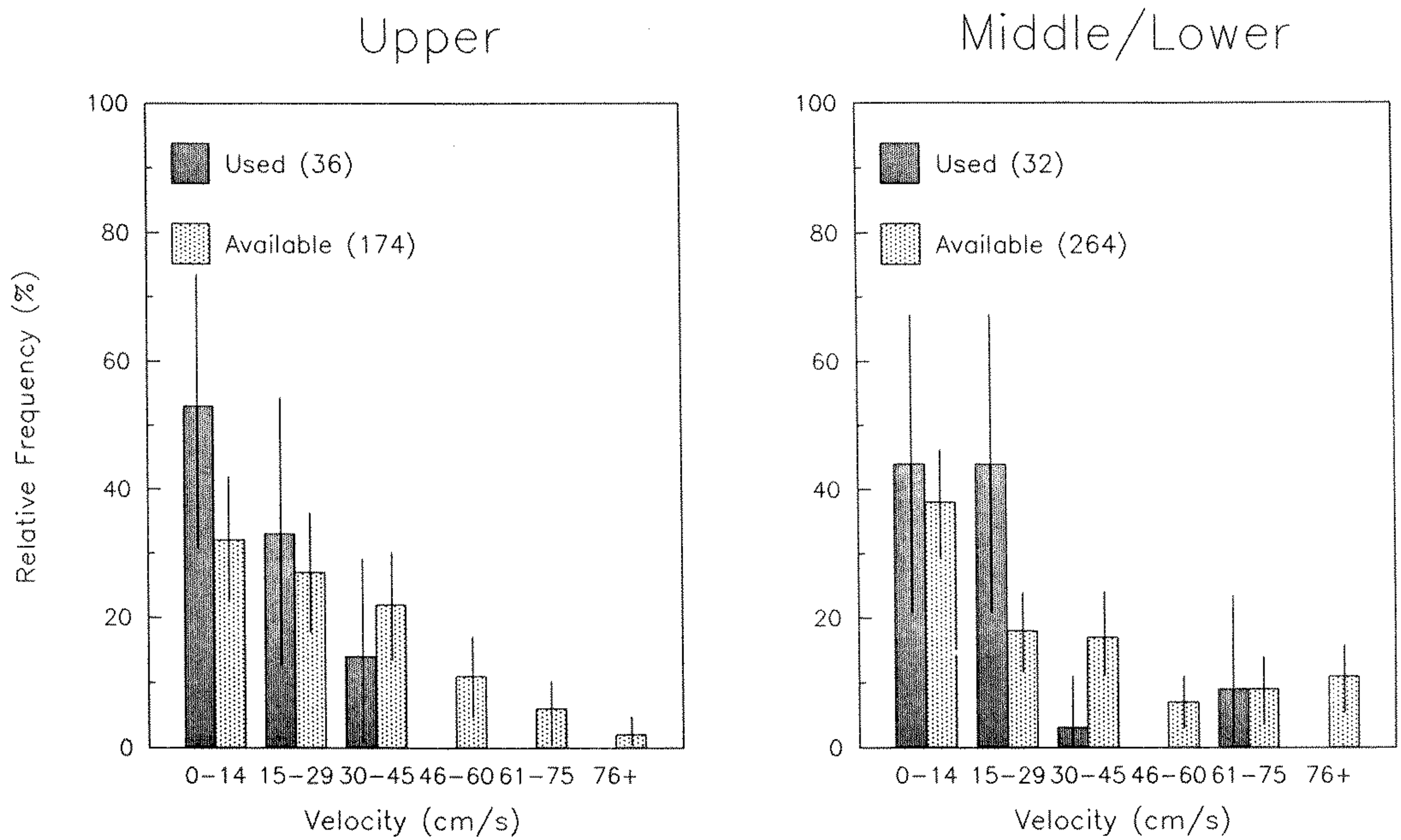

Figure 16. Point estimates and confidence intervals (95%) of winter velocities used by radio-tagged rainbow trout (>225 mm) compared to available velocities in the upper and combined middle/lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

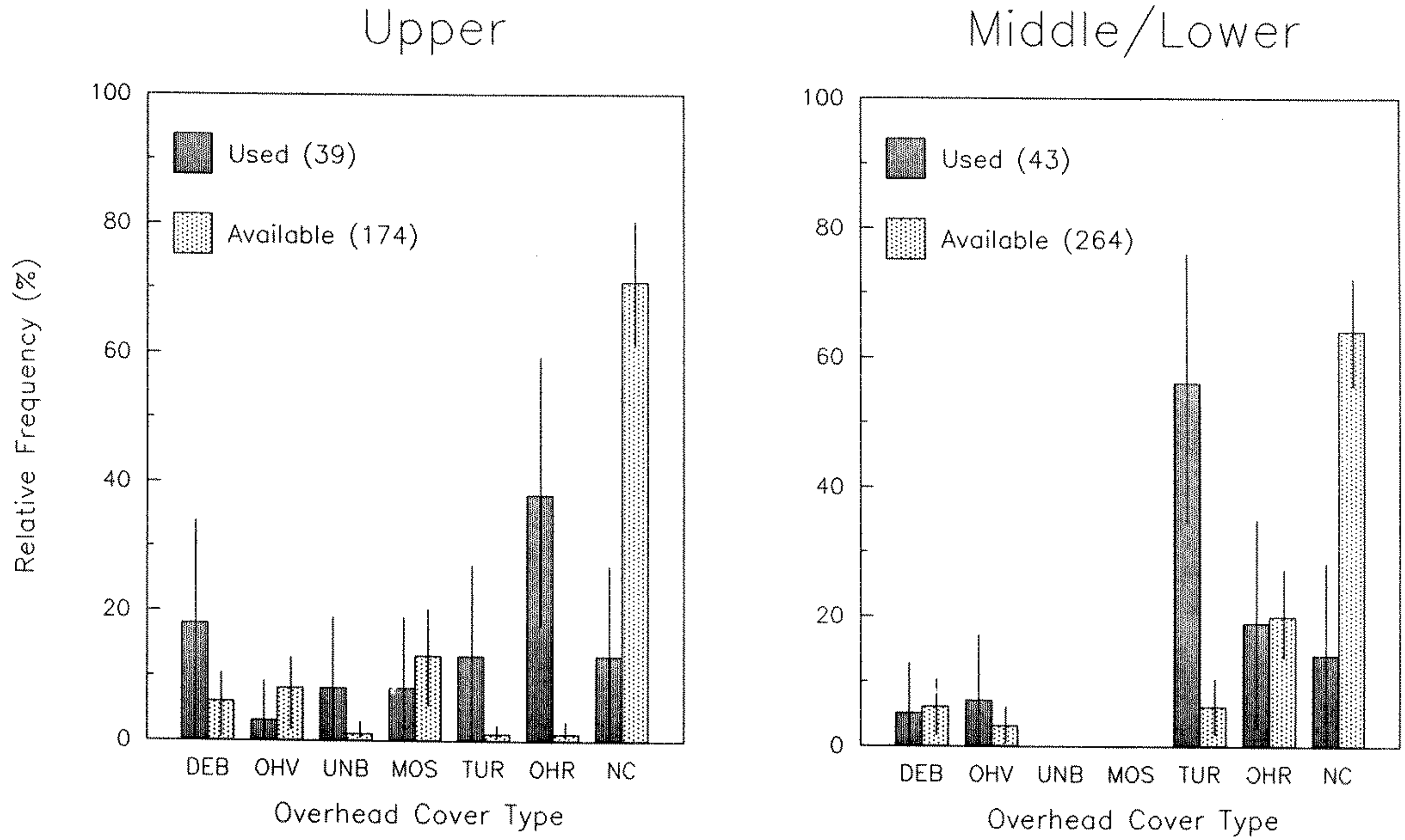

Figure 17. Point estimates and confidence intervals (95%) of winter overhead cover types used by radio-tagged rainbow trout (>225 mm) compared to available types in the upper and combined middle/lower sections, South Willow Creek, Montana. Organic debris = DEB, overhanging vegetation = OHV, undercut bank = UNB, moss = MOS, turbulence = TUR, overhanging rock = OHR, no cover = NC. Sample sizes are in parentheses.

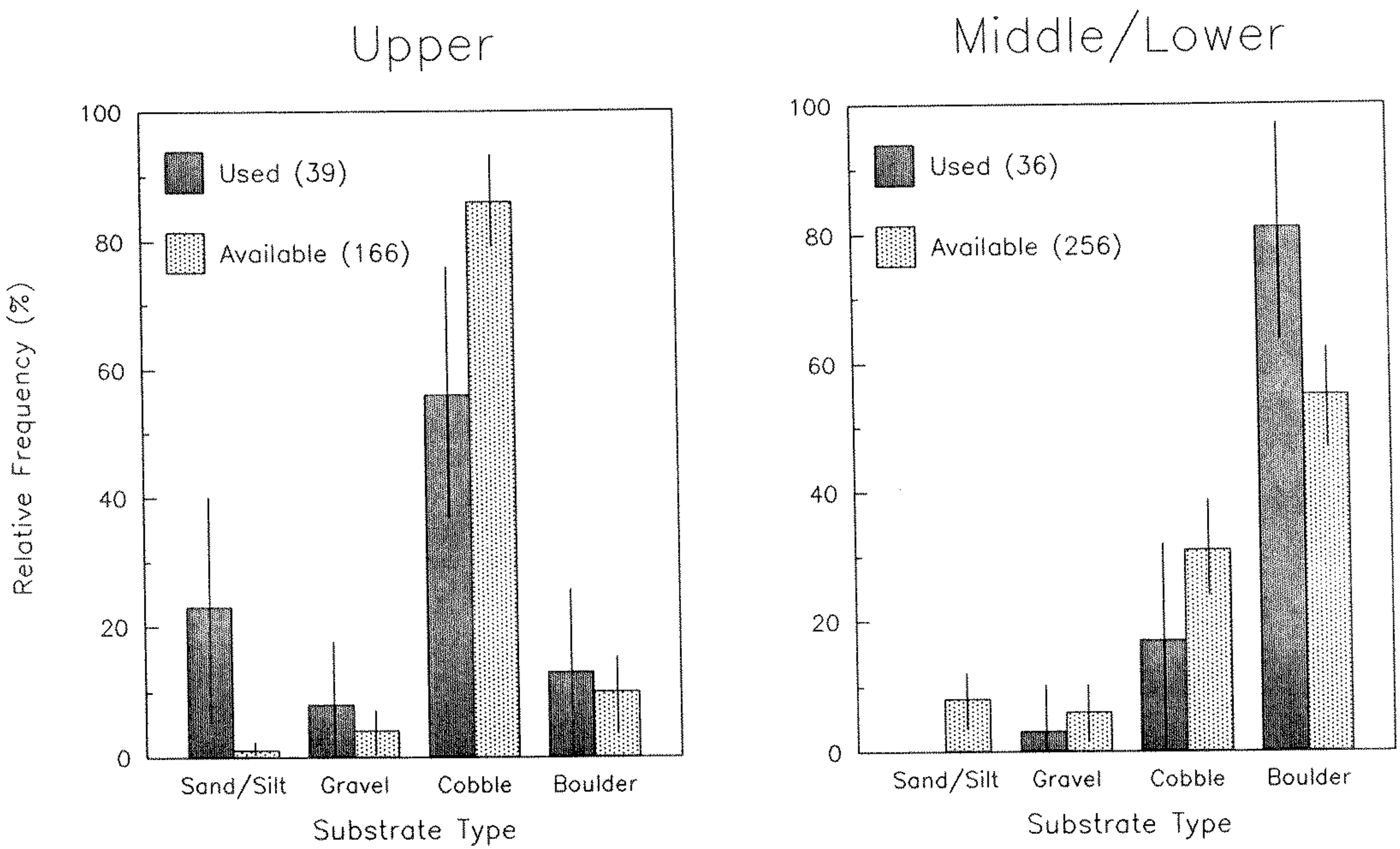

Figure 18. Point estimates and confidence intervals (95%) of winter substrate types used by radio-tagged rainbow trout (>225 mm) compared to available types in the upper and combined middle/lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

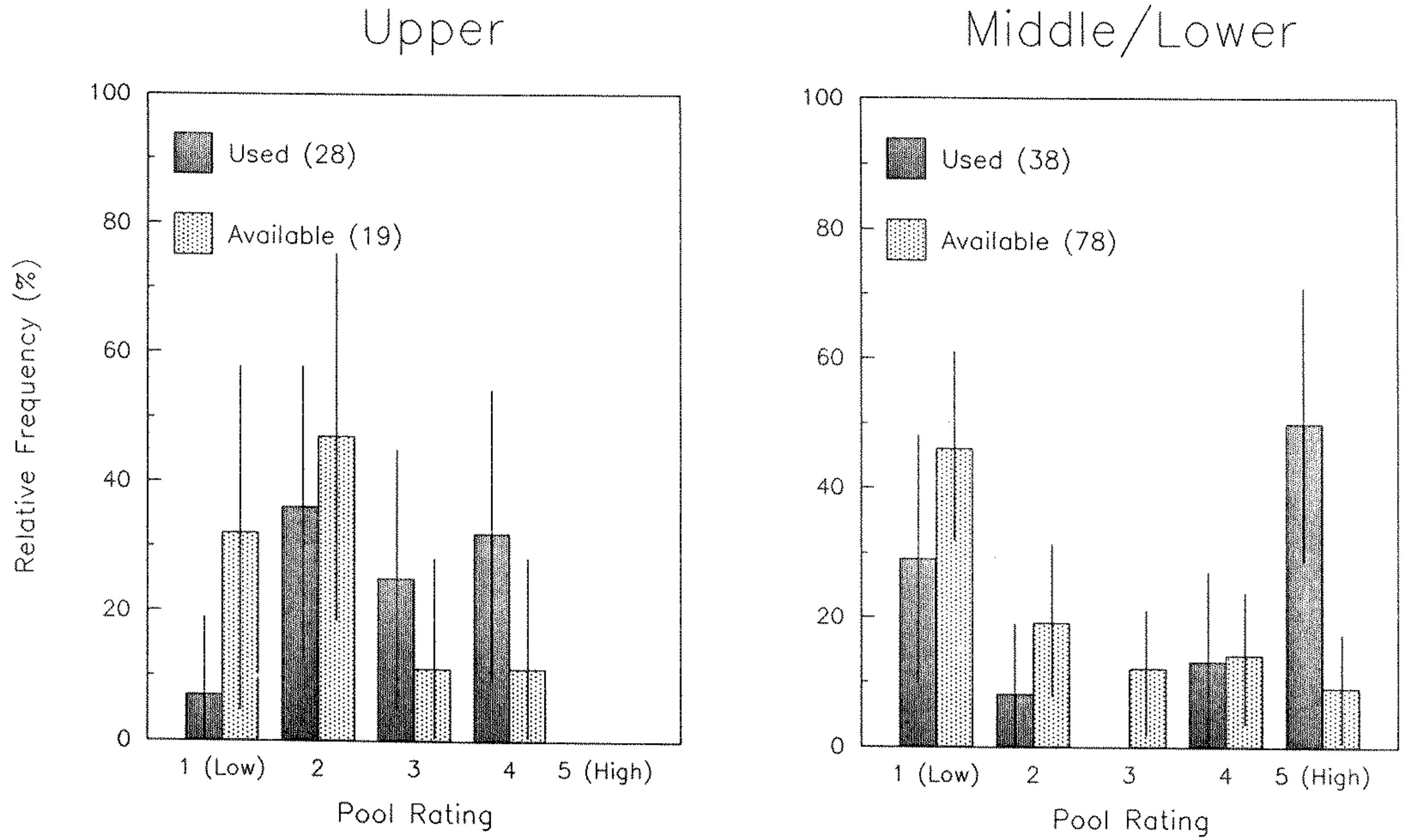

Figure 19. Point estimates and confidence intervals (95%) of rated pools used by radio-tagged rainbow trout (>225 mm) during winter compared to those available in the upper and combined middle/lower sections, South Willow Creek, Montana. Lowest quality pools = 1 and highest = 5. Sample sizes are in parentheses.

Table 8. Relative diversity indices of habitat variables measured in South Willow Creek, Montana. Variables reflect availability during winter. Low diversity = 0.00 and high diversity = 1.00 (Zar 1974).

Habitat variable	Section			
	Upper	Middle	Lower	Middle /Lower
Habitat type:	0.54	0.90	0.90	0.90
Depth:	0.72	0.88	0.80	0.85
Velocity:	0.86	0.87	0.93	0.90
Overhead cover type:	0.52	0.60	0.62	0.57
Substrate type:	0.36	0.78	0.75	0.77
Pool rating:	0.86	0.83	0.85	0.88

differences ($p<0.05$) between use and availability of substrate types (Figure 18) and rated pools (Figure 19) in the upper, lower, and combined middle/lower sections, but not in the middle section alone (Table 9).

Riffles were the most available habitat type in the upper section, composing about 75% of its wetted surface area (Figure 14). In contrast, over 65% of the area in the combined middle/lower section was estimated to be rapids or pools. Glides and pocket water were minor types in all sections.

Most sampled pools in the study area were of low quality (Figure 19). About 80% of the pools in the upper

Table 9. Summary of statistical comparisons (log-likelihood ratio [G] and chi-square [X^2] goodness-of-fit) between winter habitats used by radio-tagged rainbow trout (>225 mm) and those available in each study section, South Willow Creek, Montana. $p<0.05$ = *, $p<0.01$ = **.

Habitat variable	Section: Upper	Middle	Lower	Middle /Lower
Habitat type:				
G	58.6	18.7	68.3	73.4
p	<0.01**	<0.01**	<0.01**	<0.01**
X^2	99.0	15.0	70.6	70.7
p	<0.01**	<0.01**	<0.01**	<0.01**
df	4	4	4	4
Depth:				
G	70.7	19.9	76.8	87.4
p	<0.01**	<0.01**	<0.01**	<0.01**
X^2	321.4	33.1	205.8	204.2
p	<0.01**	<0.01**	<0.01**	<0.01**
df	3	4	4	4
Velocity:				
G	19.3	15.5	18.5	25.6
p	<0.01**	<0.01**	<0.01**	<0.01**
X^2	13.1	18.1	12.0	21.7
p	0.02*	<0.01**	0.03*	<0.01**
df	5	5	5	5
Overhead cover type:				
G	142.6	21.7	40.7	93.0
p	<0.01**	<0.01**	<0.01**	<0.01**
X^2	638.3	36.0	180.4	208.3
p	<0.01**	<0.01**	<0.01**	<0.01**
df	6	5	5	6
Substrate type:				
G	54.9	3.1	18.5	13.4
p	<0.01**	0.38	<0.01**	<0.01**
X^2	334.6	1.9	12.3	10.4
p	<0.01**	0.59	<0.01**	0.02*
df	3	3	3	3

Table 9, continued.

Habitat variable	Section: Upper	Middle	Lower	Middle /Lower
Pool rating:				
G	20.7	5.3	46.8	48.8
p	<0.01**	0.26	<0.01**	<0.01**
X^2	24.2	4.6	59.5	80.4
p	<0.01**	0.34	<0.01**	<0.01**
df	3	4	4	4

section and 65% of the pools in the combined middle/lower section were rated 2 or less. The highest-quality pools were in the lower section (Figure 28, Appendix C).

All habitat types were used by radio-tagged rainbow trout during winter, but only pools were used in greater proportions than they were available (Figure 14). Pools accounted for most of the significant differences between habitat use and availability. Over 50% of the fish locations in the upper section and 80% of the locations in the middle/lower section were in pools. Further, only high-quality pools (3 or greater) were selected (Figure 19). Except for riffles in the upper section, other habitat types were rarely used (Figure 14).

Most of the study area was <30 cm deep (Figure 15) and had velocities <46 cm/s (Figure 16). About 85% of the upper section and 65% of the middle/lower section was <30 cm deep. More than 70% of each section had velocities <46 cm/s.

Radio-tagged rainbow trout usually (>90%) occupied sites >14 cm deep (Figure 15) with velocities <46 cm/s (Figure 16) during winter. They generally selected depths >45 cm with velocities <30 cm/s, and avoided depths <15 cm with velocities >45 cm/s. Fish in the upper section used deeper water (>29 cm) less than did fish in the middle/lower section, but the upper section had less deep water available. Selected and avoided depths and velocities accounted for most of the significant differences between use and availability.

Most (>65%) of the study area lacked overhead cover (Figure 17), and most (>85%) had cobble or boulder substratum (Figure 18). Moss (*Fontinalis* spp.) was the primary cover type available in the upper section (about 15%), whereas overhanging rock was the most available cover type in the middle/lower section (about 20%). Organic debris, overhead vegetation, undercut banks, and turbulence were always rare (<10%). Cobble was most abundant in the upper section, while boulders predominated in the middle/lower section. Less than 10% of the streambed in any section was gravel or sand/silt.

During winter, radio-tagged rainbow trout mostly (>85%) used areas having some type of overhead cover (Figure 17) and generally (>65%) used the most available streambed material-cobble and boulder (Figure 18). They avoided areas that lacked cover and selected areas with overhanging rocks and turbulence. Only twice did I observe them using ice for cover. Though they selected sand/silt and avoided cobble in the upper section, they selected boulders and avoided sand/silt in the middle/lower section. I did not observe trout hiding in the substrate, but I did not see all radio-located fish. Selected and avoided cover and substrate types accounted for most of the significant differences between use and availability.

DISCUSSION

Winter Mortality

Densities of age I and older rainbow trout (>75 mm) decreased an average 32% while standing crops decreased 30% over both winters, 1984-86. Although some confidence intervals overlapped between fall and spring, I believe these decreases were real and not an artifact of sampling error. Further, I attribute a large portion of these decreases to natural mortality. Fishing mortality did not occur, and movement was minimal. Part of the decrease in standing crops could have been due to loss of body weight. However, average condition factors of larger (>125 mm) individuals did not change, and length frequency distributions suggest some overwinter growth.

Other authors have reported higher and more variable winter mortalities than I observed in South Willow Creek. Needham et al. (1945) reported 62% (range 16 to 85%) of YOY and 80% (range 48 to 91%) of older (>100 mm) wild brown trout were lost on average during four consecutive winters (August to April) in Convict Creek, California. Reductions in biomass generally paralleled reductions in numbers. Maciolek and Needham (1952) estimated 50% of marked trout died over a mild winter (November to April) in experimental channels in the same stream. In studies of wild brook trout over 11 years in Lawrence Creek, Wisconsin, Hunt (1969) reported YOY winter mortalities (September to April) averaging 46% (range 27 to 65%). Cerven (1973) estimated 97% of all ages of wild brown trout, 73% of all ages of wild cutthroat trout, and 45% of stocked catchable rainbow trout were lost over the winter (October to April) in the Temple Fork of the Logan River, Utah.

I cannot explain why mortality was less and less variable in South Willow Creek compared to these other streams. Winter has long been suspected as the season of greatest trout mortality (Hubbs and Trautman 1935; Hazzard 1941). However, the causes of mortality are poorly understood. Earlier research has suggested that predation (Maciolek and Needham 1952; Hunt 1969) or the lack of food or feeding (Maciolek and Needham 1952; Brown et al. 1953; Benson 1955; Reimers 1957; Needham and Jones 1959; Logan 1963; Chapman and Bjornn 1969) are not important factors during winter.

Other research has implicated snow and ice, and fluctuating flows associated with its formation and dispersal, as major causes of trout mortality (Needham and Slater 1944; Needham et al. 1945; Maciolek and Needham 1952; Reimers 1957; Needham and Jones 1959). Trout mortality has been observed due to: (1) crushing or asphyxiation from collapsing snowbanks and ice (Needham and Slater 1944; Needham et al. 1945); (2) stranding from severe flow fluctuations caused by anchor ice formation and dispersal (Maciolek and Needham 1952); and (3) asphyxiation from ice crystals plugging gill lamellae (Tack 1938).

I did not measure predation rates, food availability, consumption rates, or amounts of snow and ice; however, I believe they were not important winter mortality factors in South Willow Creek. Other than trout, belted kingfishers (Megaceryle alcyon) were the only predators observed in the study area, but only once during both winters. Benthic invertebrates appeared abundant, and trout were often observed feeding on drift dislodged by anchor ice. Absolute and relative mortalities were similar in the upper and lower sections, which formed extensive and sporadic anchor ice, compared to the middle section, which formed none.

Although earlier research has implicated snow and ice as a major winter mortality factor, much of this work was descriptive and lacked a quantitative basis. I am aware of only a few studies that have quantified the relationship between trout winter mortality and biotic or abiotic factors. Hunt (1969) found that survival of YOY brook trout over 11 consecutive winters was significantly and positively correlated with average body lengths in September and with hourly summations of stream temperatures above 4.5 C in January. Survival appeared to be independent of fingerling density. Lawrence Creek did not form anchor ice, however, and much of its surface remained ice-free. Hunt concluded that the survival advantage of larger body size may be related to increased resistance to temperature-induced physiological stress rather than reduced vulnerability to predation. The nature of this stress was not discussed.

Cerven (1973) found that anchor ice and snow cover in several sections of Temple Fork were not significantly related to winter mortality of stocked catchable rainbow or age I and older wild brown trout. However, anchor ice was significantly and positively correlated with YOY brown trout mortality. Cerven concluded that other environmental or physiological (e.g. stress) factors may have influenced mortality of older fish.

Cunjak (1988) concluded that early winter is a stressful period of acclimatization to rapidly changing environmental conditions, particularly declining water temperatures. Early winter (November-December) in the Credit River, Ontario, was accompanied by declining body condition, rapid depletion of energy reserves, and elevated serum glucose levels (indicating elevated stress) in wild brook and brown trout. These trends were noted in three sites that formed surface and anchor ice as well as two sites which did not. Winter mortality rates were not estimated for any of the sites.

In Convict Creek, Reimers (1963) observed accelerated mortality during winter and spring with fluctuating and rising water temperatures, respectively. Mortality of hatchery-reared rainbow trout increased progressively with declining body condition during winter, but no large mortalities were observed due to catastrophic snow or ice events. Reimers concluded that accelerated mortality may have been due to acclimatization problems, i.e. "temperature-induced catabolism beyond the limit of tolerance".

These results suggest and agree with my conclusion that trout mortality from catastrophic snow and ice events may not be as important as earlier workers believed. Ice may often be beneficial to trout (Hazzard 1941). They use it for cover (Maciolek and Needham 1952; Logan 1963; Needham and Jones 1959; Wichers 1978; Chisholm 1985), and anchor ice dislodges benthic organisms and makes them more available as food (Maciolek and Needham 1952). Food may not be digested at low water temperatures, however (Reimers 1957).

I conclude that more comprehensive and quantitative studies are needed to better define the relationships between trout mortality and changing winter stream conditions (e.g. streamflows, temperatures, and ice). Two years were not adequate to define these relationships in South Willow Creek. Valuable research might include the behavioral adaptations (e.g. feeding, moving, habitat use) and physiological responses (e.g. body condition, lipid reserves, disease resistance) of trout to changing conditions. The underlying mechanisms controlling winter mortality are probably more complex than previously believed, but understanding them would provide valuable insight for making minimum winter streamflow recommendations.

Winter Movements

Radio-tagged rainbow trout (>225 mm) moved little during winter, 1985-86, in South Willow Creek. I believe dispersal movements (i.e. immigration and emigration) were minimal, and I observed no migration to overwintering or spawning areas. Net distances moved were small (<300 m), and directions moved appeared random.

Some rainbow trout may have moved before being radio-tagged in November. However, I believe distances moved would have been small. Six of the 15 fish that were radio-tagged had fingerling tags from the previous September electrofishing; each was found in the section where it was Floy-tagged. Twelve of the 15 were recovered the following March; each was in the section where it was last located.

Tag returns and population statistics provide further evidence that winter movements of all sizes of trout in South Willow Creek were minimal. Although only 30% of the

Floy-tagged rainbow and brook trout were recaptured, most (>90%) of these remained in sections where they were tagged. For all sections during both years of the study, size structures and relative abundance were similar between fall and spring. Non-significant differences in relative abundance in the upper section may have been due to sampling error or differential mortality.

Studies in Montana and other Rocky Mountain streams support my findings that trout winter movements are minimal. Logan (1963) electrofished a section of Bridger Creek monthly to locate rainbow trout (>175 mm) tagged in October. Numbers recaptured (not reported) gradually declined through the winter but, on average, 93% of all recaptures were within 120 m of their initial tagging location. Less than 10% of the original 125 tagged fish remained in the section in April, however, and other parts of stream were not checked. Four were caught by fishermen outside the section, but the fate of others was unknown. Leathe and Enk (1985) concluded that tagged brook and cutthroat trout (>100 mm) moved little (<350 m) during winter and resided year-round in tributaries of the Swan River.

Radio-tagged brown trout (>290 mm) in the Laramie River, Wyoming, moved mostly in December, and mostly upstream, followed by progressive decreases in movements in January through March (Wichers 1978). These fish were thought to be either moving from spawning areas or moving to preferred overwintering sites, or both. No distinct relationship was found between movement and temperature or flow other than large upstream movements in October when water temperatures were most suitable for spawning. Average total movement per fish ranged from 52 m in March to 661 m in December.

Six of eight brook trout (>175 mm) radio-tagged by Chisholm (1985) in Nash Fork Creek, Wyoming, during October moved short distances downstream into a beaver pond. Four moved within a day after implant surgery and the remaining two moved within 2 weeks. Whether the movements were stress-induced is not known. Although this group and another group of 8 fish (radio-tagged and tracked the previous year) were active over each winter, net distances moved only ranged from 0 to 342 m.

The relative lack of winter movement by rainbow trout in South Willow Creek may have been related to availability of suitable winter habitat, especially cover. Beginning in September, several species of trout and juvenile salmon in Idaho streams move down from tributaries to overwinter in larger streams, often returning upstream in spring (Chapman and Bjornn 1969; Bjornn 1971; Everest and Chapman 1972). These are not seaward smolt migrations, in the case of anadromous species, nor are they thought to be caused by reduced food supply (benthic or drift), changes in flow regimes or water temperatures, or population density (Bjornn 1971). Instead, many salmonids change behavior from active feeding during summer to hiding in the substrate during winter, particularly when stream temperatures fall below 4-8 C (Hartman 1965; Chapman and Bjornn 1969; Bjornn 1971; Campbell and Neuner 1985). If adequate winter habitat is not available, trout may move downstream to locate suitable wintering areas (Bjornn 1971).

Winter Habitat Selection

During winter, 1985-86, radio-tagged rainbow trout (>225 mm) in South Willow Creek selected high-quality pools that were characterized by depths >45 cm and velocities <30 cm/s; they avoided water <15 cm deep with velocities >45 cm/s. These results generally agree with other winter studies of similar-sized but different species of trout.

Radio-tagged brown trout (>290 mm) in the Laramie River, Wyoming, occupied sites with depths ranging from 15 to 45 cm and velocities ranging from <15 to 45 cm/s (Wichers 1978). Depths >45 cm were used but not "selected". Depths and velocities used by brown trout were not statistically compared to availability. The author also measured availability during relatively high summer streamflows which may not accurately represent true winter hydraulic conditions.

Radio-tagged brook trout (>175 mm) in Telephone and

Nash Fork Creeks, Wyoming, selected low-velocity (<15 cm/s) areas that were often associated with beaver ponds (Chisholm 1985). They selected no particular depths, although sites >15 cm deep were used most. Use and availability measurements were made during summer, using transects rather than point locations, and may not be reliably compared to my results.

By diving, Cunjak and Power (1986) observed age-I-and-older brook and brown trout during three consecutive winters in the Credit River, Ontario. Most trout were in aggregations, and, like rainbow trout in South Willow Creek, were usually found in pools. Brook trout used focal point depths (measured from the water surface) that averaged 68 cm (range 25 to 150 cm); their average focal point velocity was 7 cm/s (range 1 to 23 cm/s). Brown trout used similar depths (average 69 cm, range 29 to 150 cm), but greater velocities (average 13 cm/s, range 1 to 43 cm/s). These values generally agree with my results but are not directly comparable because: (1) depths and velocities used were not statistically compared with those available and cannot be described as being "selected" or "avoided", (2) the author reported averages and not distributions, and (3) depths and velocities were measured at a fish's focal point, while I measured total depth and mean water column velocity at a fish's location. However, because most fish in the Credit

River were within 15 cm of the stream bed, their focal point depths and velocities were likely indicative of total depths and mean velocities.

Radio-tagged rainbow trout in South Willow Creek selected areas associated with overhead cover during winter, especially overhanging rocks and surface turbulence, and they avoided areas that lacked cover. Other species of trout in other parts of North America also use cover during winter. In Michigan streams, brook trout were observed in low-velocity areas associated with cover (Cooper 1953). In the Pigeon River, Michigan, Benson (1955) observed trout in quiet eddies and under banks.

Both Wichers (1978) and Chisholm (1985) concluded that cover was an important aspect of trout winter habitat suitability in Wyoming streams. These streams were completely covered with snow and ice, however, and usage of other cover types was not quantified.

In the Credit River, Ontario, most (>80%) positions occupied by brook and brown trout were beneath cover during winter (Cunjak and Power 1986). Relative to summer, they used areas with slower water velocities and greater overhead cover. Cover classifications were similar to mine except that they also included surface ice. Surface ice was often observed in the South Willow Creek study area, but only twice did I observe rainbow trout using it for cover.

Other studies have also shown that trout use surface ice and snow banks for cover during winter. Maciolek and Needham (1952) observed wild brown trout and stocked rainbow trout under surface ice, overhanging banks, willow roots, and brush in Convict Creek, California. Needham and Jones (1959) noted that trout in Convict Creek used areas close to projecting snow banks, overhanging brush, and debris. Trout in Bridger Creek, Montana, used shallow water associated with surface ice cover (Logan 1963).

Some trout and juvenile salmon overwinter in the substrate, apparently using it as a form of cover (Hartman 1965; Chapman and Bjornn 1969; Bjornn 1971; Campbell and Neuner 1985). Although I did not observe this behavior in South Willow Creek, overhanging rock was a selected cover type.

In many streams, winter cover may be the primary factor limiting salmonid abundance. Chapman and Bjornn (1969) discussed the importance of winter cover to stream salmonids, and Bjornn (1971) suggested that some populations may be limited by winter cover availability. Hunt (1971) nearly doubled the overwinter survival of brook trout in Lawrence Creek, Wisconsin, by increasing low-velocity pool areas and adding bank cover.

Although radio-tagged rainbow trout in South Willow Creek generally occupied sites with the most available substrate types (cobble and boulder) during winter, substrate selection varied between study sections. They selected sand/silt in the upper section and boulders in the lower section, but no types were selected in the middle section. I conclude that boulders, by providing overhanging rock cover, are probably the most important substrate type to large rainbow trout during winter.

Other winter studies have also reported variable selection of substrate types. Brown trout in the Laramie River used (but not necessarily selected) gravel and cobble substrate (Wichers 1978), while brook trout in Telephone and Nash Fork Creeks selected sand/silt (Chisholm 1985).

Much of the variation in trout substrate selection might be explained by the relative importance of other habitat variables in determining stream position choice. Rainbow trout in South Willow Creek selected deep, low-velocity pools that were sometimes associated with sand/silt substrate. Individuals may have chosen these locations for their depths and velocities rather than their substrate. Chisholm (1985) reported that sand/silt substrate associated with beaver ponds was often selected by brook trout during winter, but that individuals were probably using these areas because of their low-velocities and cover rather than their substrate.

Rainbow trout selection for cover and high-quality pools with deep, slow water might be explained by the need to maintain favorable energetic balances during winter.

This bioenergetics approach to understanding the mechanisms of habitat choice was formulated from summer (Bachman 1984; Fausch 1984) and noted in winter (Chapman and Bjornn 1969; Campbell and Neuner 1985; Cunjak and Power 1986) studies of other stream salmonids. Besides minimizing unprofitable energy expenditures, however, rainbow trout in South Willow Creek may have occupied positions, including those that were not selected, to avoid predators, competitors, or physical damage by ice (Chapman and Bjornn 1969). Future productive research in the laboratory and field might integrate bioenergetics with intra- and inter-specific interactions and estimates of trout mortality, movement, and habitat selection during winter.

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APPENDICES

APPENDIX A

RAINBOW TROUT LENGTH FREQUENCY DISTRIBUTIONS

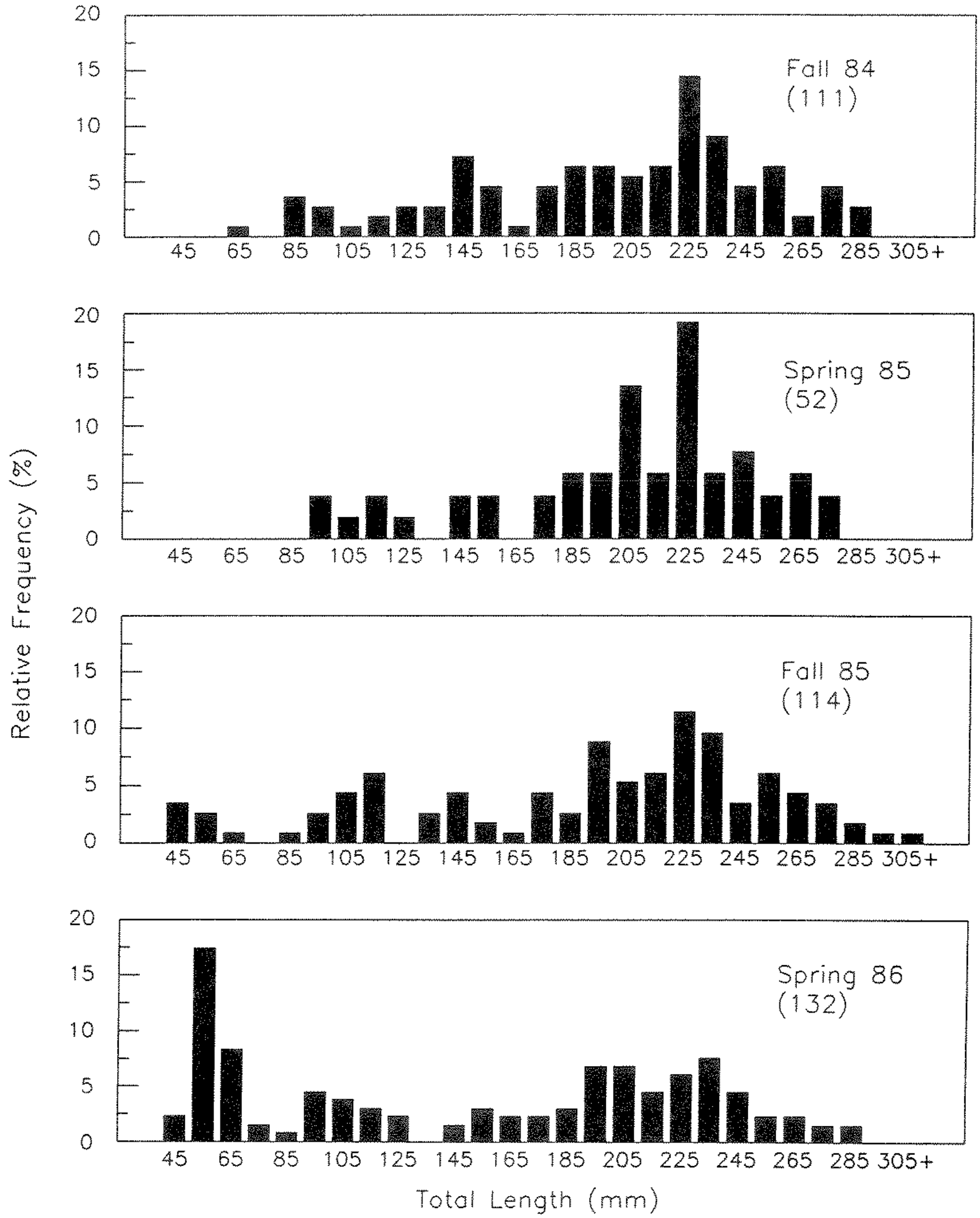

Figure 20. Length frequency distributions of rainbow trout captured in the upper section, South Willow Creek, Montana. Sample sizes are in parentheses.

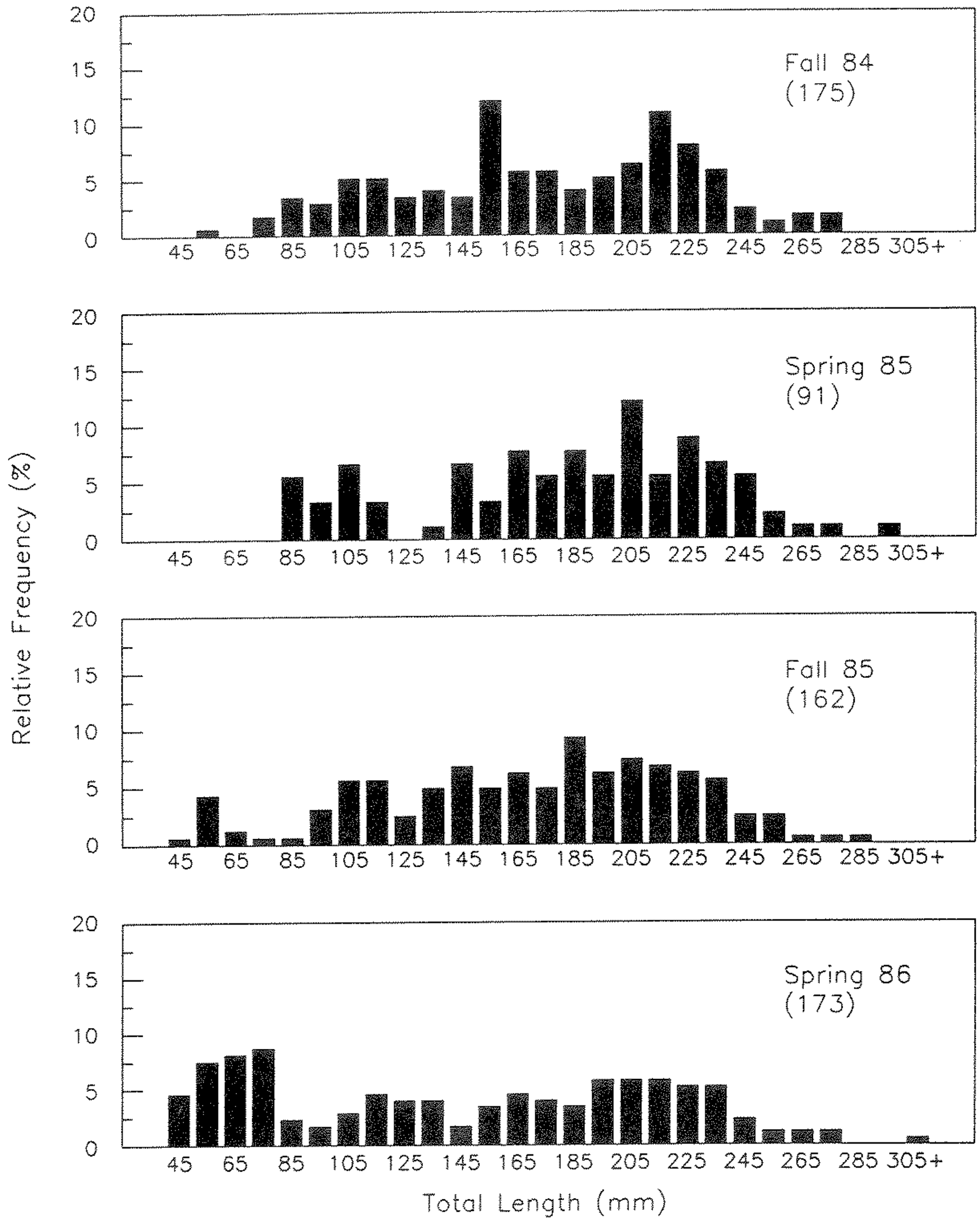

Figure 21. Length frequency distributions of rainbow trout captured in the middle section, South Willow Creek, Montana. Sample sizes are in parentheses.

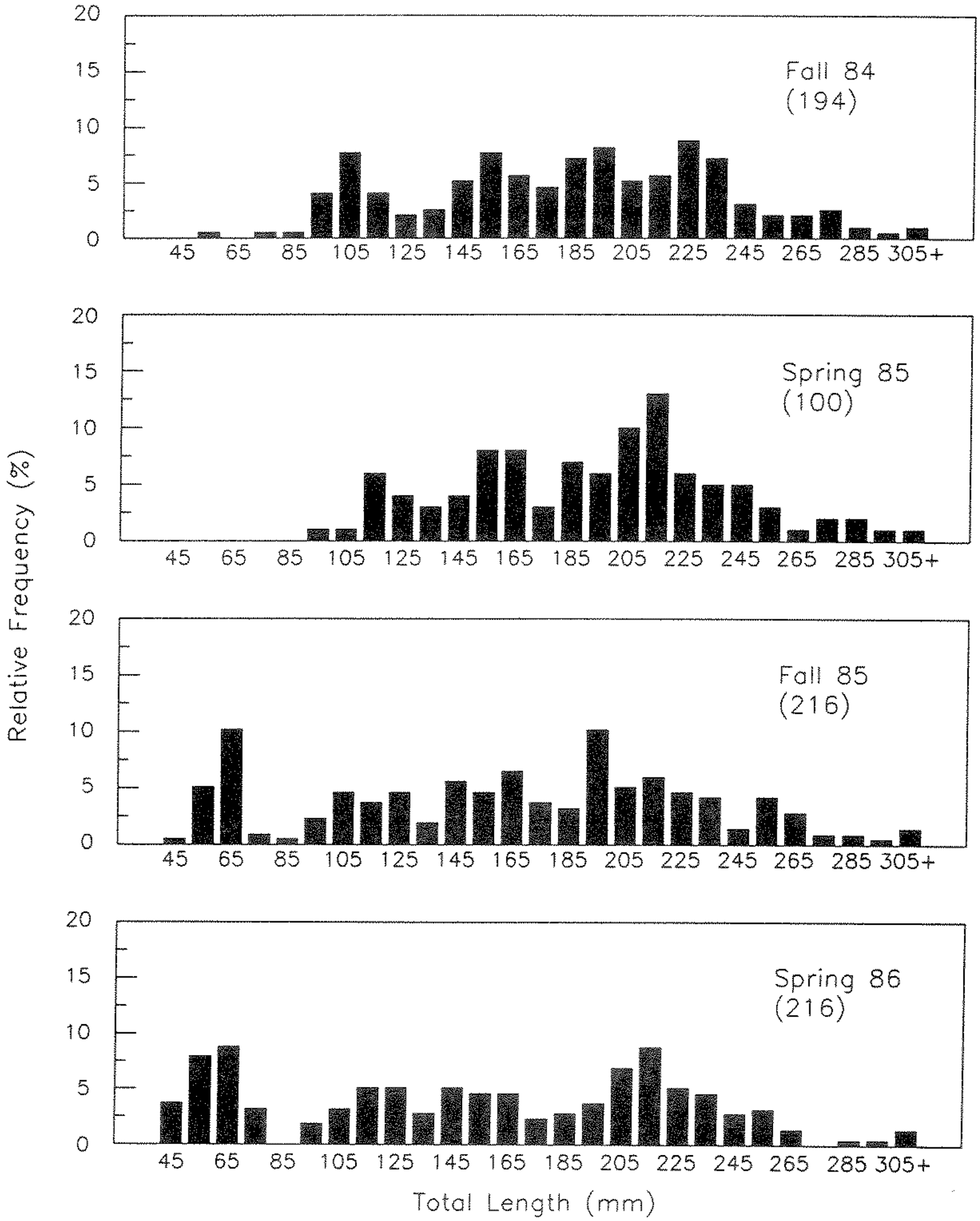

Figure 22. Length frequency distributions of rainbow trout captured in the lower section, South Willow Creek, Montana. Sample sizes are in parentheses.

APPENDIX B

RAINBOW AND BROOK TROUT DENSITIES AND STANDING CROPS

Table 10. Point estimates and confidence intervals (80%) of rainbow and brook trout densities in the three study sections, South Willow Creek, Montana. Estimates are for fish >75 mm total length.

Section	Date marked	Density (#/ha)	80% CI[a]	Change	Percent change
		Rainbow trout			
Upper	10/84	824	711-936	----	---
	4/85	515	368-662	-309	-38
	9/85	853	721-985	+338	+66
	3/86	701	637-765	-152	-18
Middle	10/84	1347	1175-1519	----	---
	4/85	772	629-914	-575	-43
	9/85	1239	1037-1441	+467	+61
	3/86	1013	890-1136	-226	-18
Lower	10/84	1782	1477-2087	----	---
	4/85	983	780-1186	-799	-45
	9/85	2097	1622-2571	+1114	+113
	3/86	1482	1293-1671	-615	-29
		Brook trout			
Upper	10/84	877	696-1059	----	---
	4/85	711	466-956	-166	-19
	9/85	652	500-804	-59	-8
	3/86	804	662-946	+152	+23

[a]80% confidence intervals (CI) are approximated by point estimates ±1.28 SD.

Table 11. Point estimates and confidence intervals (80%) of rainbow and brook trout standing crops in the three study sections, South Willow Creek, Montana. Estimates are for fish >75 mm total length.

Section	Date marked	Standing crop (kg/ha)	80% CI[a]	Change	Percent change
			Rainbow trout		
Upper	10/84	82	71-93	---	---
	4/85	53	38-69	-29	-35
	9/85	87	73-100	+34	+62
	3/86	56	49-62	-31	-36
Middle	10/84	87	78-96	---	---
	4/85	56	45-67	-31	-36
	9/85	78	69-87	+22	+40
	3/86	69	60-78	-9	-11
Lower	10/84	130	114-145	---	---
	4/85	90	72-108	-40	-30
	9/85	149	125-174	+59	+66
	3/86	103	90-116	-46	-31
			Brook trout		
Upper	10/84	47	36-58	---	---
	4/85	38	29-47	-9	-19
	9/85	42	31-53	+4	+12
	3/86	36	31-40	-6	-16

[a]80% confidence intervals (CI) are approximated by point estimates ±1.28 SD.

APPENDIX C

COMPARISONS OF MIDDLE AND LOWER SECTIONS BY HABITAT VARIABLE

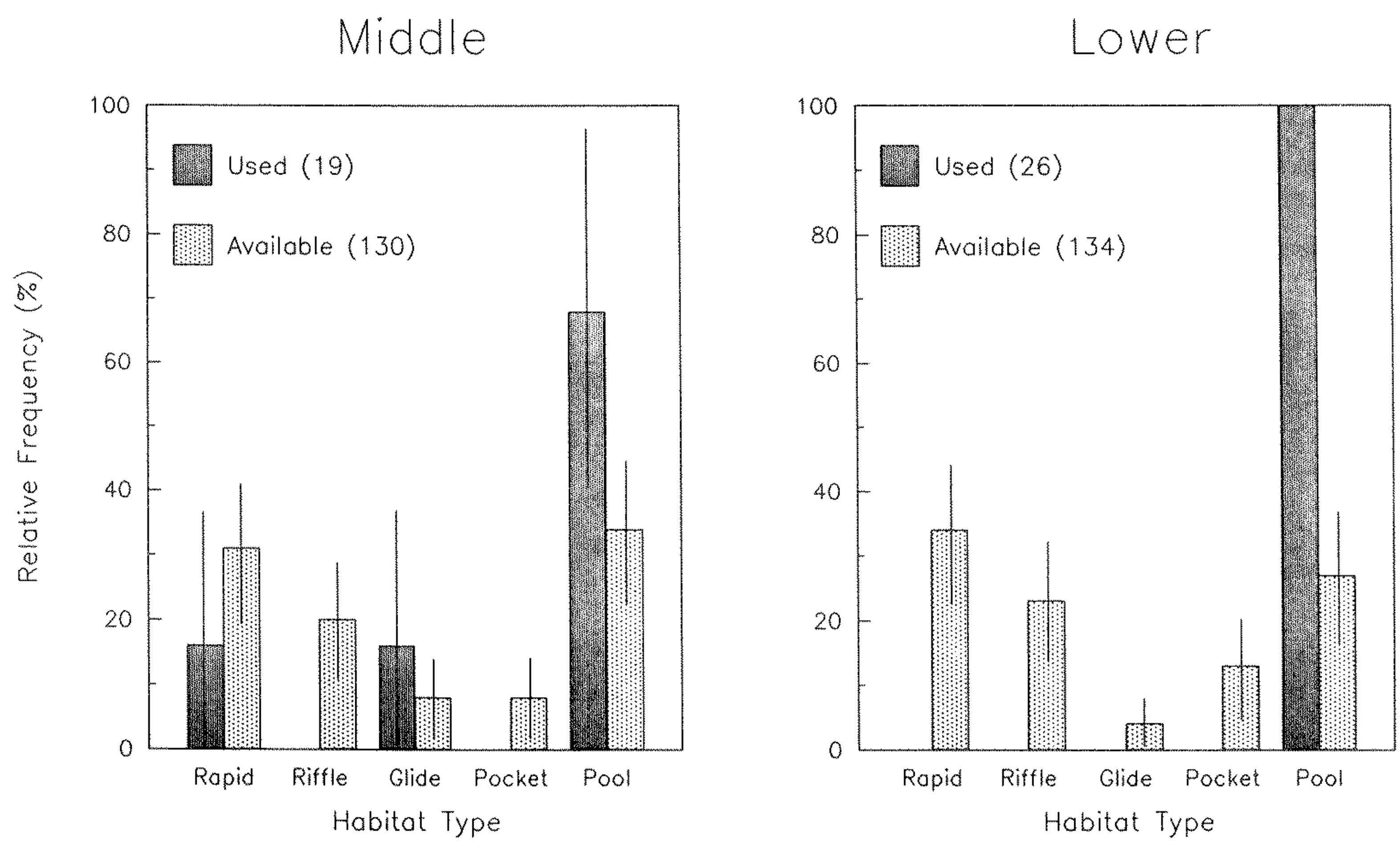

Figure 23. Point estimates and confidence intervals (95%) of winter habitat types used by radio-tagged rainbow trout (>225 mm) compared to available types in the middle and lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

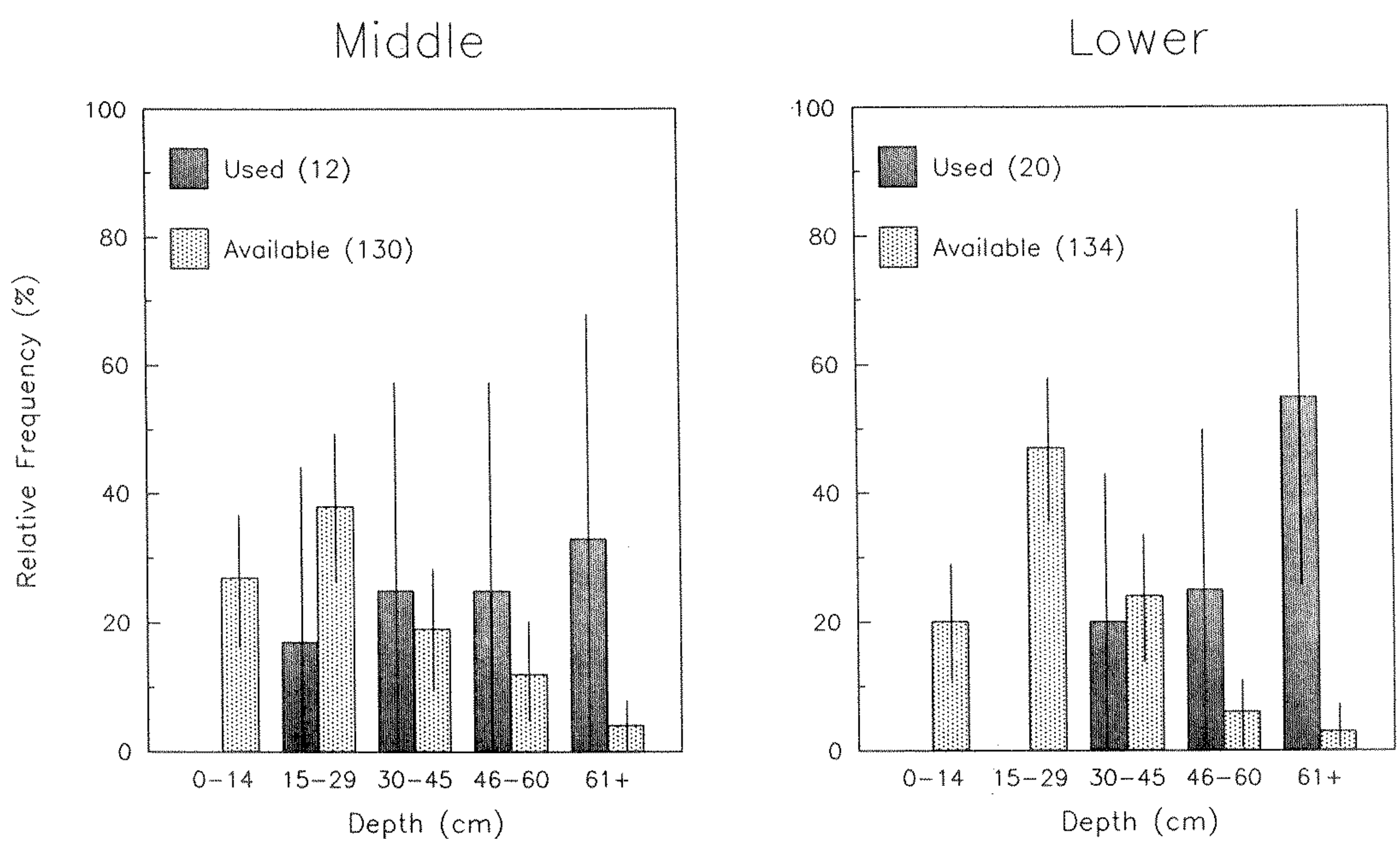

Figure 24. Point estimates and confidence intervals (95%) of winter depths used by radio-tagged rainbow trout (>225 mm) compared to available depths in the middle and lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

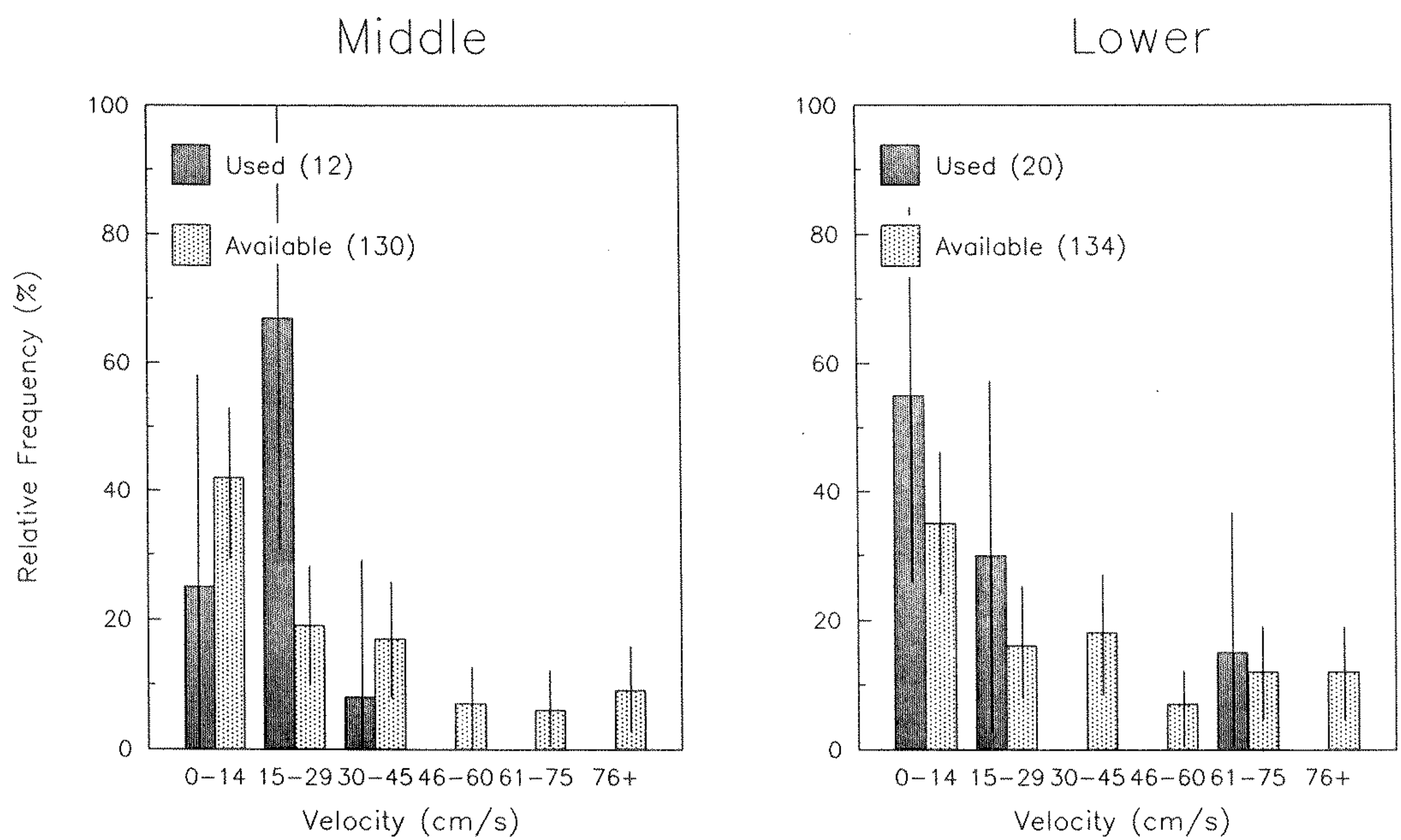

Figure 25. Point estimates and confidence intervals (95%) of winter velocities used by radio-tagged rainbow trout (>225 mm) compared to available velocities in the middle and lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

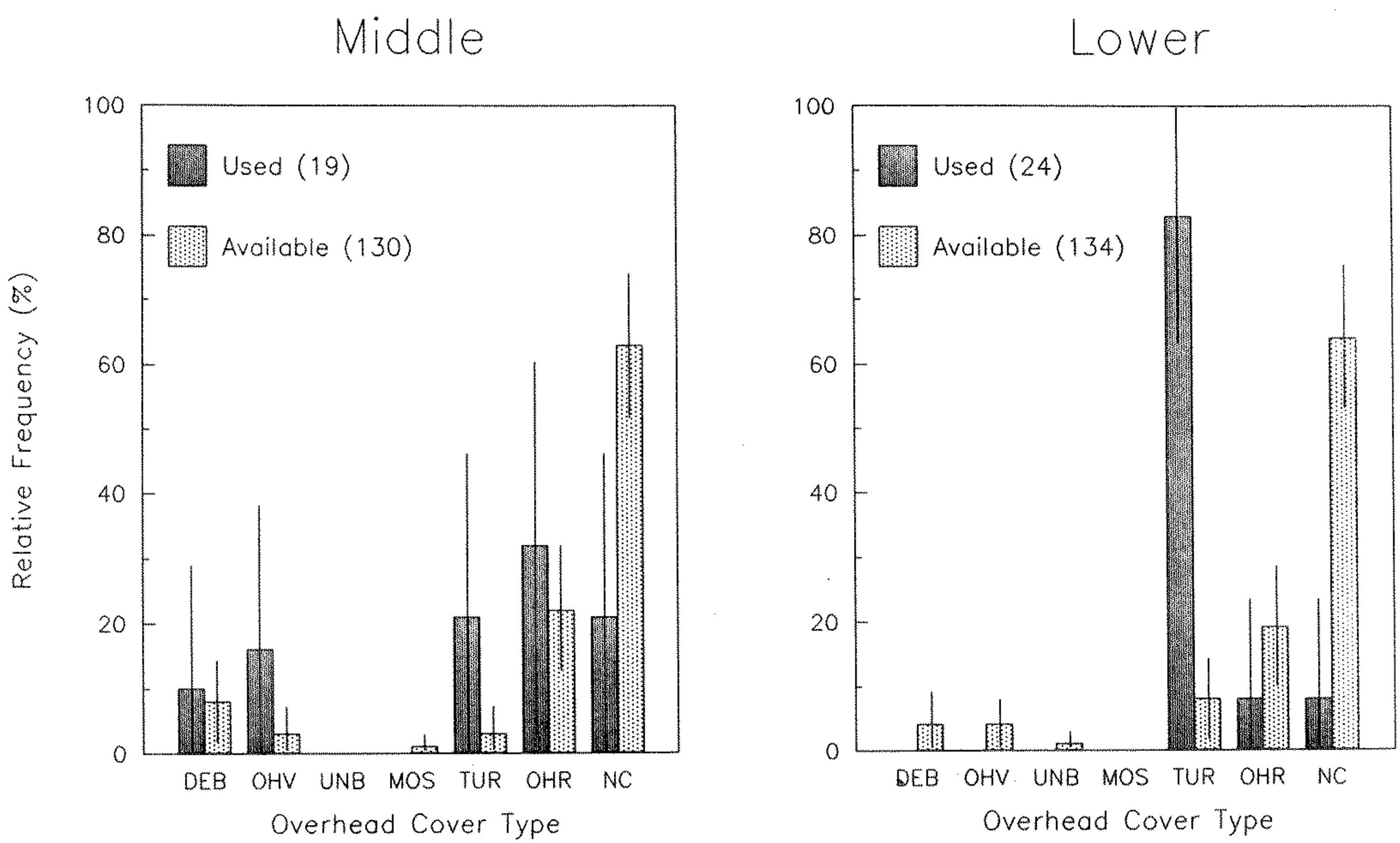

Figure 26. Point estimates and confidence intervals (95%) of winter overhead cover types used by radio-tagged rainbow trout (>225 mm) compared to available types in the middle and lower sections, South Willow Creek, Montana. Organic debris = DEB, overhanging vegetation = OHV, undercut bank = UNB, moss = MOS, turbulence = TUR, overhanging rock = OHR, no cover = NC. Sample sizes are in parentheses.

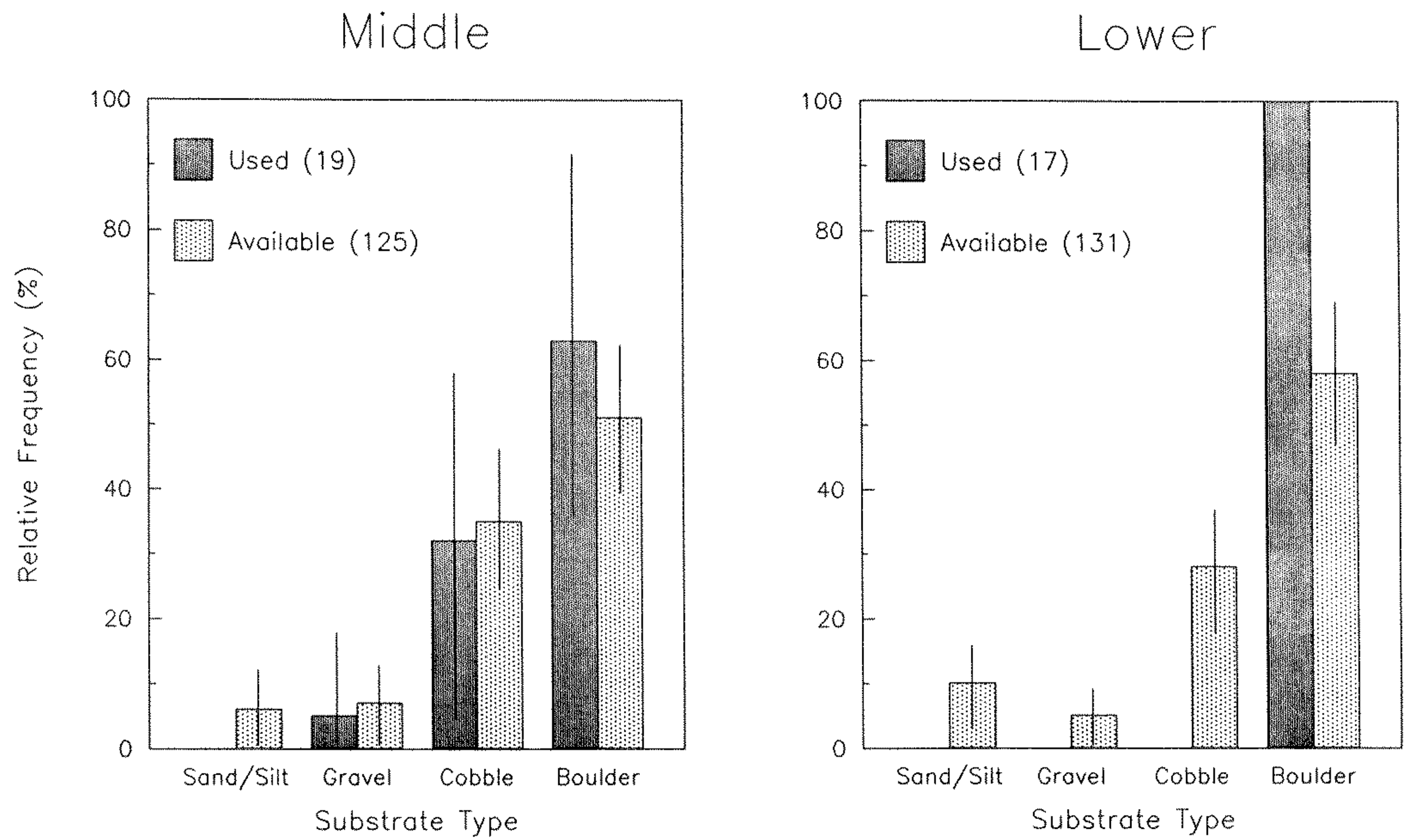

Figure 27. Point estimates and confidence intervals (95%) of winter substrate types used by radio-tagged rainbow trout (>225 mm) compared to available types in the middle and lower sections, South Willow Creek, Montana. Sample sizes are in parentheses.

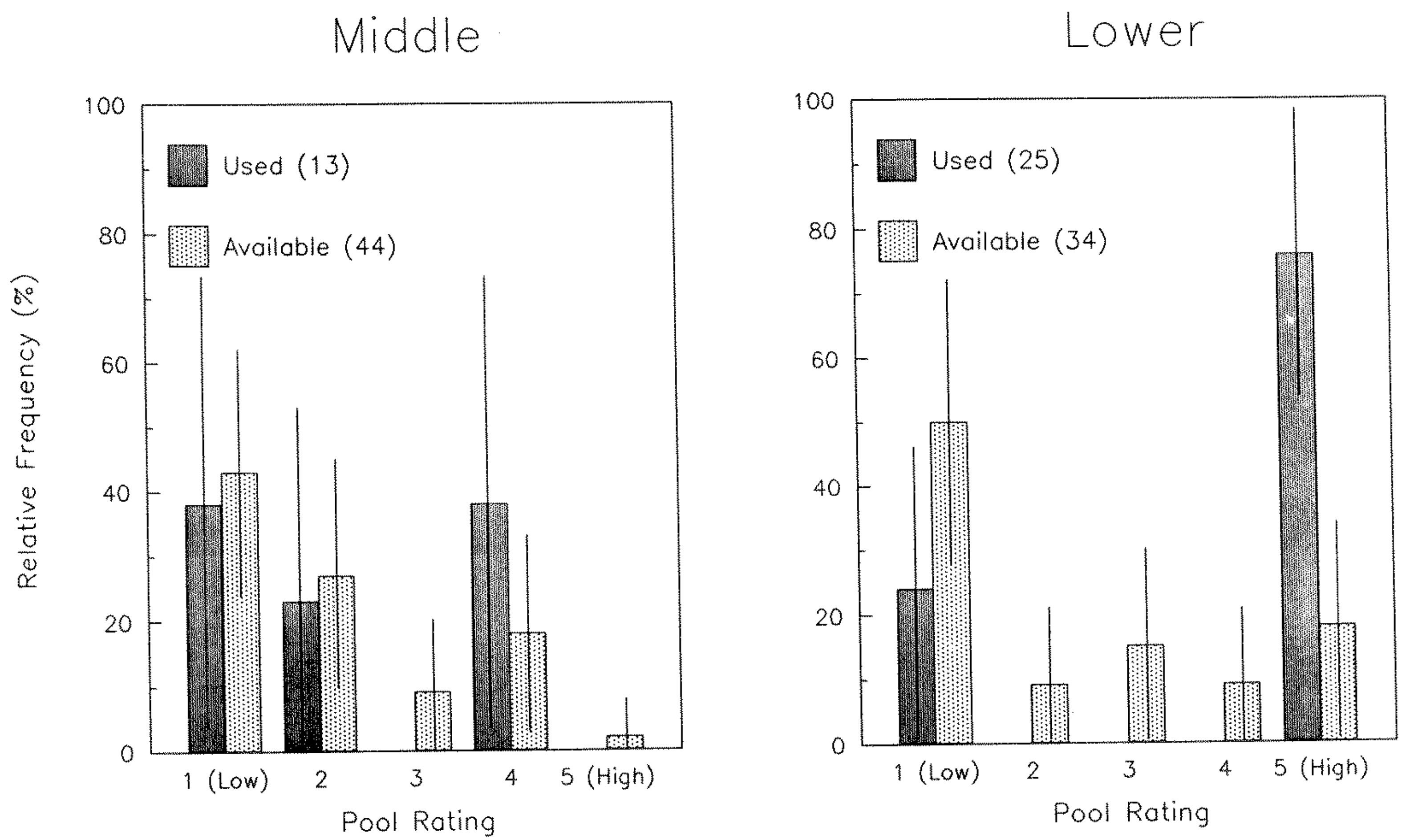

Figure 28. Point estimates and confidence intervals (95%) of rated pools used by radio-tagged rainbow trout (>225 mm) during winter compared to those available in the middle and lower sections, South Willow Creek, Montana. Lowest quality pools = 1 and highest = 5. Sample sizes are in parentheses.