WINTER HABITAT SELECTION OF CUTTHROAT TROUT
(Oncorhynchus clarki) IN A LARGE, REGULATED RIVER

by

Ronald A. Englund

A thesis submitted in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Fisheries and Wildlife

Approved:

UTAH STATE UNIVERSITY
Logan, Utah
1991
ACKNOWLEDGEMENTS

I would like to thank the Utah Division of Wildlife Resources and the U.S. Bureau of Reclamation for funding this study. I would also like to express my appreciation for the support and enthusiasm of my major professor, Timothy Modde. Committee members Jim Dobrowolski and Bill Helm were very helpful and I appreciate their time, effort, and helpful reviews. Richard Cutler was also very helpful in reviewing the statistics used for my thesis. Jack Griffith was helpful in the early design of the snorkel counts, and Jeff Kershner also provided useful input for this study.

I extend a warm thanks for the many people that helped me with field work: Mike Buntjer, Randall Filbert, Keith Lawrence, Craig Milewski, Ralph Mitchell, Ken Theis, Thom Richardson, Ken Tiffen, and Doug Young. A special thanks goes to Brian Platz, who was instrumental in ably assisting me with the snorkel counts and SCUBA dives in the treacherous Green River.

I would like to thank the two people that have always encouraged me in everything I have ever done, my parents, Stanley and Marjorie Englund. I could not have attempted this research without their support, and their support of my entire educational process has been incredible. Finally, I would to thank Davelyn Sue Kanewa for her endless support and encouragement. Without her patience and understanding, this research would have been impossible to complete. Me ke aloha pumehana, Davi.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>ii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>iv</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>v</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vi</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>STUDY SITE</td>
<td>3</td>
</tr>
<tr>
<td>METHODS</td>
<td>4</td>
</tr>
<tr>
<td>Microhabitat data collection</td>
<td>4</td>
</tr>
<tr>
<td>Macrohabitat data collection</td>
<td>6</td>
</tr>
<tr>
<td>Diel movements</td>
<td>7</td>
</tr>
<tr>
<td>Statistical analysis</td>
<td>8</td>
</tr>
<tr>
<td>RESULTS</td>
<td>9</td>
</tr>
<tr>
<td>Microhabitat use</td>
<td>9</td>
</tr>
<tr>
<td>Seasonal macrohabitat distribution</td>
<td>11</td>
</tr>
<tr>
<td>Diel movements</td>
<td>14</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>15</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>21</td>
</tr>
</tbody>
</table>
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Cutthroat trout microhabitat use (mean values) among macrohabitat types in winter 1988</td>
<td>11</td>
</tr>
<tr>
<td>2. Percent cutthroat trout behavior mode found in eddies, runs, and riffles for the winters of 1988 and 1989</td>
<td>12</td>
</tr>
<tr>
<td>3. Percent cutthroat trout observed in each macrohabitat in the winters of 1988 and 1989</td>
<td>14</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Study site and study reaches, Green River below Flaming Gorge Dam, near Dutch John, Utah</td>
<td>25</td>
</tr>
<tr>
<td>2. Proportion of substrate use for cutthroat trout in eddies, runs, and riffles</td>
<td>26</td>
</tr>
<tr>
<td>3. The proportion of depths used by cutthroat trout in eddies, runs, and riffles</td>
<td>26</td>
</tr>
<tr>
<td>4. Cutthroat trout fish elevation (distance above substrate) in eddies, runs, and riffles</td>
<td>27</td>
</tr>
<tr>
<td>5. The proportion of focal velocities used by cutthroat trout in eddies, runs, and riffles</td>
<td>28</td>
</tr>
<tr>
<td>6. Percent cutthroat trout found in each size class in eddies, runs, and riffles</td>
<td>29</td>
</tr>
<tr>
<td>7. The total amount of surface area of eddies, pools, runs, and riffles in each reach</td>
<td>30</td>
</tr>
<tr>
<td>8. Mean numbers of fish counted per linear meter in eddy macrohabitats. Vertical bars are standard error of the mean</td>
<td>31</td>
</tr>
<tr>
<td>9. Mean numbers of fish counted per linear meter in pool macrohabitats. Vertical bars are standard error of the mean</td>
<td>32</td>
</tr>
<tr>
<td>10. Mean numbers of fish counted per linear meter in run macrohabitats. Vertical bars are standard error of the mean</td>
<td>33</td>
</tr>
<tr>
<td>11. Mean numbers of fish counted per linear meter in riffle macrohabitats. Vertical bars are standard error of the mean</td>
<td>34</td>
</tr>
<tr>
<td>12. Cutthroat trout macrohabitat electivity values in eddies, pools, runs, and riffles</td>
<td>35</td>
</tr>
<tr>
<td>13. Rainbow trout macrohabitat electivity values in eddies, pools, runs, and riffles</td>
<td>36</td>
</tr>
</tbody>
</table>
ABSTRACT

Winter Habitat Selection Of Cutthroat Trout
(Oncorhynchus clarki) In A Large Regulated River

by

Ronald A. Englund, Master of Science
Utah State University, 1991

Major Professor: Dr. Timothy Modde
Department: Fisheries and Wildlife

Microhabitat use by cutthroat trout and macrohabitat use by both cutthroat and rainbow trout were studied in the Green River below Flaming Gorge Dam during the winters of 1988 and 1989. Microhabitat parameters used by cutthroat trout, such as focal velocity, depth, and fish elevation, differed significantly in eddies, runs, and riffles. Mean focal velocities in runs were 0.79 body lengths/seconds (bl/s), in riffles 0.66 bl/s, and in eddies 0.24 bl/s. Cutthroat trout size also varied significantly with macrohabitat; larger fish were found in riffles.

Macrohabitat use by cutthroat trout and rainbow trout differed significantly among species, macrohabitat types, and months. Both rainbow trout and cutthroat trout macrohabitat use shifted from lower velocity habitats during winter to faster velocity habitats in summer. Cutthroat trout and rainbow trout used macrohabitats at seasonally differing rates. Riffles were never selected in proportion to their
INTRODUCTION

Habitat selection by salmonids is a process of optimizing energetic expenditures while minimizing energetic costs and is related to body form and competition (Fausch 1984; Bisson et al. 1988). The specific location occupied by salmonids is a function of biotic factors associated with fitness and the physical structure of available habitat. Although salmonids have been described as using specific microhabitat ranges (Griffith 1972; Fausch 1984; Cunjak and Power 1986), species such as rainbow trout (Oncorhynchus mykiss) and cutthroat trout (O. clarki) are flexible in their habitat needs, existing in both lacustrine and lotic habitats during the same life stage. My study evaluated the flexibility of cutthroat trout winter microhabitat use and the variability throughout the year of macrohabitat selection by both cutthroat trout and rainbow trout in a regulated reach of the Green River.

Bisson et al. (1988) described the morphology of cutthroat trout as intermediate in shape between the steelhead, which prefers higher velocity habitats, and the coho salmon (O. kisutch), which selects slower velocity habitats. Glova (1984, 1986, 1987) observed that allopatric populations of cutthroat trout selected slow velocity habitats, but in the presence of coho salmon, were displaced into higher velocity habitats. Displacement of cutthroat trout to higher velocity habitats has its greatest impact during the winter months when most salmonids shift to slower velocity habitats (Campbell and Neuner 1985) in response to decreasing metabolic rates associated with lower
abundance, especially during high winter discharges. Cutthroat trout implanted with radiotransmitters exhibited little movement during diel monitoring and did not change their occupation of macrohabitats (37 pages).
INTRODUCTION

Habitat selection by salmonids is a process of optimizing energetic expenditures while minimizing energetic costs and is related to body form and competition (Fausch 1984; Bisson et al. 1988). The specific location occupied by salmonids is a function of biotic factors associated with fitness and the physical structure of available habitat. Although salmonids have been described as using specific microhabitat ranges (Griffith 1972; Fausch 1984; Cunjak and Power 1986), species such as rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*) are flexible in their habitat needs, existing in both lacustrine and lotic habitats during the same life stage. My study evaluated the flexibility of cutthroat trout winter microhabitat use and the variability throughout the year of macrohabitat selection by both cutthroat trout and rainbow trout in a regulated reach of the Green River.

Bisson et al. (1988) described the morphology of cutthroat trout as intermediate in shape between the steelhead, which prefers higher velocity habitats, and the coho salmon (*O. kisutch*), which selects slower velocity habitats. Glova (1984, 1986, 1987) observed that allopatric populations of cutthroat trout selected slow velocity habitats, but in the presence of coho salmon, were displaced into higher velocity habitats. Displacement of cutthroat trout to higher velocity habitats has its greatest impact during the winter months when most salmonids shift to slower velocity habitats (Campbell and Neuner 1985) in response to decreasing metabolic rates associated with lower
water temperatures (Cunjak 1988). A lack of slow water habitat in winter can adversely affect trout populations (Johnson et al. 1987) by reducing trout carrying capacity (Chapman 1966; Bustard and Narver 1975; Mason 1976; Hickman and Raleigh 1982). Although energetic refuges are important to overwintering salmonid populations, few studies have described resident salmonid winter habitat use in large lotic systems.

Previous studies on salmonid winter habitat use in streams reported cover and low water velocities to be important in maintaining juvenile salmonid populations (Tschaplinski and Hartman 1983). Juvenile coho salmon and steelhead trout were found to shift from higher water velocities and less cover in the summer to lower water velocities (< 15 cm/s) and areas of greater cover as temperatures declined to 2° C (Bustard and Narver 1975). Brook trout (Salvelinus fontinalis) moved into areas of deeper and slower water during the winter, seeking refuge from high water velocities (Chisholm et al. 1987). Habitat shifts have been observed to occur in response to lowering energetic costs as metabolic efficiency decreases with water temperature (Cunjak 1988). Salmonid behavior changes with changing environmental conditions (Dill 1983), and seasonal shifts in habitat use are common in lotic environments (Gibson 1978; Rimmer et al. 1983; Campbell and Neuner 1985; Chisholm et al. 1987). In laboratory streams, low water temperatures and increases in water velocity are responsible for microhabitat shifts of coho salmon and chinook salmon to areas of greater cover and lower water velocities (Taylor 1988). In lotic systems, rainbow trout seek areas of high water velocities to
maximize food intake in the summer months (Smith and Li 1983) but seek backwater and slow-water habitats in the winter months (Bustard and Narver 1975; Campbell and Neuner 1985). Previous studies of winter salmonid habitat selection in small streams have determined that water depth may be a limiting factor during winter months (Bustard and Narver 1975; Tschaplinski and Hartman 1983; Campbell and Neuner 1985; Cunjak and Power 1986; Swales et al. 1986; Chisholm et al. 1987; Hillman et al. 1987). However, little is known of seasonal changes in trout macrohabitat selection or cutthroat trout winter microhabitat use in large, regulated rivers.

The objectives of this study were to describe the flexibility of cutthroat trout winter microhabitat use and to determine the extent of seasonal shifts in Colorado River cutthroat trout (*O. c. clarki*) and rainbow trout macrohabitat use in the Green River below Flaming Gorge Dam. Specifically, my objectives were to describe 1) microhabitat use among macrohabitats by cutthroat trout, 2) cutthroat trout microhabitat use associated with fluctuating discharges, 3) seasonal cutthroat trout and rainbow trout macrohabitat use, 4) cutthroat trout winter diel activity and macrohabitat use.

**STUDY SITE**

The study area included the 18.3 km section of the Green River from the Flaming Gorge Dam to the confluence of Red Creek (Figure 1). The elevation of the river bed ranged from 1705 m at the Flaming Gorge Dam Base to 1670 m at Red Creek. Water temperatures ranged from 3-6° C during the winter and 13-17° C during the summer. Discharges
released from the Flaming Gorge Dam vary from a low of 22.7 m³/s to a high of 110 m³/s. The study area was divided into four representative reaches based on geomorphology, dominant macrohabitat type, and river gradient (Figure 1). Within each reach the river was separated into macrohabitat types defined either as eddies, pools, runs, or riffles/rapids (Helm 1985; Upper Colorado River Basin Database 1987). Reach A contained the highest frequency of slow velocity eddy and pool habitats, Reach B consisted primarily of fast riffles and runs, Reach C was dominated by runs, and Reach D was largely pool habitat.

METHODS

Microhabitat Data Collection

Microhabitat was defined as the specific location or area in the river where a fish was located. Five variables were used to define microhabitat: focal velocity, water column depth, substrate size, cover type, and fish elevation (Griffith 1972). Focal velocity was the water velocity at the fish's snout (Griffith 1972) and was measured by a diver equipped with a Montedoro-Whitney PVM-2A current meter probe. An onshore technician recorded the velocity from a meter connected to the velocity probe. Ten-second velocity averages were used for each observation. The current meter probe was attached to a 2-m steel rod, which exceeded the minimum 1.5-m Morantz et al. (1986) recommended to avoid erroneous velocity measurements. Water column depth was the distance from the substrate to the surface of the river. In depths greater than 2-m, the water column depth was measured with a depth gauge on the diver's air gauge and with the current meter probe in
shallower waters. The Brusven substrate index was used to describe substrate size (Bovee 1982). Fish elevation represented the elevation of the fish above the substrate and was estimated to the nearest cm. Fish length was estimated by the diver. Observers equipped with SCUBA entered at the downstream end of a macrohabitat and moved slowly upstream while maintaining a low profile on the river bottom. Macrohabitat types sampled with SCUBA included eddies, runs, and riffles. Snorkeling was used in shallower portions of runs and riffles. When collecting microhabitat data, the diver selected the first fish sighted that was not noticeably affected by the diver's presence. Each individual fish was observed for 1-2 minutes to determine its focal point, or center of activity and feeding (Griffith 1972, Bustard and Narver 1975), before microhabitat variables were measured.

In addition to microhabitat variables, fish behavior mode was also recorded. Behavior mode was classified as either drift feeding, random swimming or stationary swimming. Fish in low velocity areas and swimming without orientation to the current were described as random swimming, while fish maintaining a single position by swimming with observable orientation to the current were designated as stationary swimming (Gosse 1981, 1982). Fish actively engaged in the capture of food were described as drift feeding.

Cutthroat trout microhabitat use data were collected from January 1 to March 15 during the winters of 1988 and 1989. Microhabitat data were sampled equally from the randomly selected eddies, runs, and riffles in reaches A, B, and C in the winter of 1988. In 1988,
microhabitat sampling was evenly divided among low (22.7-45 m$^3$/s), medium (46-80 m$^3$/s), and high (80-110 m$^3$/s) discharges. In the winter of 1988, discharges varied daily from 22.7 m$^3$/s to 110 m$^3$/s. Due to a drought in the Green River drainage beginning in 1988, only constant low flows were discharged from Flaming Gorge Dam (22.7 m$^3$/s) during the winter of 1989. Reach B was not sampled in 1989 because low discharges prevented transportation to the dive sites.

Macrohabitat Data Collection

Seasonal macrohabitat selection and distribution of cutthroat trout and rainbow trout in reaches A through D were determined from diver observations in randomly selected macrohabitat types (eddies, pools, runs, riffles) on 11 dates between 1988 and 1989. The same macrohabitats were sampled through time, with one pass made for each macrohabitat sampled. Macrohabitat types were sampled in proportion to their abundance in the Green River study area. Two divers counted fish with each diver maintaining equal spacing on the opposite ends of a 2-cm diameter, 4.5-m PVC pipe (Schill and Griffith 1984). Because visibility in the Green River was usually at least 4-m, the length of the PVC pipe reduced duplicate counts by divers and maintained a consistent counting lane. Each diver counted fish directly downstream and to the side opposite of the other diver. Fish in the middle were not counted to further reduce duplicate counts (Schill and Griffith 1984).
Diel Movements

Winter diel cutthroat trout macrohabitat selection was monitored using radiotelemetry during the winters of 1988 and 1989. Cutthroat trout were captured from the Green River by angling and electrofishing. To ensure fish were collected from different habitats in the river, trout were captured by both electrofishing in shallow areas (< 2-m) and angling in deeper areas (> 2-m) of the river. Immediately following capture, fish were marked with an external color-coded tag to allow underwater identification. After tagging, the cutthroat trout were placed in a fish cage and, after a one-hour recovery period, anaesthetized with MS-222 and implanted with 30 mHz radio transmitters. Fish were released into the river after they appeared to be swimming strongly. Fish were allowed a three-week acclimation period before data collection began.

In the winter of 1988, transmitters with an expected life of 90 days were used, while smaller 30-day transmitters were used for 8 small cutthroat trout in 1989. A total of 16 cutthroat trout in four different size classes were implanted with radio transmitters in both the winters of 1988 and 1989.

Monitoring of implanted fish over a 24-h period occurred seven times in the two winters. Due to assumed mortalities or loss of the radio transmitter signal, a total of six cutthroat trout were monitored in the winters of 1988 and 1989. Fish location was monitored every two to three hours during the 24-h period. Triangulation points were marked with double stakes on the river bank. Macrohabitat location, mean water column velocity, water depth, and substrate size were
recorded at the triangulation point. Measurements were taken after the
diel monitoring period was completed. To quantify cutthroat trout
movements, diel changes were measured on river maps traced from aerial
photographs.

Statistical Analysis
Cutthroat trout microhabitat data were normally distributed
(Kolmogorov-Smirnov test, NS) and variances were homogeneous
(Bartlett's test, NS). The SAS software program was used for these
tests, and the Number Cruncher Statistical System (NCSS) software
program was used for all remaining tests. An unbalanced design, one-
way analysis of variance (ANOVA) was used to determine if cutthroat
tROUT size significantly differed among eddies, runs, or riffles.
Linear regression was used to describe whether facing velocity was
dependent on discharge during the winter of 1988, the only year that
a range of different discharges occurred. A one-way ANOVA was used to
determine if mean focal velocity, water column depth, and fish
elevation differed among eddies, runs, and riffles. When differences
existed, Fisher's LSD test identified these differences. Focal
velocity was converted into body lengths/second to more accurately
represent the energy demands of the fish.

Seasonal macrohabitat use for cutthroat trout and rainbow trout
was determined by the total number of fish counted in a macrohabitat
type and dividing by the total length (meters) of the macrohabitat
sampled. Electivity was used to determine if seasonal macrohabitat use
by rainbow and cutthroat trout varied among macrohabitat types.
Chesson's $\alpha$, calculated from the following equation was used as the electivity index:

$$\alpha^i = \frac{(r_i/p_i)}{\sum_{i=1}^{n} (r_i/p_i)}.$$

In the above equation, $r$ is the relative amount of available macrohabitat and was determined by the length in meters of each macrohabitat sampled, and $p$ is the relative use of each habitat type (Lechowicz 1982). A three-way ANOVA comparing fish numbers/meter by macrohabitat, fish species, and month was used to determine if cutthroat trout and rainbow trout differed in macrohabitat selection and monthly use of macrohabitat types. To stabilize variances, total fish numbers counted in a macrohabitat type each month were transformed to the square root of fish numbers/length of macrohabitat sampled.

Time categories relative to daily trout activity were determined by dividing the day between sunrise and sunset into five intervals and the remaining period into five additional intervals for a total of ten daily time intervals. The average distance and standard error each cutthroat trout moved was calculated for each time period.

RESULTS

Microhabitat Use

Association of cutthroat trout to substrate in different macrohabitat types showed no clear pattern of use (Figure 2). Cutthroat trout in eddies tended to be associated with either fine substrates or large boulders. Trout in runs and riffles were associated more with cobble- and boulder-sized substrate.
Results of linear regression indicated no dependence of focal velocity to discharge from fish observed in riffles ($r^2 = 0.048, P = 0.63$), runs ($r^2 = 0.061, P = 0.12$), or eddys ($r^2 = 0.002, P = 0.80$). A one-way ANOVA detected differences in the use of depths ($F_{(2,67)} = 12.9, P < 0.001$), focal velocities ($F_{(2,67)} = 16.7, P < 0.001$), and fish elevations ($F_{(2,7)} = 20.7, P < 0.001$) among macrohabitat types by cutthroat trout during the winter of 1988 (Table 1). Fisher's LSD detected no difference in microhabitat variables between run and riffle macrohabitats (Table 1), while differences were detected between eddies relative to both runs and riffles. Cutthroat trout used the greatest depths in eddies, and used shallower depths in runs and riffles (Table 1, Figure 3). More than 50% of the cutthroat trout were found between 1.5-2.5-m in eddies, while greater than 94% of the fish observed in riffles were found in water less than 1.5-m deep. Depth occupied in runs was intermediate to that of eddies and riffles. Cutthroat trout were found in lower elevations in riffles and runs, and at higher elevations in eddies (Table 1, Figure 4). Cutthroat trout used lower focal velocities in eddies than in runs and riffles. Most velocities (96%) used in eddies were less than 1.0 bl/s, while 23.6% and 37.6% of velocities were greater than 1.0 bl/s, respectively, in riffles and runs (Figure 5).

Size distribution of cutthroat trout differed among macrohabitat types (Figure 6). One-way ANOVA detected differences between the mean size of fish found in riffles, runs, and eddies ($F_{(2,145)} = 14.16, P < 0.001$). Average fish size in eddies was 33-cm (±9.1 SD), 33.2-cm (±7.5 SD) in runs, and 44.2-cm (±5.7 SD) in riffles. Fisher's LSD detected
a difference between cutthroat trout size in riffles from those in eddies and runs ($P = 0.01$). Cutthroat trout behavior mode also varied

Table 1.—Cutthroat trout microhabitat use (mean values) among macrohabitat types in winter 1988. Asterisks (*) denote $P < 0.05$; NS = not significant.

<table>
<thead>
<tr>
<th>Macrohabitat Parameter</th>
<th>Eddy (67)</th>
<th>Run (64)</th>
<th>Riffle (17)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Focal Velocity (bl/s)</td>
<td>0.26 *</td>
<td>0.84 NS</td>
<td>0.97 NS</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>2.46 *</td>
<td>1.22 NS</td>
<td>1.11 NS</td>
</tr>
<tr>
<td>Fish Elevation (m)</td>
<td>0.91 *</td>
<td>0.24 NS</td>
<td>0.30 NS</td>
</tr>
</tbody>
</table>

with macrohabitat type. Fish in riffles and runs were found almost exclusively in the (Table 2) stationary swimming mode, while fish in eddies were most often observed in the random swimming mode. Drift feeding did not occur frequently in any habitat but was most common in riffles (Table 2).

**Seasonal Macrohabitat Distribution**

Based on aerial photographs taken at a $22.7 \text{ m}^3/\text{s}$ discharge, total macrohabitat surface area within each reach varied, with the greatest area of slower water velocity macrohabitats such as eddies and pools occurring in reach A (Figure 7). Reach B had the greatest area of higher velocity riffles, and contained little slow water habitat. Reach C contained the greatest area of runs, and reach D consisted mainly of pools.

Both rainbow trout and cutthroat trout used lower velocity macrohabitats at a greater rate when discharge was high and variable.
during 1988. Higher velocity macrohabitats were used to a greater extent during low, stable discharges in 1989 (Figures 8-11).

Table 2.--Percent cutthroat trout behavior mode found in eddys, runs, and riffles for the winters of 1988 and 1989.

<table>
<thead>
<tr>
<th>Behavior Mode (%)</th>
<th>Eddy</th>
<th>Run</th>
<th>Riffle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random Swimming</td>
<td>65.7</td>
<td>4.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Stationary Swimming</td>
<td>29.7</td>
<td>90.8</td>
<td>88.9</td>
</tr>
<tr>
<td>Drift Feeding</td>
<td>4.5</td>
<td>4.6</td>
<td>11.1</td>
</tr>
</tbody>
</table>

In the winter of 1989, fish counts were generally higher each month in all habitat types except for eddies, when compared to the previous winter (Figures 8-11). Changes in underwater visibility due to fluctuating flows were probably responsible for the wide range of fish counts. During periods of high fluctuating discharges in 1988, underwater visibility usually ranged from 4-5-m. Visibility was 11-m or more during the low, constant flows of 1989. This could account for the higher number of fish counted in pools in the winter of 1989 (Figure 9). There was variation in the number of fish counted in runs, but a general non-significant trend of increasing numbers in runs from winter to summer months was noted for cutthroat trout (Figure 10). Fish counts were the most constant in riffles, with numbers of both cutthroat and rainbow trout increasing from winter to summer months (Figure 11).

Macrohabitat electivity was greatest for eddies, both by cutthroat and rainbow trout; especially during the high discharge winter of 1988 (Figures 12, 13). Eddies were highly selected in ten
of eleven months by cutthroat trout and nine of eleven months by rainbow trout. Electivity for pools was highest in February 1989. Trout did not select pool macrohabitats during periods of high flows, but increased selection of pools during the low-flow 1989 winter. Selection of eddies was high in both winter and spring for cutthroat trout.

Macrohabitat selection varied by season and discharge regime, with a general non-significant trend toward increasing selection of faster water macrohabitats during summer months. Relative selection of runs and riffles was lowest during periods of high discharges, such as the winter of 1988, for both cutthroat trout and rainbow trout. Cutthroat trout did not consistently select runs until discharges became low and constant after September, 1988; this contrasts with greater selection of runs by rainbow trout. Although riffles were never used extensively by cutthroat trout, electivity (α) increased from a low of 0.024 in March, 1988 to a high of 0.168 in September, 1989. Selection of riffles by both cutthroat trout and rainbow trout was higher during the low-flow winter of 1989 than during the high-flow winter of 1988.

A measure of the total use of each macrohabitat type by cutthroat trout in the winters of 1988 and 1989 was determined by multiplying the mean number of fish counted/linear meter during the winter months by the total length of available macrohabitat in the Green River (Table 3). In the winter of 1988, the slow-water macrohabitats, eddies and pools, accounted for greater than 60% of the cutthroat trout observed. During the low-flow winter of 1989 less than 55% of cutthroat trout used slow-water macrohabitats.
Table 3.--Percent cutthroat trout observed in each macrohabitat in the winters 1988 and 1989.

<table>
<thead>
<tr>
<th>Macrohabitat</th>
<th>Winter 1988</th>
<th>Winter 1989</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eddy</td>
<td>19.8</td>
<td>11.9</td>
</tr>
<tr>
<td>Pool</td>
<td>40.7</td>
<td>42.6</td>
</tr>
<tr>
<td>Run</td>
<td>38.9</td>
<td>40.5</td>
</tr>
<tr>
<td>Riffle</td>
<td>0.6</td>
<td>4.9</td>
</tr>
</tbody>
</table>

Relative trout densities (fish/m) were significantly different among macrohabitats, between species, and over time. A three-way ANOVA detected differences in rainbow trout and cutthroat trout densities among macrohabitats ($F_{(3,30)} = 2.56, P < 0.01$). Rainbow trout relative densities were greater than those of cutthroat trout ($F_{(3,30)} = 11.25, P < 0.001$). Also, both rainbow trout and cutthroat trout densities were different among count dates ($F_{(10,30)} = 2.75, P < 0.05$). Rainbow trout selected higher velocity macrohabitats such as runs and riffles in a greater percentage than cutthroat trout. Runs were selected in percentages greater than availability by cutthroat trout only when discharges were relatively low and stable after September 1988. Electivity of riffles by rainbow trout was greater than cutthroat trout electivity values for eight of eleven months. Cutthroat trout electivity values for slow-water eddy macrohabitats were greater than those of rainbow trout for 10 of 11 months.

**Diel Movements**

Due to transmitter failure and probable fish mortality, only three cutthroat trout in the winter of 1988 and four in the winter of 1989 were monitored over a twenty-four hour diel period. Of the seven fish
monitored through twenty-four hour periods, none moved from the initially occupied macrohabitat type during the observation period. Mean distance moved and standard errors were calculated from six fish. One fish was monitored twice due to transmitter failure in all other implanted fish. The distance moved between monitoring periods was not measured for one of the seven cutthroat trout due to measurement difficulties caused by high flows. Although mean distances moved within a macrohabitat type were variable during the twenty-four period, movements were small and ranged from 4-8-m (Figure 14).

**DISCUSSION**

Microhabitat occupied by cutthroat trout in the Flaming Gorge Dam tailwaters differed among macrohabitat types. Although availability was not measured, microhabitat use by cutthroat trout appeared to respond to microhabitat availability with focal velocity lowest and water depth greatest in eddies, and conversely fish in riffles occupied the highest velocity and shallowest microhabitats. Eddies in the Green River are slow, counter-currents formed below riffles and adjacent to runs, and represent hydraulic refuges for fish that are located close to higher velocity habitats which have higher invertebrate drift rates (Everest and Chapman 1972; Smith and Li 1983). High use of eddies by cutthroat trout may represent a cost-minimizing energetic strategy.

Cutthroat trout macrohabitat selection in the Green River differed between winters. During periods of higher discharges, cutthroat trout used lower velocity macrohabitats, but increased their use of faster velocity macrohabitats during periods of lower discharges. Similarly,
in a Pennsylvania stream, Bachman (1984) determined brown trout used discrete, energy-saving foraging sites, while Fausch (1984) found salmonids established intraspecific heirarchies with dominant fish maintaining positions allowing maximum potential energetic gains. Mean focal velocities in runs were more than three times greater than that of mean focal velocities in eddies. Greater than 96% of focal velocities used in eddies were less than 1.0 bl/s, indicating cutthroat trout were expending less energy in eddies as compared to runs and riffles. Although eddies comprised only 3.7 percent of the total available macrohabitat in the Flaming Gorge tailwater, 11.9% (winter 1989) to 19.8% (winter 1988) of cutthroat trout counted during the winter months were located in eddies. Eddies provided an important velocity refuge for cutthroat trout, especially during winters with high discharges.

Flexibility in habitat use by the Colorado River cutthroat trout is evident by their establishment in both lakes and rivers (Martinez 1988). Substantial percentages of cutthroat trout were found in run and riffle macrohabitats, even though these macrohabitats were often selected in lower proportions than eddies and pools. If macrohabitats are combined into two general velocity categories of high (riffles and runs) and low (eddies and pools) velocities, percentages of cutthroat trout found in high velocity macrohabitats were approximately 40% for the winters of 1988 and 1989. Fish in low velocity macrohabitats have less available food and lower energetic costs, while fish in high velocity macrohabitats have higher energetic costs but also have access to greater prey densities. Thus cutthroat trout may exhibit two
behavioral modes during the winter in the Flaming Gorge Tailwater. Diel monitoring of winter cutthroat trout movements suggested that fish spend most of their time in a single macrohabitat type. Gosse (1982) reported similar results in the Green River and found significant differences in focal velocity use between cutthroat trout observed in the stationary swimming mode as compared to the random swimming mode. Stationary swimming was usually found in high velocity macrohabitats, as compared to random swimming which was found only in low velocity macrohabitat types.

Cutthroat trout found in riffles were significantly larger than those occupying eddies and runs. Although fish in eddies were similar in size to fish in runs, velocities used in runs were significantly greater. Energetic factors probably contribute to the incidence of larger fish being found in riffles, and may exclude smaller cutthroat trout from high velocity riffle macrohabitats. For example, a fish 25 cm would swim at a rate of 2 bl/s in a 50 cm/s water velocity, while a 50 cm fish could maintain its position at only 1 bl/s. Similar size-dependent hierarchical use of habitat due to intraspecific competition between age classes was found for brown trout in a small Swedish stream (Bohlin 1977, 1978).

Seasonality was another major factor influencing trout macrohabitat selection. Electivity for both cutthroat trout and rainbow trout shifted from low velocity macrohabitat types in the winter to high velocity macrohabitat types in the summer. Electivity of eddies was high in almost all months for cutthroat trout, while rainbow trout preferred high velocity macrohabitats. Rainbow trout
selected riffle macrohabitats in greater proportions than cutthroat trout, and this is consistent with predictions based on body form (Bisson et al. 1988). Similar seasonal shifts have been reported for other salmonid populations, with brown and brook trout in Ontario streams using areas of lower water velocities in the winter relative to summer (Cunjak and Power 1986). Hicks and Watson (1985) reported seasonal movements of rainbow and brown trout in a New Zealand river. In Cascade Mountain streams in Washington, numbers of rainbow trout using pool habitats during winter doubled compared to those in pools during the summer (Campbell and Neuner 1985).

Seasonal changes in macrohabitat selection by cutthroat trout in the Green River may be due to a combination of energetic factors caused by changes in temperature. As temperatures decline in the fall, salmonids undergo a stressful period of acclimatization accompanied by declining body condition and fat reserves (Cunjak 1988). To cope with declines in energetic reserves, salmonids may seek areas of lower-water velocities as metabolic deficits occur when temperatures decrease in the fall (Cunjak and Power 1987). Similarly, cutthroat trout in the Green River selected lower water velocity macrohabitat types in the colder winter months. Temperature affects salmonid sustained swimming speeds more than burst speeds (Brett 1964) and this temperature effect is probably linked to seasonal changes in cutthroat trout macrohabitat selection in the Green River. Thus, regardless of flow regime, salmonids may seek areas of lower velocities in rivers as an energy-minimization strategy.
Cutthroat trout did not highly select runs until discharge rates were low and stable after September 1988. Cutthroat trout also selected riffles in greater proportions during periods of lower discharges. Rainbow trout selection of riffles showed a similar trend with lower use during periods of high discharge.

The response of salmonids to changes in discharge has been variable. Reductions in discharge of up to 95% decreased rainbow trout densities by 40% in simulated stream channels in Oregon (White et al. 1981). Heggenes (1988) found that increases in peaking discharges of 4-100 times did not displace brown trout from a small Norwegian stream. Stream discharge appeared to effect fish activity in a small coastal stream in British Columbia, with juvenile coho salmon entering into low velocity side channels during winter freshets (Bustard and Narver 1975). Tschaplinski and Hartman (1983) found juvenile coho salmon populations in British Columbia streams to be reduced by nearly 75% after major increases in stream discharge. No differences were found among brook and brown trout physiological measures of stress in a stable, spring-fed section of river as compared to a naturally fluctuating section of the same Ontario river (Cunjak 1988).

Individuals within the same population of cutthroat trout in the Green River occupied different microhabitats, with microhabitat use differing by macrohabitat location. The macrohabitats sampled in the Green river consisted of two general categories, high and low velocity. Microhabitat use was different in low velocity macrohabitats as compared to high velocity run and riffle areas. Thus, cutthroat trout microhabitat use varied widely according to the macrohabitat type.
inhabited. Ehlinger (1990) determined bluegill sunfish (*Lepomis macrochirus*) exhibited similar patterns of differential habitat use, with some individuals foraging in open-water habitats, and others in littoral areas. These behavioral differences were correlated with morphological differences in bluegill pectoral fin size.

The results of this study indicated adult cutthroat trout macrohabitat and microhabitat selection were flexible in a large-regulated river. Cutthroat trout microhabitat use was dependent upon the macrohabitat inhabited, which may be influenced by seasonality and size of fish. In winter, cutthroat trout exhibited two different spatial use patterns, with some fish selecting low prey density macrohabitats with lower energetic costs, and other fish selecting high prey density macrohabitats with greater energy costs.
REFERENCES


Gibson, R.J. 1978. The behavior of juvenile atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) with regard to temperature and water velocity. Transactions of the American Fisheries Society 107:703-712.


Figure 1.-(A) Study site. (B) Study reaches, Green River below Flaming Gorge Dam, near Dutch John, Utah.
Figure 2.--Proportion of substrate use for cutthroat trout in eddies, runs, and riffles.

Figure 3.--The proportion of depths used by cutthroat trout in eddies, runs, and riffles.
Figure 4.--Cutthroat trout fish elevation (distance above substrate) in eddies, runs, and riffles.
Figure 5.--The proportion of focal velocities used by cutthroat trout in eddies, runs, and riffles.
Figure 6.--Percent cutthroat trout found in each size class in eddies, runs, and riffles.
Figure 7.--The total amount of surface area of eddies, pools, runs, and riffles in each reach.
Figure 8.--Mean numbers of fish counted per linear meter in eddy macrohabitats. Vertical bars are standard error of the mean.
Figure 9.--Mean numbers of fish counted per linear meter in pool macrohabitats. Vertical bars are standard error of the mean.
Figure 10.--Mean numbers of fish counted per linear meter in run macrohabitats. Vertical bars are standard error of the mean.
Figure 11.--Mean numbers of fish counted per linear meter in riffle macrohabitats. Vertical bars are standard error of the mean.
Figure 12. -- Cutthroat trout macrohabitat electivity values in eddies, pools, runs, and riffles.
Figure 13.—Rainbow trout macrohabitat electivity values in eddies, pools, runs, and riffles.
Figure 14.--Diel movements of six cutthroat trout in the winters of 1988 and 1989.