May 6, 1991

Dr. Robert Behnke
Dept. of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523

Dear Dr. Behnke:

This is a long overdue letter in response to your interest in my thesis research on spatial interaction of coast cutthroat and steelhead trout. I am enclosing a copy with my compliments.

Your predictions regarding segregation of these species were born out by my findings. In addition to their segregation within a drainage, I found that cutthroat (probably of sea-run origin) in the Smith River used different microhabitats when sympatric with steelhead than did their allopatric counterparts.

I have attempted to postulate on the evolutionary significance of divergent life history and ecological traits exhibited by cutthroat trout throughout their common range with steelhead. Your comments or criticisms would be most appreciated.

Sincerely,

Bill Mitchell

MICROHABITAT UTILIZATION AND SPATIAL SEGREGATION OF JUVENILE COASTAL CUTTHROAT AND STEELHEAD TROUT IN THE SMITH RIVER DRAINAGE, CALIFORNIA

by

William T. Mitchell

A Thesis
Presented to
The Faculty of Humboldt State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

April, 1988

ABSTRACT

Diving surveys of the Smith River drainage, California, in summer, 1982-1983, revealed that juvenile coastal cutthroat trout (Salmo clarki clarki) and steelhead trout (Salmo gairdneri) segregate broadly within the drainage and into different microhabitats along reaches where they occur sympatrically. In summer, 1983, physical microhabitat utilized by sympatric and allopatric cutthroat and steelhead trout was characterized in terms of depth, velocity, and substrate size over broad stream areas and at individual fish locations. Comparisons were made between sympatric and allopatric populations to assess the degree of overlap in microhabitat use and the potential for spatial interaction.

Both species exhibited a general positive relationship between body size and the physical variables. Thus, the greatest potential for spatial interaction existed between trout of similar size. Within their respective streams, allopatric cutthroat <10 cm and sympatric steelhead <10 cm occupied the same type of habitat (riffles and margins of channel) where they used similar current velocities, indicating a high potential for spatial interaction. Cutthroat within this size range, however, were found only in small tributaries above natural falls and log jams and in upper reaches of the drainage above major concentrations of juvenile steelhead. Sympatric cutthroat >10 cm utilized microhabitats comparable in velocity and depth characteristics to those utilized by equal-sized allopatric cutthroat. Sympatric cutthroat >10 cm and steelhead >10 cm segregated with respect to depth and water velocity; in sympatry cutthroat >10 cm generally occupied deep, slow-water pool areas while steelhead >10 cm occupied shallower, swifter water in runs, rapids, and heads of pools.

Microhabitat segregation of sympatric cutthroat and steelhead trout during summer is attributed to differential behavioral responses to cover and current velocity. Behavioral flexibility demonstrated by sympatric and allopatric cutthroat suggests that differences observed in sympatry may be due in part to interaction. Broad spatial segregation of coastal cutthroat and steelhead trout is attributed to differences in adult migratory behavior and spawning preferences. Segregation of adult spawners serves to maintain reproductive isolation and segregate juveniles during the early rearing period when microhabitat requirements are most similar. Stable coexistence of cutthroat and steelhead trout thus appears to be a result of selective segregation which separates the two species broadly within a drainage. In areas of sympatry, differences in microhabitat use are attributed to selective and interactive mechanisms.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. Terry Roelofs for serving as chairman of my graduate committee and lending assistance and guidance throughout my graduate studies. I also thank my committee members, Dr. Roger Barnhart and Dr. Robert VanKirk, for reviewing the manuscript and making valuable criticisms. I am especially grateful for the time, energy, and funds given by Mr. Eric Gerstung, Coordinator of the Threatened Salmonids Project, California Department of Fish and Game. Successful completion of the field work would not have been possible without his support and personal interest. Special thanks go to the following persons for their valuable assistance in the field: Glenn Yoshioka, Robert Franklin, Brian Winter, and Dave McLeod. I wish to thank Gordon Reeves for his suggestions concerning the statistical analysis, Pat Collins for his computer assistance, and Kyra Klobucar for typing the final manuscript. Thanks also go to Don Kelley for permitting the use of computer equipment and software during my employment with his firm.

I gratefully acknowledge the support provided by California Trout during the field surveys, and its part in prompting this study. I also express my gratitude to the Marin Rod and Gun Club for providing a generous scholarship which allowed me to devote full attention to thesis work during the data analysis and writing phases.

This work was performed as part of Dingell-Johnson Project F33R-9, Restoration and Maintenance of Native and Threatened Salmonids, California Department of Fish and Game, and was supported by Federal Aid to Fish Restoration funds, United States Fish and Wildlife Service.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

APPENDIXES

TABLE OF CONTENTS (CONTINUED) Page

TABLE OF CONTENTS (CONTINUED)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

INTRODUCTION

Coastal cutthroat trout (Salmo clarki clarki Richardson) and anadromous coastal rainbow (steelhead) trout (Salmo gairdneri Richardson) are native to Pacific Coast drainages of North America. The historical range of the coastal rainbow trout extends from the Rio del Presidio in Mexico to the Kuskokwim River, Alaska (Behnke 1979). The coastal cutthroat trout occupies a more restricted range extending from the Eel River in northern California (DeWitt 1954) to Prince William Sound, Alaska (Scott and Crossman 1973). Throughout the area of range overlap, sympatric populations of coastal cutthroat and steelhead trout are common. This represents the only major incidence of sympatry among western North American trouts (Behnke 1979). Coexistence of these closely related congeners without the occurrence of mass hybridization has generally been attributed to behavioral and ecological differences (Behnke 1972). Differences in spawning habitat and spawning time appear to be of primary importance in maintaining reproductive isolation (Needham and Gard 1959; Behnke 1979; Campton 1981).

Spatial segregation of cutthroat and steelhead spawners is reflected in the distribution of juveniles. In British Columbia coastal streams, Hartman and Gill (1968) found that juvenile steelhead occurred predominantly in large streams and those which dropped steeply in their lower reaches whereas cutthroat occurred predominantly in small streams and those with slight gradients in their lower reaches. Where both species occurred, cutthroat were found primarily in small tributaries and headwaters and steelhead in lower main stem reaches. Accounts from Washington, Oregon, and California also identify small streams as important cutthroat spawning areas (Cramer 1940; DeWitt 1954; Sumner 1962; Lowry 1965; Nicholas 1978a; Johnston 1981).

Although migratory populations of steelhead and coastal cutthroat may effectively segregate at spawning, juveniles frequently occur along the same stream lengths during their freshwater rearing period. For example, cutthroat composed a minor portion of samples collected in lower stream reaches of British Columbia drainages supporting both species (Hartman and Gill 1968). In Oregon, cutthroat parr exhibit variable lengths of stream residency and degrees of seaward migration following initial downstream migration from natal streams as yearlings (Sumner 1962; Lowry 1965; Giger 1972). In the Alsea River, substantial downstream migrations of parr in the spring terminate in lower stream reaches or the estuary where further rearing takes place prior to seaward migration typically at age three or four (Giger 1972). Juvenile steelhead typically spend two to three years in freshwater before smolting occurs (Withler 1966). In view of their similar sizes, morphology, and rearing requirements, cutthroat and steelhead trout may compete for stream resources (e.g., food and space) or otherwise interact because of similar habitat requirements.

Conventional competition theory states that two species drawing upon common resources (i.e., having similar ecological niches) in limited supply cannot coexist indefinitely (Lotka 1925; Volterra 1926; Gause 1964). Accordingly, coexistence of ecologically-similar species is frequently attributed to niche segregation. Brian (1956) recognized two types of segregation, selective and interactive. The first is governed by innate behavioral responses to environmental stimuli which effectively separate species along dimensions of habitat, food, or time. The second occurs when selective segregation is incomplete and species interact in their attempt to secure common resources. Svardson (1949) stated that interacting species are forced to magnify their ecological differences, resulting in a niche shift or restriction of a species to its "adaptive peak", defined as those conditions to which it is best adapted or competitively superior. The hypothetical end product of interaction should be selective segregation (Nilsson 1967).

Selective and interactive processes of habitat segregation have been inferred in a number of studies of the ecological relationships of sympatric salmonids in streams.

Everest and Chapman (1972) found that spatial interaction between juvenile chinook salmon (_Oncorhynchus tshawytscha_) and steelhead trout was minimized by temporal differences in habitat utilization arising through differential spawning and emergence times. Lister and Genoe (1970) observed a similar form of selective segregation for underyearling chinook and coho salmon (_O. kisutch_). Hartman (1965) demonstrated experimentally the role of social interaction in segregation of underyearling coho salmon and steelhead trout. Other examples of interactive segregation of stream-dwelling salmonids have been given by Lindroth (1957), Kalleberg (1958), and Saunders and Gee (1964).

In summer, 1982, I conducted diving surveys of the major forks and tributaries of the Smith River to determine the distribution and abundance of cutthroat trout and to gain insight into their behavior and habitat preferences. In the following summer, surveys were continued in upper reaches of the drainage and small tributaries using both diving and electrofishing techniques.

In late summer and early fall, 1983, I investigated microhabitat utilization by cutthroat trout in streams where they occurred with steelhead trout and in reaches where cutthroat occurred alone. The objectives were as follows:

1. To quantitatively define and compare the physical microhabitats used by juvenile coastal cutthroat trout and steelhead trout in allopatry and sympatry.

2. To assess the degree of overlap in microhabitat use and the potential for spatial interaction.
3. To identify possible mechanisms that act to maintain segregation and permit coexistence.

STUDY AREA

The Smith River drainage encompasses 1,627 km^2 of Del Norte County in northwestern California and 236 km^2 of southwestern Oregon (Figure 1). The Smith River and all its tributaries from the Oregon-California border to the Pacific Ocean have been included in the California and Federal Wild and Scenic Rivers Systems. This designation provides for protection and enhancement of the scenic, recreational, fishery, and wildlife resources of the Smith River and its immediate environment. As a result, the Smith River has remained one of the few unregulated streams in California.

The Smith River originates on the western slope of the Siskiyou Mountains at elevations ranging up to 1,830 m above sea level. Three main forks descend through steep, v-shaped canyons to the main stem which flows across a narrow coastal plain to the estuary. The Smith River extends 73 km from the headwaters of the Middle Fork to the Pacific Ocean. Stream gradients range from 2 m/km at the coast to over 19 m/km at the headwaters (Iwatsubo and Washabaugh 1982).

The majority of the upper watershed, which comprises the three forks, lies within Six Rivers National Forest. Jedediah Smith and Del Norte Coast Redwoods State Parks,

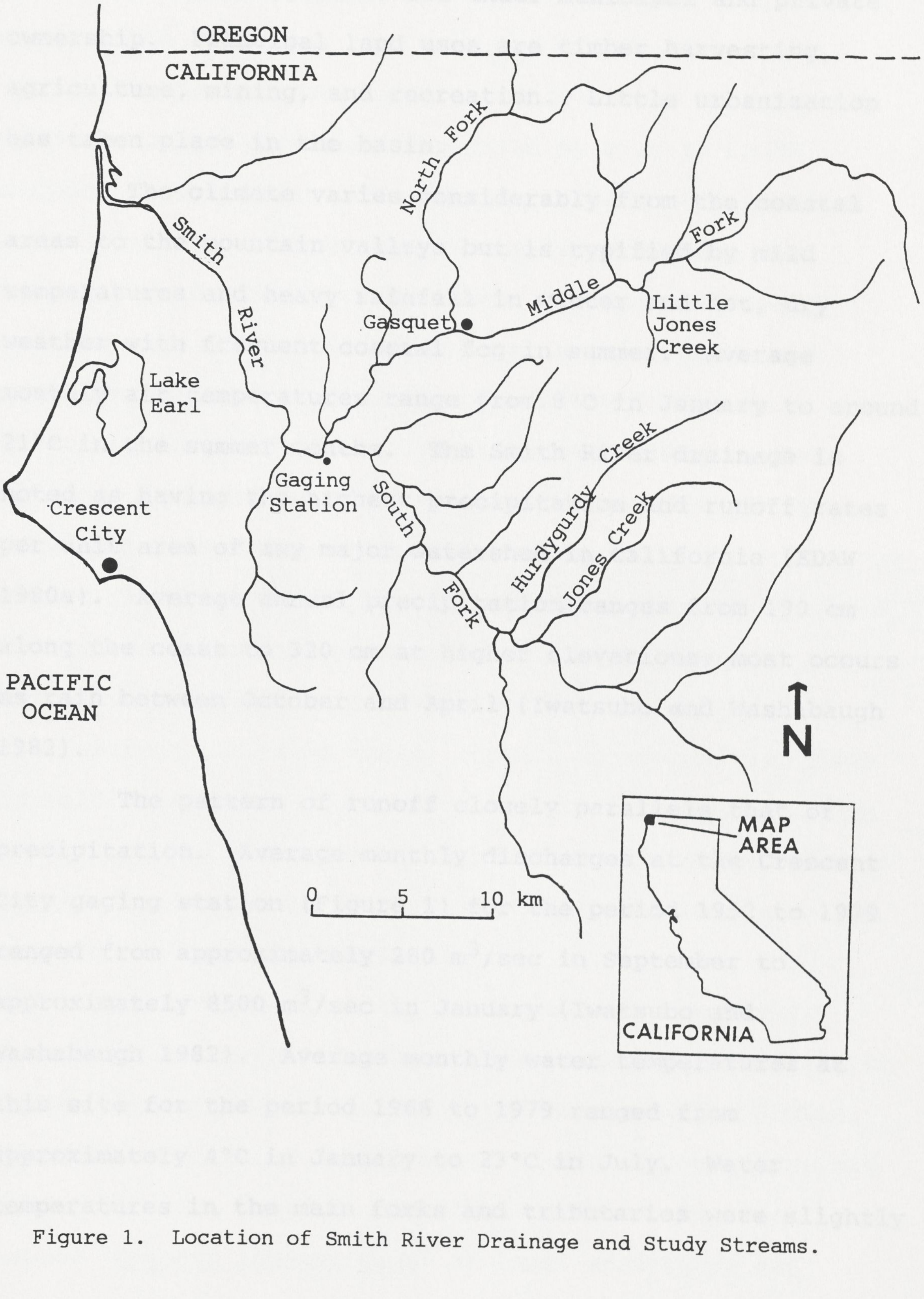

Figure 1. Location of Smith River Drainage and Study Streams.

both part of Redwood National Park, border the lower reaches. Remaining lands are under municipal and private ownership. Principal land uses are timber harvesting, agriculture, mining, and recreation. Little urbanization has taken place in the basin.

The climate varies considerably from the coastal areas to the mountain valleys but is typified by mild temperatures and heavy rainfall in winter and hot, dry weather with frequent coastal fog in summer. Average monthly air temperatures range from 8°C in January to around 21°C in the summer months. The Smith River drainage is noted as having the highest precipitation and runoff rates per unit area of any major watershed in California (EDAW 1980a). Average annual precipitation ranges from 190 cm along the coast to 320 cm at higher elevations; most occurs as rain between October and April (Iwatsubo and Washabaugh 1982).

The pattern of runoff closely parallels that of precipitation. Average monthly discharges at the Crescent City gaging station (Figure 1) for the period 1952 to 1979 ranged from approximately 280 m^3/sec in September to approximately 8500 m^3/sec in January (Iwatsubo and Washabaugh 1982). Average monthly water temperatures at this site for the period 1966 to 1979 ranged from approximately 4°C in January to 23°C in July. Water temperatures in the main forks and tributaries were slightly lower; in this study I recorded peak daily temperatures in the main forks ranging from 17° to 21°C during July and August, 1982.

The Smith River Basin is underlain by parts of two major geological provinces separated by a north-south trending thrust fault. The eastern three quarters of the basin lies within the Klamath Mountains Province, the western portion in the Coast Ranges Province. These provinces are characterized by a series of roughly north-south trending belts of rock separated by faults and decreasing in age from east to west (EDAW 1980a). The eastern and central part of the basin are underlain by the two westernmost belts of the Klamath Mountains Province, the Western Paleozoic-Triassic and the Western Jurassic. These belts contain a complex assemblage of metavolcanic, metasedimentary, and ultramafic rocks of marine origin. Late Jurassic intrusive rocks, varying in composition from ultramafic to siliceous, occur along the eastern margin of the basin. The western part of the basin along the coast consists predominantly of Jurassic-Cretaceous sandstone and shale of the Franciscan Formation.

The diverse climatic, geologic, and topographic setting of the Smith River basin has created one of the most complex vegetation patterns in North America (EDAW 1980a). Twenty-one species of conifers and 12 plant communities are recognized. The dominant coniferous species are coast redwood (<u>Sequoia sempervirens</u>) at lower elevations and

Douglas fir (Pseudotsuga menziesii) at higher elevations. Hardwoods include red alder (Alnus rubra), madrone (Arbutus menziesii), tanoak (Lithocarpus densiflora), canyon live oak (Quercus chysolepis), and bigleaf maple (Acer macrophyllum). An extensive understory of shrubs is present throughout the basin. Shrub communities dominate hot, dry ridges and old clearcut areas.

The Smith River supports one of the most important anadromous fisheries in California (EDAW 1980a). Fall chinook salmon (Oncorhynchus tshawytscha), coho salmon (O. kisutch), and winter steelhead trout constitute the principal sport catch. Coastal cutthroat trout support a small tidewater fishery in spring and fall, and provide limited angling opportunities in upper parts of the drainage during summer. Other anadromous species include American shad (Alosa sapidissima), green sturgeon (Acipenser medirostris), Pacific lamprey (Lampreta tridentata), and eulachon (Thalichthys pacificus). Threespine sticklebacks (Gasterosteus aculeatus), sculpins (Cottus sp.), and suckers (Catostomus sp.) occur in lower reaches of the drainage.

Study Sites

Three streams within the Smith River drainage were selected for study: Hurdygurdy Creek, a tributary of the South Fork; Little Jones Creek, a tributary of the Middle Fork; and a section of the upper Middle Fork (Figure 1).

Hurdygurdy Creek

Hurdygurdy Creek heads at an elevation of 1,280 m and flows southwest for 25 km to its confluence with the South Fork Smith River at an elevation of 180 m. The drainage area is approximately 75 km^2. Stream discharge at the mouth typically ranges from 0.5 m^3/sec in September to 190 m^3/sec in December (Six Rivers National Forest files 1981-1982. Supervisors Office, Eureka, California). Water temperatures at midday during the study period (mid-July to late-September) averaged 15°C. Afternoon temperatures peaked at 18°C. I selected five study reaches, four within 6 km of the mouth and one approximately 15 km from the mouth. Stream gradient in these reaches averages 20 m/km.

Extensive logging and road construction has occurred, particularly in the upper half of the drainage. Whereas most slopes are dominated by Douglas fir and mixed conifers, clearcut areas in the upper basin are vegetated largely by brush. Slopes commonly exceed 30%, reaching a maximum of 70% in the upper basin. Numerous active debris slides are present along inner gorge areas (EDAW 1980b). The lower 8 km of Hurdygurdy Creek is accessible by County Route 405. Approximately 75% of the basin is in public ownership (Six Rivers National Forest). The remaining area is privately owned land in the middle and upper basin.

Hurdygurdy Creek provides spawning and rearing habitat for steelhead trout, chinook salmon, and coastal cutthroat trout. In the lower reaches, the Forest Service is conducting stream habitat improvement work primarily aimed at enhancing spawning and rearing habitat for salmon and steelhead.

Little Jones Creek

Little Jones Creek heads at an elevation of 980 m and flows in a northerly direction, joining the Middle Fork Smith River at an elevation of 270 m. Approximately 8 km in length, this stream drains an area of 26 km^2. Minimum discharges of 0.1 and 0.2 m^3/sec were recorded in September, 1977 and 1978 (EDAW 1980b). Water temperature during minimum flow periods typically ranges from 13-15°C. I selected two study reaches located approximately 1 km and 2 km above the mouth, respectively. Stream gradient averaged 17 m/km in the upper study reach, increasing to over 20 m/km near the mouth.

The Little Jones Creek drainage has been extensively clearcut and roaded. Much of the former Douglas fir-dominant forest has been replaced by brush (EDAW 1980b). An extensive alder thicket borders the stream along much of its lower reaches. The majority of the basin slopes exceed 50%, creating a moderate to high soil erosion hazard. Past and present slide activity is evident throughout the basin. Little Jones Creek is accessible along the upper three quarters of its length by Forest Route 17N08. The land in the drainage is both publically and privately owned.

In summer, 1982, I discovered that Little Jones Creek supported a resident cutthroat trout population isolated above a 5 m bedrock falls located near the stream mouth. In general, this stream differs considerably from most larger Smith River tributaries by its low flow and gradient, extensive canopy, abundant instream wood debris (e.g., logs, branches, root wads) and leaves. Much of the gravel in the main stem is compacted by silt and unsuitable for spawning. In the lowermost reaches, the stream drops through a steep gorge area where gradient, exposure, substrate, and hydraulic character more closely resemble that of larger tributaries.

Upper Middle Fork

I selected two study reaches located approximately 14 km from the source of the Middle Fork at an elevation of 440 m. The drainage area at this point is approximately 46 km^2. Minimum summer discharges vary around 0.2 and 0.3 m^3/sec. Stream gradient averages 20 m/km.

Access along this reach is afforded by Forest Route 18N07 which continues to parallel the stream for 1.5 km above the study reach before diverging and ascending along Knopki Creek, a major branch of the upper Middle Fork. Above its confluence with Knopki Creek, the Middle Fork is unroaded and considered wild (EDAW 1980b). Anadromous salmonid spawning and rearing habitat in this segment is rated excellent (EDAW 1980b). Entirely in public ownership, the Knopki Creek drainage has been roaded for logging along most of its length and receives comparatively heavy recreational use during the summer.

Within the study reaches, juvenile steelhead were the only salmonids observed during summer surveys. Comparatively swift currents and boulder-bedrock channels characterize these reaches.

MATERIALS AND METHODS

In summer, 1983, data were collected over broad stream areas and at individual fish locations following the basic methodologies of Everest and Chapman (1972). These authors termed these methods habitat and microhabitat analysis, respectively.

Habitat Analysis

This method was used to describe and compare general patterns of habitat use between sympatric and allopatric coastal cutthroat and steelhead trout. Physical habitats were characterized in terms of mean water velocity, depth, and substrate size. A single 30-40 m long study site was established on each of three streams: Hurdygurdy Creek, which supported sympatric populations of coastal cutthroat and steelhead trout; Little Jones Creek, which supported an allopatric resident cutthroat population; and the upper Middle Fork Smith River where steelhead were locally allopatric. Each site extended from the head of a pool downstream until shallow water (<15 cm deep) precluded underwater observations.

Habitat data were collected in August and early September, 1983. At each study site, a grid was constructed by extending a ruled nylon cord across the width of the stream and securing surveying tape to the stream bottom at 3 m intervals. This procedure was repeated at 3 m intervals along the length of each study reach. A number and letter, corresponding to a row and column position within the grid, was printed on each piece of tape. The day after completion of the grid, I recorded fish distribution by direct underwater observation using a face mask and snorkel. I entered the water at the downstream end of the grid section and proceeded slowly upstream, recording the species, size class, and position of fish onto a roughened plexiglass slate bearing a diagram of the grid. Fish were assigned to one of three size classes: <5 cm, 5-10 cm, or >10 cm body length. These size classes corresponded to age 0+, age 0+ and 1+, and age 1+ trout, respectively. A single pass was made in the morning between 0900 and 1100, and repeated in the afternoon between 1500 and 1700. All data recorded on plexiglass slates were later transferred to data sheets.

On subsequent days, physical parameters were measured at 1.5 m intervals on the grid and at shorter intervals in areas where gradients noticeably increased. Water velocity (recorded to the nearest cm/sec) and depth (recorded to the nearest cm) were measured with a Pygmy current meter and top-setting rod. Mean water velocities were obtained by taking measurements at 0.6 of the total depth from the surface when depth was equal to or less than 76 cm, or by averaging measurements taken at 0.8 and 0.2 of the total depth when depth exceeded 76 cm. Dominant substrate types were mapped and assigned to the following size categories: <2 cm sand and gravel, 2-5 cm gravel, 5-20 cm cobble, 20-40 cm cobble, and >40 cm boulder. Stream width was measured at 3 m intervals with the nylon cord used in constructing the grid.

Measurements of depth and mean velocity within the grid were used to create contour maps stratified into 20 cm depth contour intervals and 15 cm/sec velocity contour intervals, respectively. These maps were then photocopied onto clear acetate overlays and superimposed upon base maps depicting substrate and shoreline contours. By combining contour maps in this manner, I was able to identify various habitat units (termed habitat "sets" by Everest and Chapman 1972), each represented by an area in which individual contour intervals overlapped. Clear overlays of fish positions were then superimposed, and the number, species, and size class of fish within each "set" were recorded. A polar planimeter was used to measure the total area enclosed by each contour interval (i.e., habitat stratum). The number of trout of each species and size class within each interval was determined to obtain a measure of fish density in relation to each variable separately.

Data Analysis

Habitat utilization by each trout group was evaluated with respect to each variable separately using a habitat specific utilization index (Bisson et al. 1981):

$$U_h = \frac{D_h - D_t}{D_t}$$

where D_h = average fish density in a particular habitat; and D_t = average density over the entire stream area. Values of the index range from negative one, indicating absence from a habitat, to positive infinity as fish density within a habitat increases. This coefficient provides a measure of utilization that indicates whether a given type of habitat is selected (positive values), avoided (negative values), or used in proportion to its abundance (zero).

Discriminant analysis was used to describe differences in microhabitat use between species and size classes both within and between sites. The results are presented in a graphical form which depicts group differences along a single or reduced set of habitat variables. These new variables, termed canonical discriminant functions, are linear combinations of the original variables and have the property of maximally separating group means (Klecka 1980). The utility of discriminant analysis lies in its ability to discriminate between groups and to identify the parameters by which they are separated. In the present study, it provided a means of assessing the degree of habitat differentiation between trout groups as well as identifying the variables which contributed most to group differences. Discriminant analysis was also used to test for differences in habitat use between morning and afternoon observation periods for each species and size class.

Each contour interval, which defined a range of values for a given variable, was given an integer rank according to its relative magnitude (beginning with 1). Each observation for a given trout group consisted of three integer values representing a habitat set in which members of that group were found irrespective of their density within that set. Therefore, this analysis is essentially a comparison of habitat utilization based on presence or absence rather than the relative numbers of fish.

Graphical representations of the results allowed examination of group differences in terms of scores generated from the discriminant functions. Each group is represented by a centroid (i.e., group mean), denoted by a solid circle, and a range of scores represented by a horizontal line. The relative positions of the centroids and ranges depicted group differences in habitat utilization. Identification of those variables weighing most heavily in group separation was based on examination of the pooled within-groups correlations between the discriminant functions and the original variables (i.e., structure coefficients). The degree of habitat differentiation between groups was evaluated with the canonical correlation coefficient and Wilks' lambda, both of which are measures of group discrimination (Klecka 1980). Wilks' lambda was converted into an approximation of the chi-square distribution for significance testing. Discriminant analysis was performed by a CDC Cyber 170/720 computer using the SPSS (Statistical Package for the Social Sciences) subprogram DISCRIMINANT (Klecka 1975).

Qualitative and quantitative differences in habitat can confound attempts to evaluate differences in habitat selection between sympatric and allopatric trout groups. Possible stream effects were assessed by comparing the habitat composition of study sites with respect to each variable separately and by evaluating differences with respect to all variables simultaneously using discriminant analysis.

Microhabitat Analysis

In habitat analysis, fish distribution was examined in relation to broad distinctions in physical habitat. In order to define more precisely the physical conditions selected by individual fish a microhabitat analysis was employed. In each study stream, two or more 40-60 m reaches, one of which included the grid section of the previous analysis, were sampled. Two additional reaches were established on Jones Creek, a tributary of the South Fork Smith River which resembled Hurdygurdy Creek in both physical character and species composition (Figure 1). An effort was made to sample from a wide range of available habitats.

Data on microhabitat utilization by sympatric and allopatric trout were collected in September and October, 1983. The sampling method consisted of visually locating individual fish which exhibited holding behavior at a specific site or feeding station (i.e., focal point). I entered the water at the downstream end of the selected reach and proceeded upstream until a holding fish came into view. After observing its behavior for up to three minutes to ensure that it was not disturbed by my presence I recorded the species and size class of the fish, its distance above the substrate, and its distance from the nearest fish (the latter two estimated in relation to total depth). After recording these data, I cautiously approached the fish as closely as possible to determine the point on the stream bottom over which it was holding. This point was marked with surveying tape bearing a number and letter for data reference. This sampling method resulted in a minimum of disturbance, allowing me to repeat the procedure immediately after marking a focal point. After completion of a single pass, the following physical parameters were measured at the focal points: substrate size, total depth, mean velocity, surface velocity, facing velocity (measured at point in water column where fish was holding), maximum velocity within 0.6 m, and distance from nearest cover. Depth, velocity, and substrate size were measured in the manner described in the preceding section. Measurements of fish distance above the substrate and from the nearest fish were computed from the relative measurements and the actual total depth. Discriminant analysis was used to describe differences in microhabitat utilization between species and size classes both within and between sites. A t-test was used to test for differences between means for each habitat variable separately.

RESULTS

Diving Surveys

In summer, 1982, I commonly observed from five to ten cutthroat per stream kilometer in the major forks and tributaries of the Smith River. Estimated body lengths of cutthroat in these reaches ranged from 10 cm to 45 cm. In the following summer, we found that the abundance of cutthroat was generally greater in upper reaches of the drainage. Highest population densities were found in reaches above major log jams and falls. Only in these isolated reaches and in smaller tributaries did we observe cutthroat less than 10 cm in length.

During our surveys, certain patterns of habitat use and behavior became apparent. Cutthroat and steelhead trout were typically segregated along reaches where both species were present. Underyearling steelhead were most abundant along shallow channel margins and in pool tail-outs. Yearling and older steelhead typically occupied deeper areas of the channel immediately adjacent to swift surface currents. They were commonly observed maintaining positions at the heads of pools where they exhibited active drift feeding. Sympatric cutthroat of equal or larger size were also typically observed in deeper pool areas but frequently near the bottom in areas removed from surface currents. My observations of feeding behavior were limited to occasions when cutthroat were seen pursuing or seizing young salmonids in open water. In Little Jones Creek, allopatric cutthroat were more surface oriented than sympatric individuals. Although the physical character of Little Jones Creek differed considerably from other surveyed reaches, cutthroat behavior and habitat use appeared to be comparable to that of steelhead inhabiting larger, swifter streams.

Habitat Analysis

Hurdygurdy Creek

No significant differences were detected between morning and afternoon patterns of habitat utilization for individual trout size classes at the Hurdygurdy Creek site (Wilks' lambda>0.8; p>0.4). Therefore, data from the two observation periods were pooled prior to further analysis.

Differences in habitat use among steelhead size classes in Hurdygurdy Creek were characterized by association of larger fish with deeper, faster water and larger substrate (Figure 2, Appendix A). Differences were most pronounced between steelhead >10 cm long and the two smaller size classes, and were due primarily to occupation of deeper areas by larger steelhead.

Coefficients of habitat utilization calculated for each variable separately further illustrate the general positive relationship between body size and the physical variables (Figure 3). The degree of habitat use by

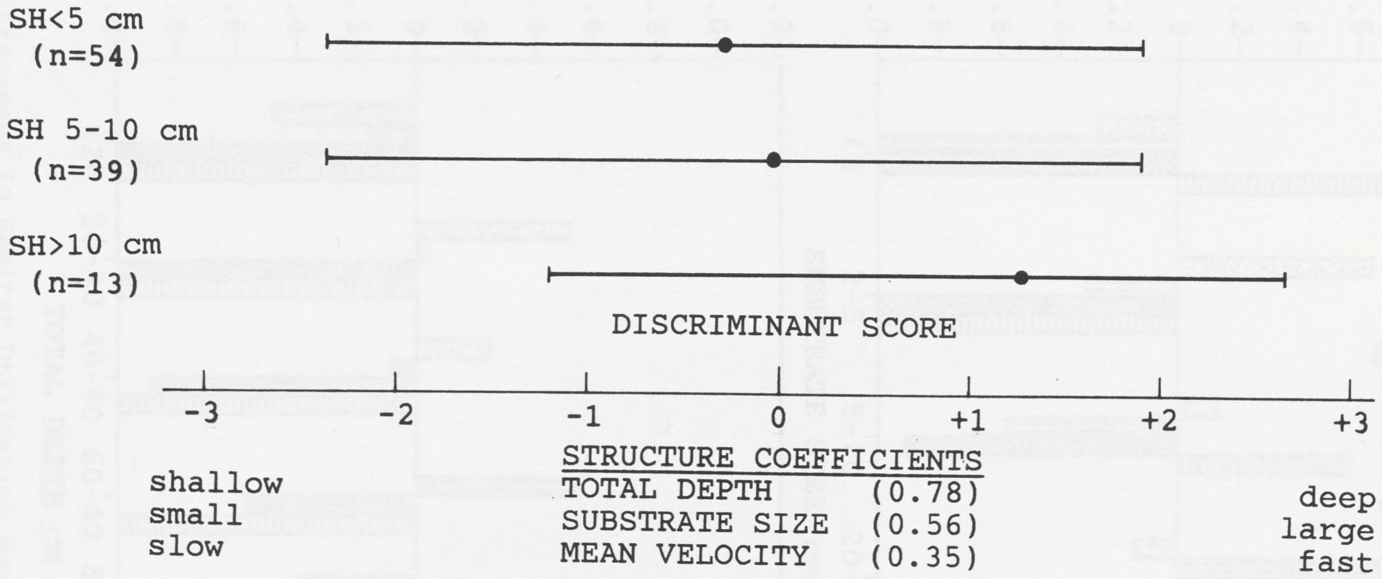

Figure 2. Differences in Habitat Utilization among Three Steelhead (SH) Size Classes in Hurdygurdy Creek Based on Means and Ranges of Scores on a Single Linear Composite (Discriminant Function) of the Habitat Variables. The Magnitude of the Structure Coefficients, in Parentheses, Reflect the Relative Contribution of Individual Variables to Group Differences. Positive Coefficients Indicate that Increasing Scores on the Discriminant Function Correspond to Habitats of Increasing Depth, Substrate Size, and Current Velocity. See Appendix A for Statistical Summary.

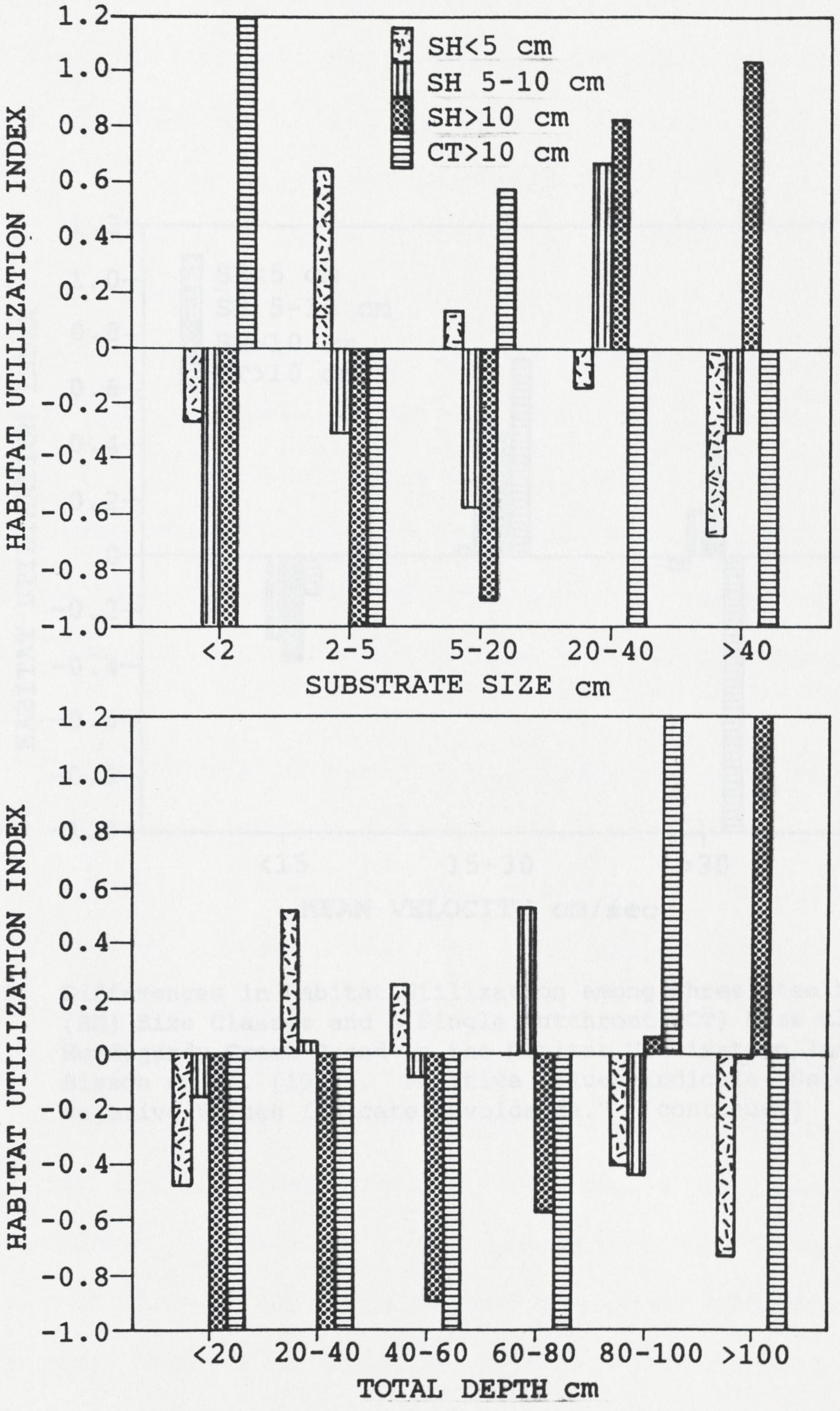

Figure 3. Differences in Habitat Utilization among Three Steelhead (SH) Size Classes and a Single Cutthroat (CT) Size Class in Hurdygurdy Creek Based on the Habitat Utilization Index from Bisson et al. (1981). Positive Values Indicate "Selection", Negative Values Indicate "Avoidance."
]

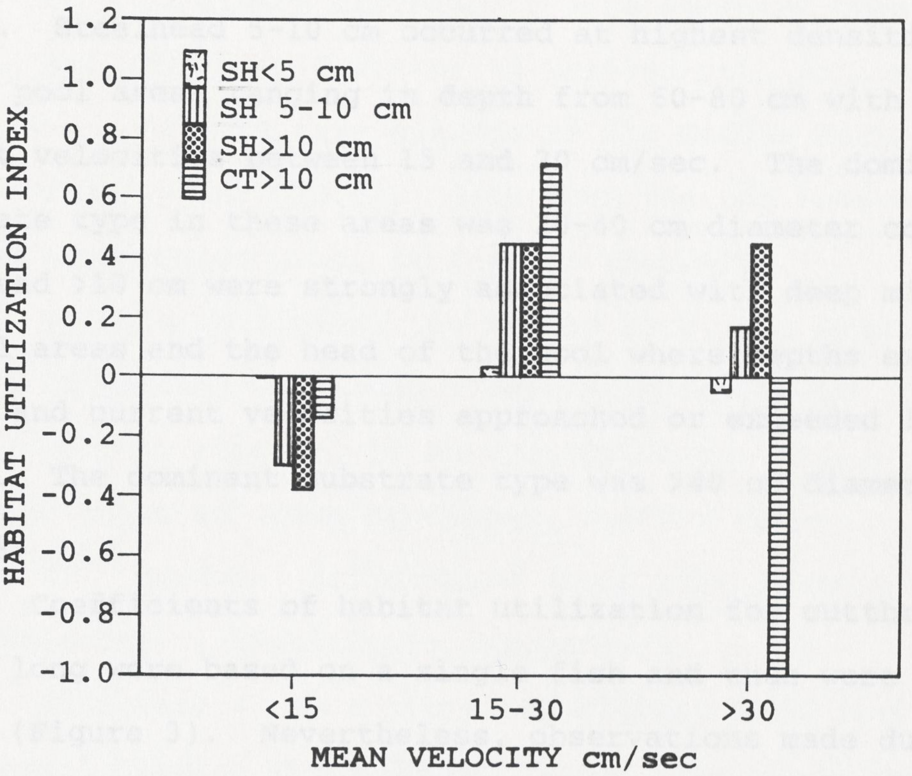

Figure 3. Differences in Habitat Utilization among Three Steelhead (SH) Size Classes and a Single Cutthroat (CT) Size Class in Hurdygurdy Creek Based on the Habitat Utilization Index from Bisson et al. (1981). Positive Values Indicate "Selection", Negative Values Indicate "Avoidance." (continued)

steelhead <5 cm long was greatest along channel margins and in the tail of the pool where depths ranged from 20-40 cm and mean current velocities from 15-30 cm/sec. The bottom substrate in these areas was predominantly 2-5 cm diameter gravel. Steelhead 5-10 cm occurred at highest densities in deeper pool areas ranging in depth from 60-80 cm with mean current velocities between 15 and 30 cm/sec. The dominant substrate type in these areas was 20-40 cm diameter cobble. Steelhead >10 cm were strongly associated with deep mid-channel areas and the head of the pool where depths exceeded 100 cm and current velocities approached or exceeded 30 cm/sec. The dominant substrate type was >40 cm diameter boulder.

Coefficients of habitat utilization for cutthroat >10 cm long were based on a single fish and thus were highly skewed (Figure 3). Nevertheless, observations made during previous diving surveys indicated that the location of the individual within the pool was typical of that occupied by cutthroat living sympatrically with juvenile steelhead. This habitat type was characterized by relatively deep water (80-100 cm) and intermediate mean current velocities (15-30 cm/sec). Substrate types over which the single fish was observed during the morning and afternoon observation periods were sand <2 cm diameter and gravel-cobble 5-20 cm diameter. Discriminant analysis, based on only two data points for cutthroat trout (i.e., morning and afternoon observations), indicated that association with finer substrate was the main difference separating cutthroat from steelhead trout at the Hurdygurdy site (Appendix A).

Middle Fork Smith River

No significant differences were detected between morning and afternoon patterns of habitat utilization for individual steelhead size classes at the Middle Fork site (Wilks' lambda>0.8; p>0.5). Data from the two observation periods were pooled prior to further analysis.

In this section of the Middle Fork, the general pattern of habitat use among steelhead size classes was similar to that observed in Hurdygurdy Creek; larger steelhead occupied areas of deeper, swifter water (Figure 4). However, differences among size classes were not statistically significant (Appendix A).

Steelhead <5 cm occurred at highest densities near the channel margins where depths ranged from 20-40 cm and mean current velocities averaged less than 15 cm/sec (Figure 5). Steelhead 5-10 cm selectively utilized portions of the channel having depths of 60-80 cm and current velocities of 15-30 cm/sec. Steelhead >10 cm occupied deeper, mid-channel areas where depths and current velocities exceeded 80 cm and 30 cm/sec, respectively.

Little Jones Creek

As at other sites, no significant differences were detected between morning and afternoon patterns of habitat

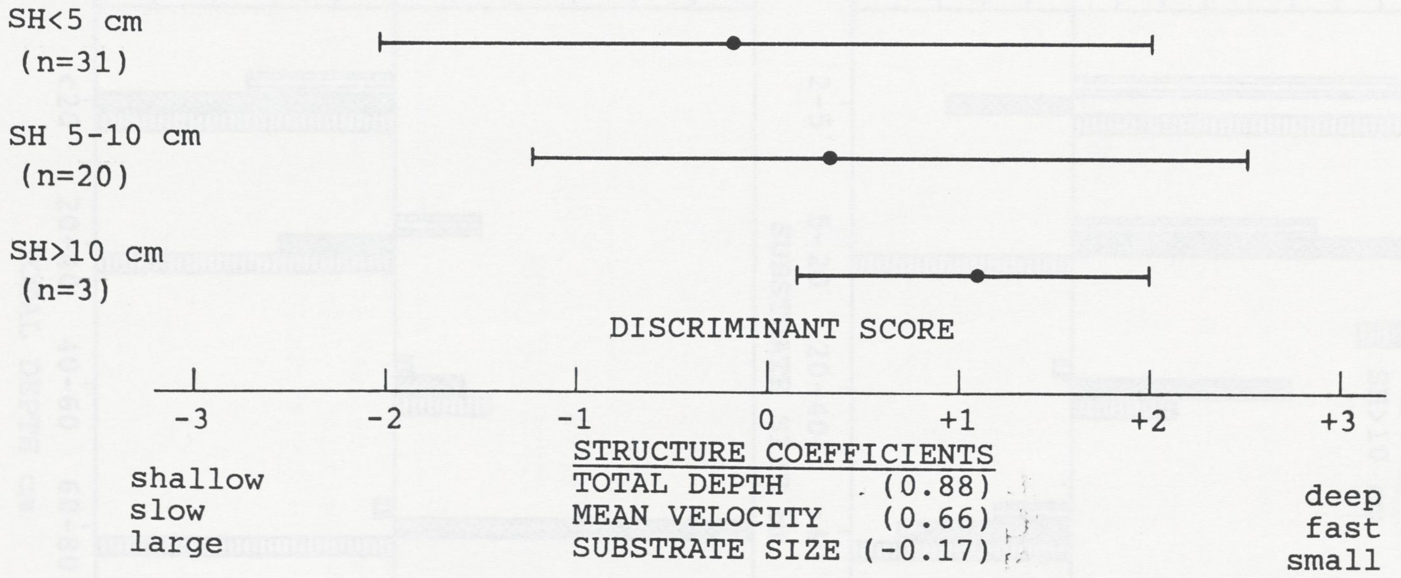

Figure 4. Differences in Habitat Utilization among Three Steelhead Size Classes in the Middle Fork Smith River Based on Means and Ranges of Scores on a Single Linear Composite (Discriminant Function) of the Habitat Variables. The Magnitude of the Structure Coefficients, in Parentheses, Reflect the Relative Contribution of Individual Variables to Group Differences. The Sign of the Coefficient (+ or -) Indicates Whether the Associated Variable Increases or Decreases with Increasing Scores on the Discriminant Function. See Appendix A for Statistical Summary.

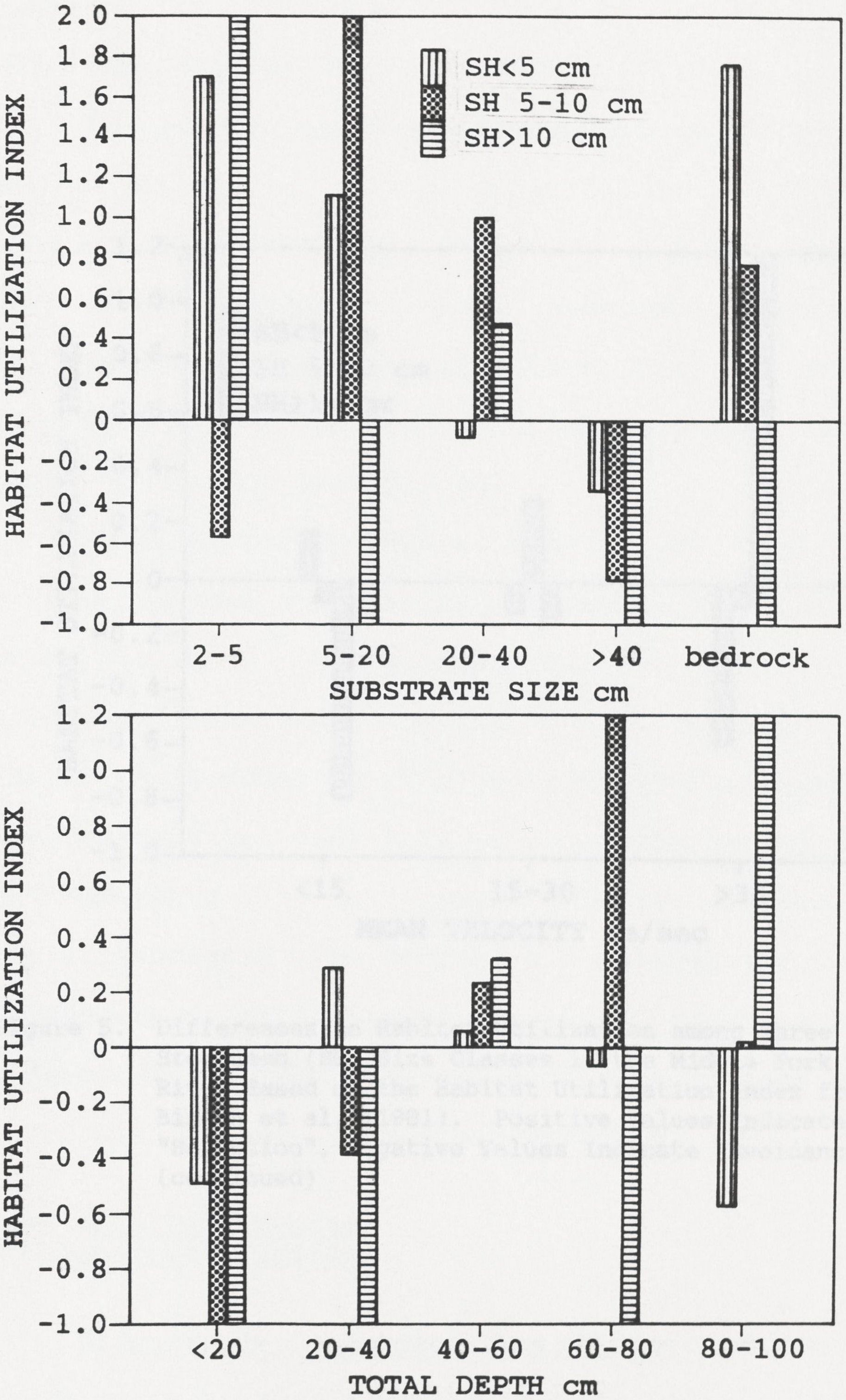

Figure 5. Differences in Habitat Utilization among Three Steelhead (SH) Size Classes in the Middle Fork Smith River Based on the Habitat Utilization Index from Bisson et al. (1981). Positive Values Indicate "Selection", Negative Values Indicate "Avoidance."

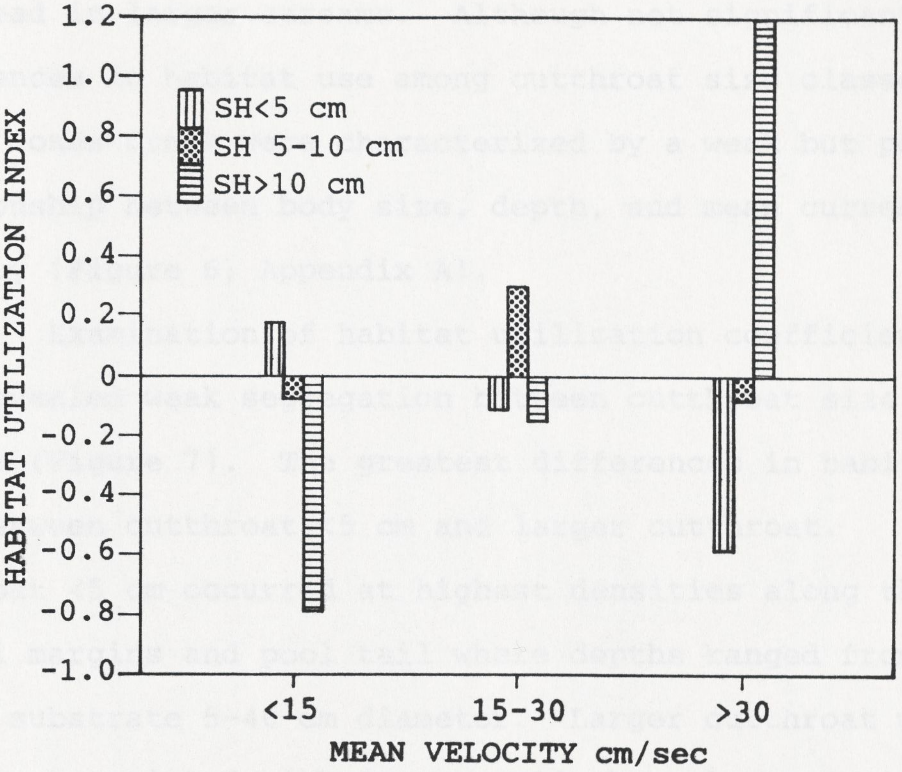

Figure 5. Differences in Habitat Utilization among Three Steelhead (SH) Size Classes in the Middle Fork Smith River Based on the Habitat Utilization Index from Bisson et al. (1981). Positive Values Indicate "Selection", Negative Values Indicate "Avoidance." (continued)

utilization for individual cutthroat size classes at the Little Jones site (Wilks' lambda>0.9; p>0.5).

The general distribution pattern of allopatric cutthroat was similar to that observed for juvenile steelhead in larger streams. Although not significant, differences in habitat use among cutthroat size classes in Little Jones Creek were characterized by a weak but positive relationship between body size, depth, and mean current velocity (Figure 6; Appendix A).

Examination of habitat utilization coefficients also revealed weak segregation between cutthroat size classes (Figure 7). The greatest differences in habitat use were between cutthroat <5 cm and larger cutthroat. Cutthroat <5 cm occurred at highest densities along the channel margins and pool tail where depths ranged from 20-60 cm and substrate 5-40 cm diameter. Larger cutthroat were strongly associated with deeper, mid-channel areas and the pool head where depths ranged from 60-80 cm and substrate 2-5 cm diameter. Little separation of size classes was detected with respect to current velocity.

Between-Site Differences in Habitat Utilization

Differences in Habitat Composition. Major differences in habitat composition were revealed by examining the relative area of each substrate, depth, and velocity stratum within the three sites (Table 1). There was considerable variation in bottom substrate composition

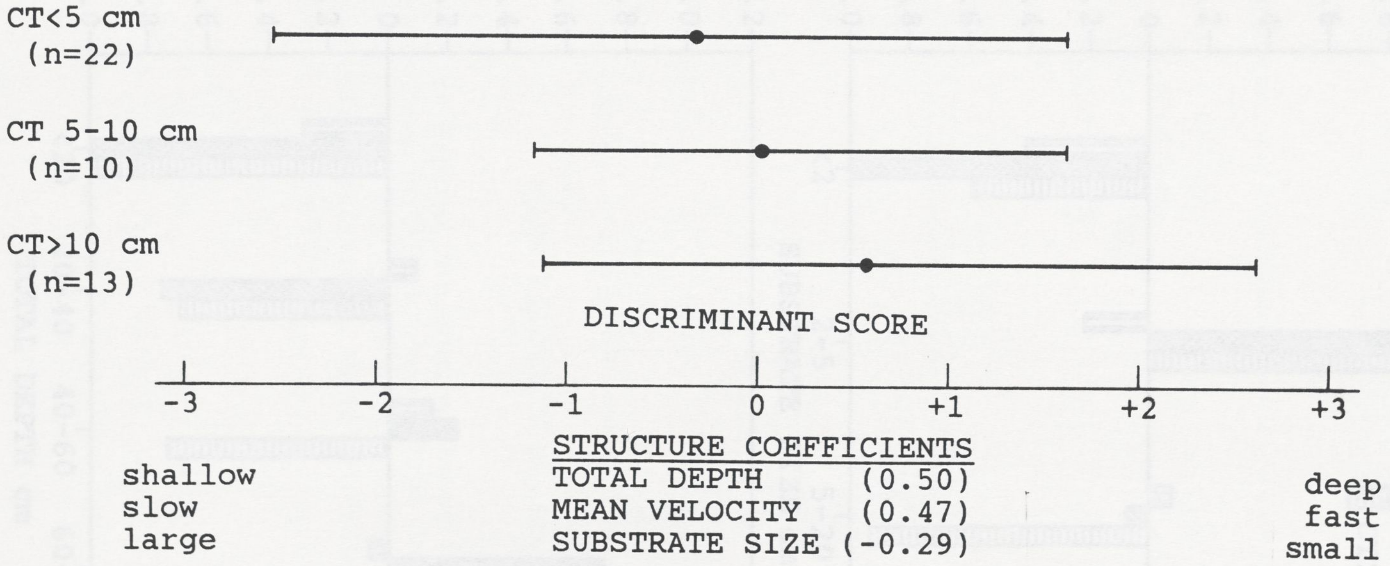

Figure 6. Differences in Habitat Utilization among Three Cutthroat Size Classes in Little Jones Creek Based on Means and Ranges of Scores on a Single Linear Composite (Discriminant Function) of the Habitat Variables. See Appendix A for Statistical Summary.

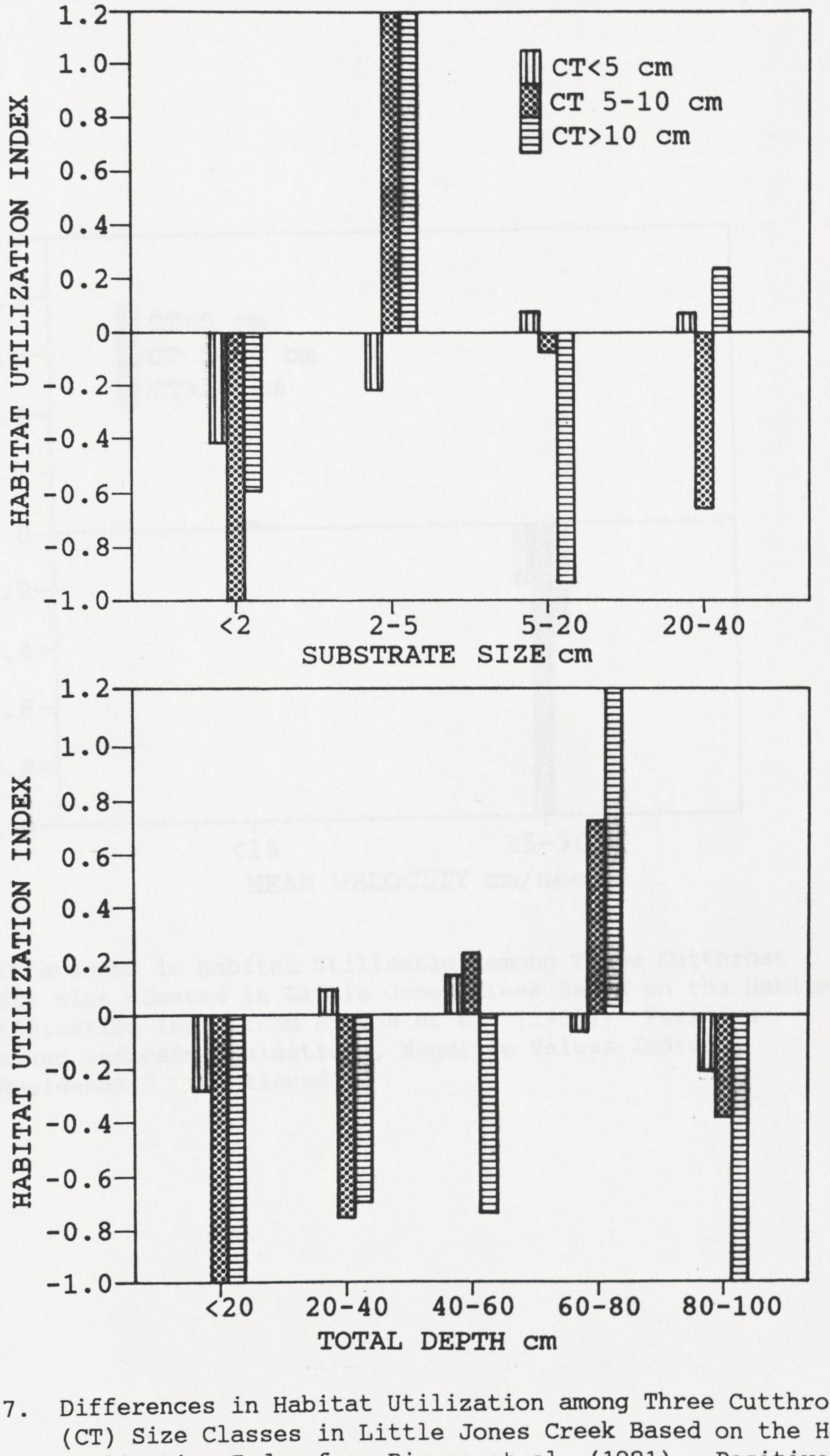

Figure 7. Differences in Habitat Utilization among Three Cutthroat (CT) Size Classes in Little Jones Creek Based on the Habitat Utilization Index from Bisson et al. (1981). Positive Values Indicate "Selection", Negative Values Indicate "Avoidance."
]

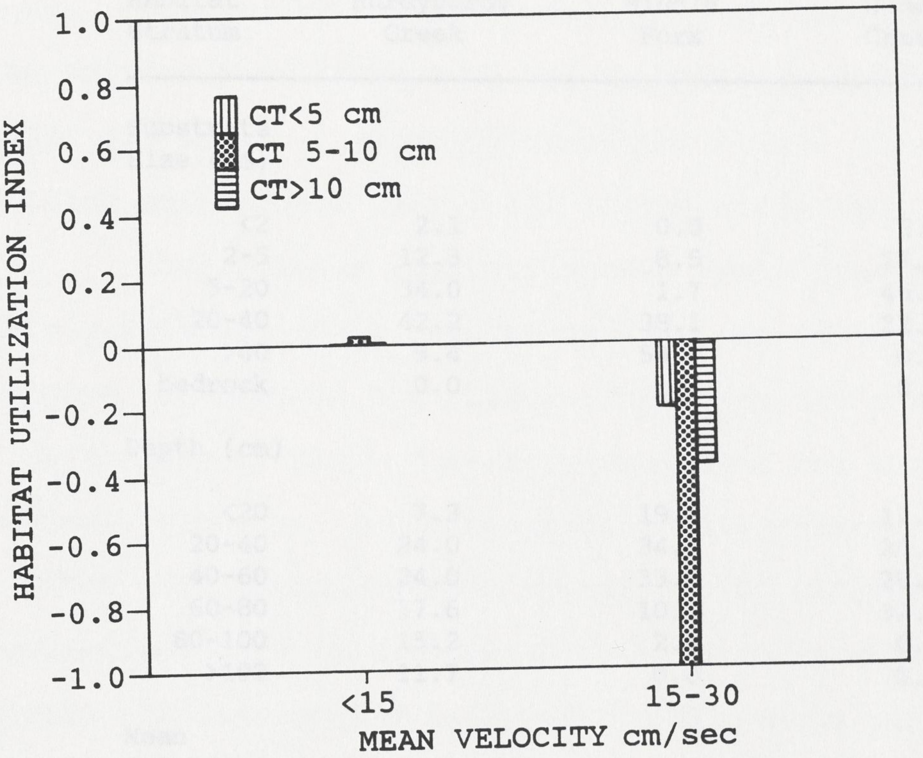

Figure 7. Differences in Habitat Utilization among Three Cutthroat (CT) Size Classes in Little Jones Creek Based on the Habitat Utilization Index from Bisson et al. (1981). Positive Values Indicate "Selection", Negative Values Indicate "Avoidance." (continued)

Table 1. Percentage of Total Area Comprised by Each Habitat Stratum of Substrate Size, Depth, and Mean Water Velocity by Study Site.

Habitat Stratum	Hurdygurdy Creek	Middle Fork	Little Jones Creek
Substrate Size (cm)			
<2	2.1	0.0	5.3
2-5	12.3	8.5	27.3
5-20	34.0	1.7	45.3
20-40	42.2	38.1	22.0
>40	9.4	50.0	0.0
bedrock	0.0	1.7	0.0
Depth (cm)			
<20	7.3	19.3	12.0
20-40	24.0	34.7	20.7
40-60	24.0	33.0	28.0
60-80	17.6	10.2	32.7
80-100	15.2	2.8	6.7
>100	11.7	0.0	0.0
Mean Velocity (cm/sec)			
<15	54.8	64.2	98.0
15-30	30.5	19.3	2.0
>30	14.7	16.5	0.0

among sites. Major differences included the preponderance of substrate over 20 cm in diameter at the Middle Fork site, and the preponderance of substrate less than 20 cm at the Little Jones site. Average depth was greatest in Hurdygurdy Creek, followed by Little Jones Creek and the Middle Fork. The Little Jones Creek site was markedly different from the other two sites in velocity characteristics; the <15 cm/sec stratum encompassed nearly all of the study area.

Discriminant analysis showed that sites differed mainly with respect to substrate size and velocity (Figure 8; Appendix B). Little Jones was the most distinct site because of smaller average substrate and lower average current velocity. Interpretation of differences in trout habitat utilization between sympatric and allopatric populations were thus tempered by consideration of possible stream effects, particularly when differences were along habitat dimensions by which two sites appreciably differed.

Sympatric versus Allopatric Steelhead. Habitat utilization by sympatric (Hurdygurdy Creek) and allopatric (Middle Fork) steelhead of equal size was compared using discriminant analysis. In general, steelhead in Hurdygurdy Creek were associated with deeper, swifter water than equal size steelhead in the Middle Fork, thus paralleling observed differences in habitat composition between these sites. Differences were, however, statistically significant between steelhead <5 cm only (Appendix C).

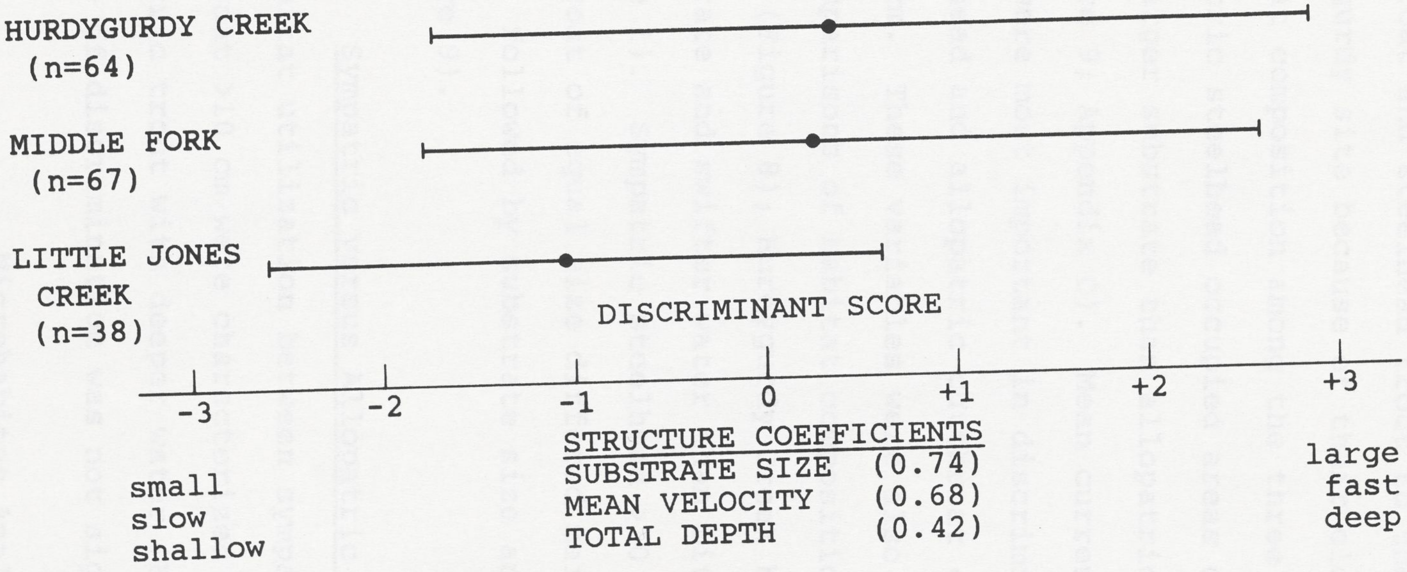

Figure 8. Differences in Habitat Composition among Three Study Sites on the Smith River Based on Means and Ranges of Scores on a Single Linear Composite (Discriminant Functions) of the Habitat Variables. See Appendix B for Statistical Summary.

Sympatric Steelhead versus Allopatric Cutthroat. I chose to limit comparisons of habitat utilization between cutthroat and steelhead trout to the Little Jones and Hurdygurdy site because of their closer similarity in habitat composition among the three sites. In general, sympatric steelhead occupied areas of deeper, swifter water and larger substrate than allopatric cutthroat trout (Figure 9; Appendix C). Mean current velocity and substrate size were most important in discrimination of sympatric steelhead and allopatric cutthroat <5 cm and 5-10 cm. These variables were also important discriminators in comparisons of habitat composition between these two sites (Figure 8); Hurdygurdy Creek had, on average, larger substrate and swifter water than Little Jones Creek (Table 1). Sympatric steelhead >10 cm and allopatric cutthroat of equal size differed mainly with respect to depth, followed by substrate size and mean velocity (Figure 9).

Sympatric versus Allopatric Cutthroat. Differences in habitat utilization between sympatric and allopatric cutthroat >10 cm were characterized mainly by association of sympatric trout with deeper water (Figure 10) although the degree of discrimination was not significant (Appendix C).

Microhabitat Analysis

Microhabitat analysis afforded an opportunity to sample over a greater range of habitats than those

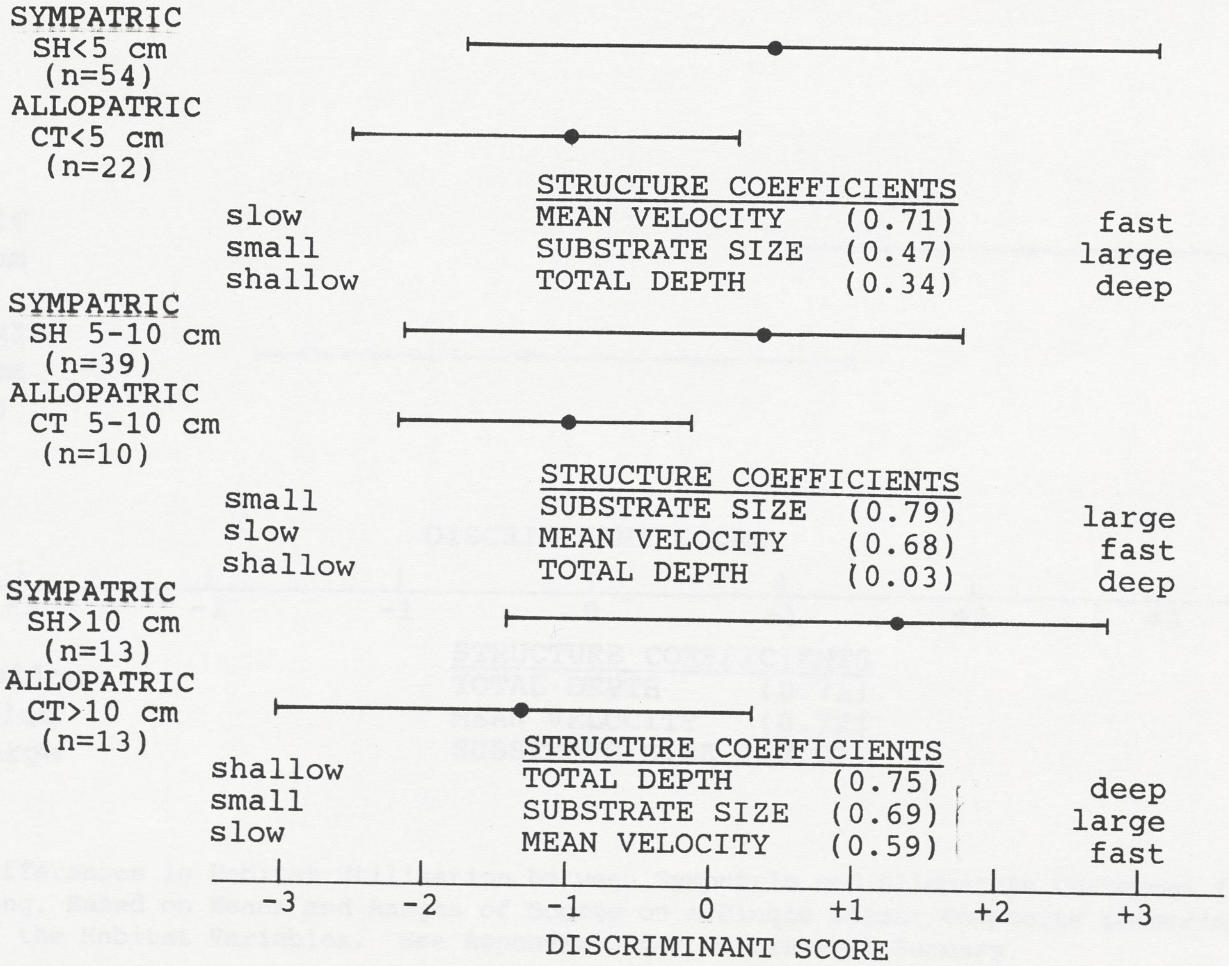

Figure 9. Differences in Habitat Utilization between Sympatric and Allopatric Steelhead and Cutthroat Trout of Equal Size Based on Means and Ranges of Scores on Single Linear Composites (Discriminant Functions) of the Habitat Variables. See Appendix C for Statistical Summary.

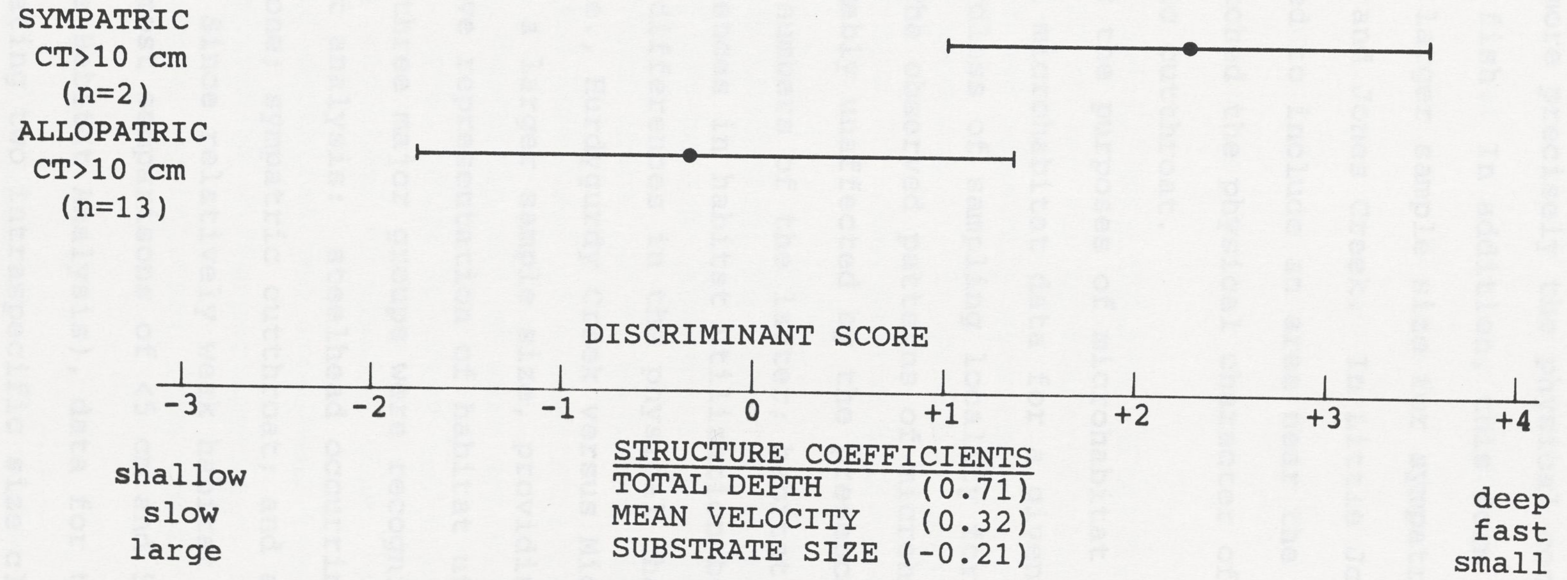

Figure 10. Differences in Habitat Utilization between Sympatric and Allopatric Cutthroat Trout >10 cm Long, Based on Means and Ranges of Scores on a Single Linear Composite (Discriminant Function) of the Habitat Variables. See Appendix C for Statistical Summary.

represented at gridded sites in the previous analysis, and to define more precisely the physical conditions selected by individual fish. In addition, this form of sampling provided a larger sample size for sympatric cutthroat in Hurdygurdy and Jones Creek. In Little Jones Creek, sampling was extended to include an area near the mouth which more closely matched the physical character of streams occupied by sympatric cutthroat.

For the purposes of microhabitat analysis, I chose to pool all microhabitat data for a given steelhead size class regardless of sampling locality for the following reasons: The observed patterns of microhabitat utilization were presumably unaffected by the presence of cutthroat due to the low numbers of the latter; habitat analysis suggested that differences in habitat utilization between sites were related to differences in the physical character of stream reaches (i.e., Hurdygurdy Creek versus Middle Fork); pooling resulted in a larger sample size, providing a more comprehensive representation of habitat utilization. Therefore, three major groups were recognized in microhabitat analysis: steelhead occurring within the sympatric zone; sympatric cutthroat; and allopatric cutthroat. Since relatively weak habitat discrimination was evident in most comparisons of <5 cm and 5-10 cm size classes (see Habitat Analysis), data for these groups were pooled, creating two intraspecific size classes for microhabitat analysis (i.e., <10 cm and >10 cm).

Intra- and interspecific differences in microhabitat selection were described using discriminant analysis. Certain variables were excluded from the analysis because of missing data points or because of inconsistencies in the manner in which they were measured. These were maximum velocity within 0.6 m, distance from nearest cover, and distance from nearest fish.

Sympatric Steelhead and Cutthroat. Sympatric steelhead <10 cm and >10 cm differed significantly in microhabitat use primarily with respect to water velocity (Figure 11; Appendix D); in general, larger steelhead faced swifter currents in areas having higher mean and surface velocities.

Depth accounted, in large part, for differences in microhabitat use between sympatric cutthroat and steelhead trout; cutthroat trout >10 cm occupied significantly deeper water than did steelhead of either size class (Figure 11). In addition, cutthroat >10 cm were associated with slower water (i.e., focal point velocity and mean velocity) than that used by steelhead of similar size. An actual vertical separation of cutthroat and steelhead trout was indicated by their utilization of different depths at focal points that were, on average, equidistant from the bottom (Appendixes E and F).

Allopatric Cutthroat. The degree of microhabitat discrimination between <10 cm and >10 cm size classes of

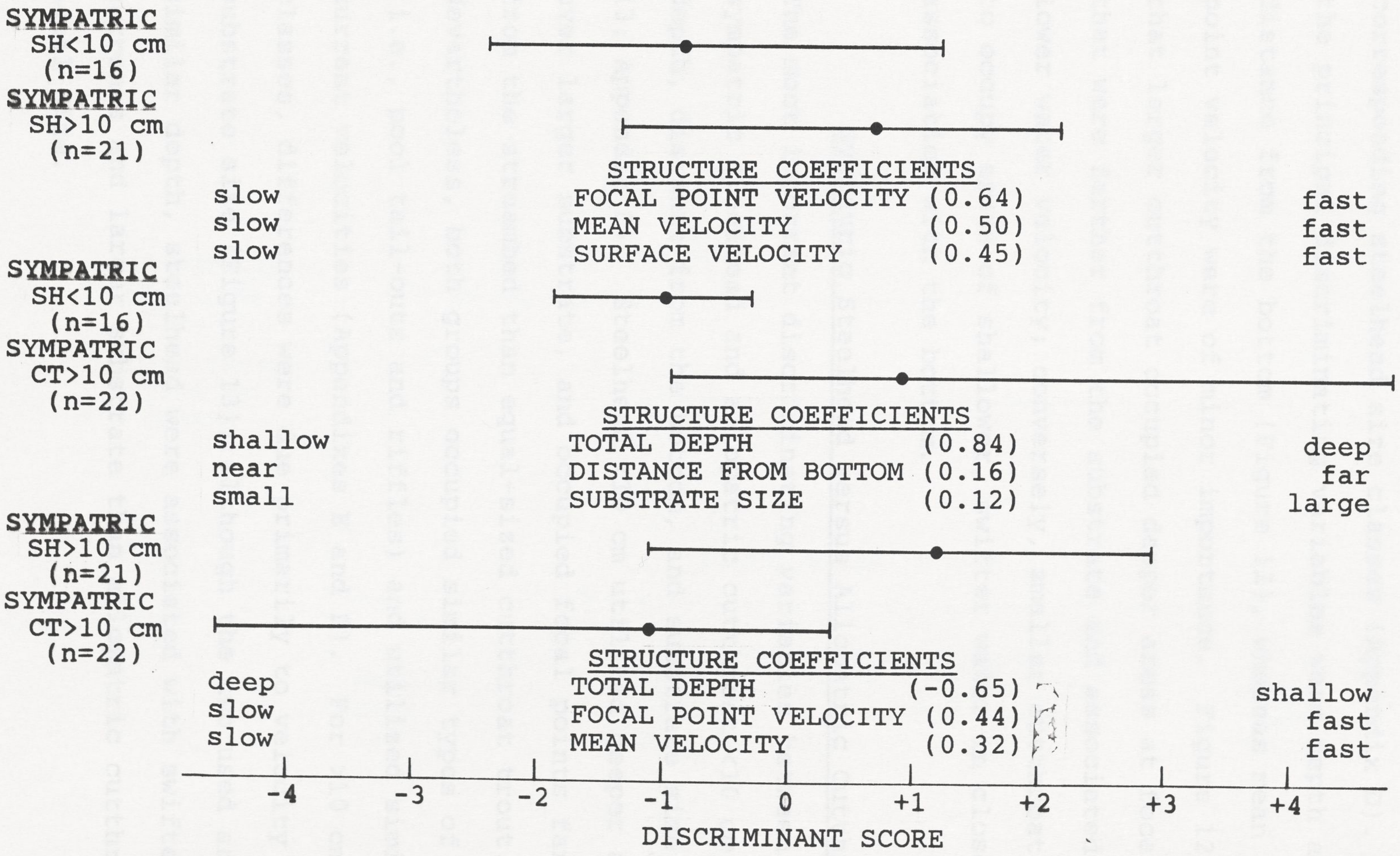

Figure 11. Differences in Microhabitat Utilization between Sympatric Steelhead and Cutthroat Trout Size Classes Based on Means and Ranges of Scores on Single Linear Composites (Discriminant Function) of the Microhabitat Variables. The Magnitude of the Structure Coefficients, in Parentheses, Reflect the Relative Contribution of Individual Variables to Group Differences. The Sign of the Coefficient (+ or -) Indicates Whether the Associated Variable Increases or Decreases With Increasing Scores on the Discriminant Function. See Appendixes D and E for Statistical Summaries.

allopatric cutthroat was similar to that exhibited between corresponding steelhead size classes (Appendix D). However, the principal discriminating variables were depth and distance from the bottom (Figure 12), whereas mean and focal point velocity were of minor importance. Figure 12 shows that larger cutthroat occupied deeper areas at focal points that were farther from the substrate and associated with lower water velocity; conversely, smaller cutthroat tended to occupy areas of shallower, swifter water in closer association with the bottom.

Sympatric Steelhead versus Allopatric Cutthroat. The most important discriminating variables between sympatric steelhead and allopatric cutthroat <10 cm were depth, distance from the bottom, and substrate size (Figure 13; Appendix D). Steelhead <10 cm utilized deeper areas over larger substrate, and occupied focal points farther from the streambed than equal-sized cutthroat trout. Nevertheless, both groups occupied similar types of habitat (i.e., pool tail-outs and riffles) and utilized similar current velocities (Appendixes E and F). For >10 cm size classes, differences were due primarily to velocity and substrate size (Figure 13); although the two used areas of similar depth, steelhead were associated with swifter currents and larger substrate than allopatric cutthroat of equal size.

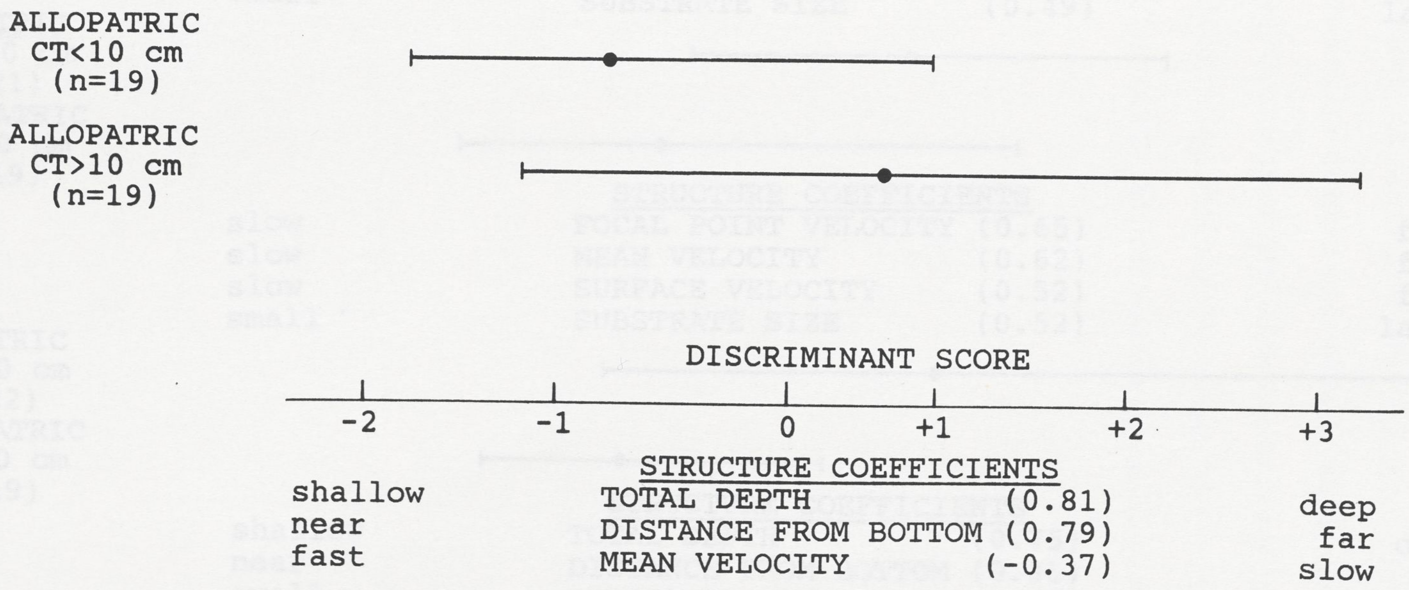

Figure 12. Differences in Microhabitat Utilization between Allopatric Cutthroat <10 cm and >10 cm in Length (Little Jones Creek) Based on Means and Ranges of Scores on a Single Linear Composite (Discriminant Function) of the Habitat Variables. See Appendixes D and E for Statistical Summaries.

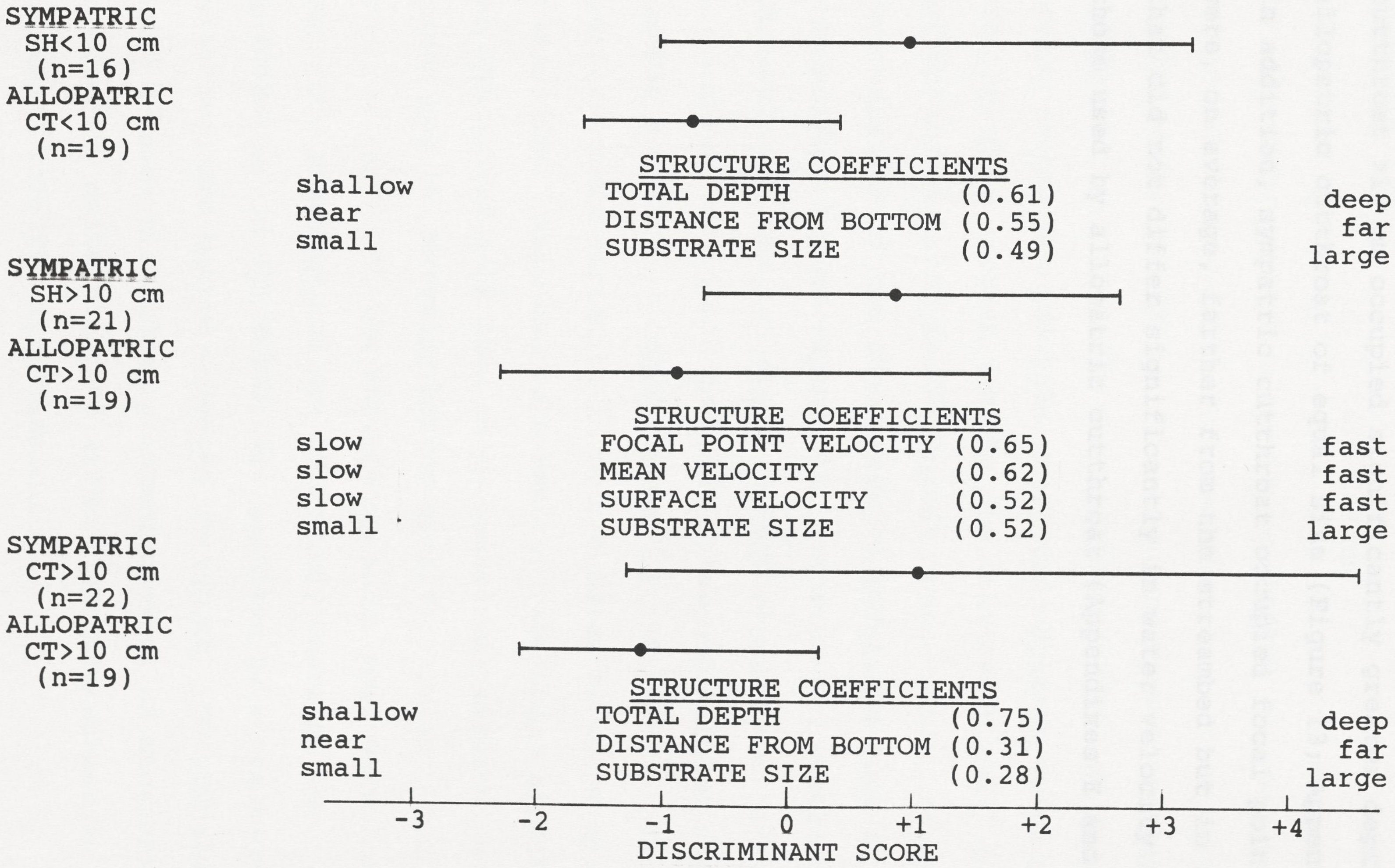

Figure 13. Differences in Microhabitat Utilization between Sympatric and Allopatric Steelhead and Cutthroat Trout of Equal Size Based on Means and Ranges of Scores on Single Linear Composites (Discriminant Functions) of the Habitat Variables. See Appendixes D and E for Statistical Summaries.

Sympatric versus Allopatric Cutthroat. Sympatric cutthroat >10 cm occupied significantly greater depths than allopatric cutthroat of equal size (Figure 13; Appendix D). In addition, sympatric cutthroat occupied focal points that were, on average, farther from the streambed but in areas that did not differ significantly in water velocity from those used by allopatric cutthroat (Appendixes E and F).

DISCUSSION

Microhabitat analysis provided a broader and more representative sample of stream characteristics selected by individual trout groups than that obtained using habitat analysis. For example, restriction of sampling to a single reach in habitat analysis prevented adequate description of the physical habitat used by the relatively small population of cutthroat trout in Hurdygurdy Creek. This resulted in overemphasis of the importance of substrate size in comparisons between sympatric cutthroat and steelhead trout. In addition, the failure to detect significant differences in habitat use within the same reach and between reaches was probably due to an inability of habitat analysis to discern smaller scale variation in microhabitat to which fish were responding. This may have been of particular significance at the Middle Fork site where relatively shallow, swift water and an irregular bottom profile resulted in a complex flow pattern. At the Hurdygurdy site, mean water column velocity probably did not adequately describe the differences in the velocities utilized by surface-oriented steelhead and bottom-oriented cutthroat. Nevertheless, habitat analysis aided in interpretation of microhabitat results by defining broad differences in habitat utilization based on relative fish densities.

Both habitat and microhabitat analysis revealed shifts in habitat occupancy with increasing body size. Movements of juvenile salmonids to areas of progressively deeper, swifter water and larger substrate with growth have been well documented (Lister and Genoe 1970; Everest and Chapman 1972; Griffith 1972; Hanson 1977; Symons and Heland 1978), and have generally been attributed to changes in space, food, and cover requirements (Chapman and Bjornn 1969). This relationship was most pronounced in pools of the largest tributaries studied (e.g., Hurdygurdy Creek) where marked gradients of depth and velocity corresponded with relatively discrete spatial distributions of steelhead size classes, with larger individuals occurring at greater distances from the stream margins. In contrast, significant spatial overlap and weak habitat discrimination among cutthroat size classes at the Little Jones site reflected the more homogeneous physical character of pools in this stream, particularly with respect to current velocity.

Contrary to that observed for juvenile steelhead in larger tributaries, depth assumed more importance than velocity in microhabitat discrimination of cutthroat size classes in Little Jones Creek. Furthermore, velocity was inversely related to trout size, reflecting the predominance of larger trout in pools and smaller trout in shallower, swifter water habitats. A similar relationship was observed for age 0+ and 1+ cutthroat trout in a headwater stream on the Olympic Peninsula, Washington (June 1981). In Little

Jones Creek, this general distribution pattern corresponded with that described for cutthroat in small streams above migration barriers in western Washington in which underyearlings selectively utilized low gradient riffles while yearling and older trout were strongly associated with pool habitat (Bisson et al. 1981).

The extent to which disparity in stream size and physical character influenced observed differences in habitat utilization between allopatric cutthroat in Little Jones Creek and steelhead in larger tributaries is unknown. Association of cutthroat trout with shallower, slower water and smaller substrate in pools may simply reflect their occurrence in smaller stream environments and not necessarily predisposed differences in habitat selection. This is suggested by the results of habitat analysis which show that differences in habitat occupancy between corresponding size classes of allopatric cutthroat and sympatric steelhead paralleled major between-site differences in habitat composition. Hence, microhabitat utilization by allopatric cutthroat may not adequately describe the potential microhabitat niche of cutthroat in the absence of steelhead. Furthermore, trout populations effectively separated by a barrier falls would be expected to differ behaviorally as a consequence of genetic isolation and differential selective pressures (Northcote 1969). The potentially confounding influence of such differences is inherent with attempts to detect species interactions by evaluating patterns of resource use under natural conditions of sympatry and allopatry. Because of the lack of a true control, there is no certainty that the observed differences between sites are due to the presence or absence of one species (Connel 1975). On these grounds, interpretations of similarities and differences in microhabitat utilization between sites should be tempered by consideration of possible stream effects.

Because of similar size-related shifts in microhabitat use detected in populations of juvenile steelhead and cutthroat trout in general, the potential for spatial interaction would be greatest between individuals of comparable size. Within their respective streams, allopatric cutthroat and sympatric steelhead <10 cm occupied the same type of stream habitats (i.e., pool tail-outs and riffles) where they utilized similar current velocities. In western Washington, Bisson et al. (1981) found that age 0+ cutthroat both above and below migration barriers displayed similar affinities for low gradient riffles, citing decreased utilization of such habitats and diminished growth rates in anadromous zones as evidence of the competitive dominance of age 0+ steelhead trout.

Stream simulation studies have offered additional evidence of the behavioral and ecological similarities of juvenile steelhead and cutthroat trout. Behavioral interaction between sympatric age 0+ steelhead trout and coho salmon during spring and summer (Hartman 1965) was also shown to occur between age 0+ cutthroat trout and coho, resulting in a similar pattern of habitat segregation (Glova 1978). Hanson (1977) found that age 0+ cutthroat and steelhead trout exhibited similar distribution patterns when alone in laboratory stream channels. In sympatric tests, steelhead displaced cutthroat from riffles when the former had prior residency. Thus, the potential for spatial interaction between age 0+ cutthroat and steelhead trout appears to be large. In the Smith River drainage, however, spatial interaction is minimized by complete or partial segregation of juveniles into different parts of the drainage during the early rearing period.

Sympatric cutthroat trout, represented by individuals >10 cm, segregated by depth from both steelhead size classes (<10 cm and >10 cm). The results of microhabitat comparisons between cutthroat and steelhead >10 cm reflected association of cutthroat trout with deep, slow-water pool areas and steelhead trout with shallower, swift water areas (i.e., heads of pools, deep runs and rapids). A similar distribution pattern has been observed in western Cascade streams supporting resident trout populations (Nicholas 1978a) and in a southeastern Alaskan stream-lake system (Jones 1977). In several streams in western Washington, age 1+ steelhead selected rapids, cascades, and glides, while age 1+ and 2+ cutthroat generally avoided these habitats in favor of pools (Bisson et al. 1981).

Microhabitat analysis showed that sympatric and allopatric cutthroat >10 cm faced similar water velocities but at different depths. Diving observations within their respective streams revealed that these groups generally occupied the deepest portions of pools. Because pools in sympatric areas were generally larger and deeper, effects due to stream size may be significant. It is possible that specific behavioral responses or tolerances to current velocity may restrict cutthroat in larger, swifter flowing streams to greater pool depths, resulting in segregation from strongly rheotactic steelhead trout.

Another consideration is the differential responses to cover exhibited by these two species. In a small Montana stream, Lewis (1969) found that among a number of physical variables characterizing pool habitat, current velocity and cover accounted for most of the variation in numbers of trout longer than 17.5 cm. Whereas cover assumed greater importance for brown trout (<u>S</u>. <u>trutta</u>), current velocity was the most important variable for rainbow trout. The strong association of juvenile steelhead with high current velocities is thought to be largely related to food supply (i.e., abundance of drifting organisms), although associated cover components of depth and turbulence may also contribute in releasing holding behavior (Chapman and Bjornn 1969; Everest and Chapman 1972; Pearlstone 1976). Cutthroat trout, like brown trout, generally exhibit a strong cover-seeking response. Older cutthroat are known to utilize heavy cover in deep areas adjacent to the current (Chapman and Bjornn 1969). Bisson et al. (1981) reported strong positive associations of yearling and older cutthroat with large wood debris, undercut banks, and depth. In the Smith River, larger tributaries such as Hurdygurdy Creek, where cutthroat and steelhead are sympatric, are subjected annually to scouring winter flows which effectively clear the channel of large wood debris and bank cover. Consequently, stream cover components are limited to depth, surface turbulence, and instream boulders. Because of this relatively low degree of structural complexity, there may be little opportunity for interspecific differences in cover-velocity preferences to express themselves. Within pools, these differences appear to be manifested largely by vertical segregation, with cutthroat occupying sites in deeper, slower water and steelhead positioned in shallower, swifter water. This interpretation of the observed distribution patterns implies that spatial segregation of cutthroat and steelhead trout is effected largely by innate differences in microhabitat responses, and would therefore constitute an example of selective segregation.

Evaluation of dietary differences between sympatric cutthroat and steelhead trout was not undertaken in this study. Examination of the stomach contents from a small sample of cutthroat trout in addition to a number of diving observations, however, suggested that they were feeding to a large extent on large benthic organisms (e.g., crayfish, salamanders) and fish, the most important of which appeared to be young chinook salmon. In the main forks and larger tributaries of the Smith River, juvenile salmon were observed in pools holding positions or schooling in open water during the summer months prior to outmigration. I suspect that at this time they are quite vulnerable to predation and would provide an ample food supply for the relatively small numbers of cutthroat trout observed in these waters. The piscivorous habit of coastal cutthroat trout is well documented (Ricker 1941; Idyll 1942; Armstrong 1971; Giger 1972; Scott and Crossman 1973). Their occurrence in deep pool areas removed for productive surface currents and their roving behavior provided additional evidence of their reliance on prey other than invertebrate drift. In contrast to sympatric cutthroat trout, allopatric cutthroat appeared to feed mainly on surface and drifting foods (largely terrestrial insects). Wydoski and Whitney (1979) noted the opportunistic feeding habits of cutthroat trout in Oregon waters.

The observed differences in habitat utilization and feeding habits between sympatric and allopatric cutthroat trout in the Smith River reflect a certain behavioral flexibility characteristic of temperate freshwater fish in general (Larkin 1956). In view of the close similarities in morphology and behavior of cutthroat and steelhead trout, this flexibility suggests a potential for broad overlap in resource utilization as demonstrated for other salmonids in sympatry and under conditions of natural and experimentally-induced allopatry (Hartman 1965; Glova and Mason 1977; Griffith 1974; Bisson et al. 1982). For example, Hanson (1977) failed to find appreciable quantitative differences in habitat utilization between allopatric populations of cutthroat (S. clarki lewisi) and steelhead trout in small and large northern Idaho streams. For these reasons, and because of possible stream effects on habitat use, the possibility that interactive mechanisms are involved in segregation of cohabiting coastal cutthroat and steelhead cannot be dismissed.

Interactive segregation of stream dwelling salmonids is typically mediated by territoriality or social dominance characterized by aggression and mutually recognized threat displays (Newman 1956; Kalleberg 1958). This type of interaction falls under the broad category termed interference because one individual or species typically controls access to resources within a given area or habitat (Brian 1956; Nilsson 1967). Interaction between species will be magnified when resources are in short supply, the outcome of which will either be total exclusion of one species or segregation into different habitat or food niches through behavioral differences (Nilsson 1963, 1965). A number of studies have emphasized the importance of habitat segregation as a means by which sympatric salmonids partition stream resources, invoking both interactive and selective processes (Lindroth 1957; Hartman 1965; Lister and Genoe 1970; Everest and Chapman 1972; Glova 1978). Examination of the spatial relationships of sympatric cutthroat and steelhead trout during summer suggests that steelhead, by virtue of their dominant drift-feeding role in large streams, may exclude cutthroat from areas receiving high inputs of drifting foods, forcing them to occupy marginal localities offering fewer drift-feeding opportunities. Therefore, the effect of interaction would be to accentuate species differences in microhabitat utilization and food preferences. Consequently, cutthroat trout may be forced to exploit a smaller but exclusive share of the available resources. Their capacity to prey on fish and other large organisms would appear to be an important means of reducing potential interaction. Moreover, their persistence in streams dominated by steelhead may be ascribed in general to a broad niche breadth.

A similar niche shift was indicated in a study of the diets and growth of allopatric and sympatric lake populations of rainbow and cutthroat trout in British Columbia (Nilsson and Northcote 1981). In the presence of rainbow, which were largely limnetic feeders, cutthroat fed more on littoral prey and were more piscivorous than allopatric cutthroat. Their larger size in sympatry also indicated a dietary shift from smaller limnetic prey items to larger benthic organisms and fish in littoral zones. These findings, along with the marked aggressiveness of rainbow demonstrated in laboratory aquaria, led the authors to suggest that food segregation in sympatry was maintained through interaction. They also suggested that the marked shift in food habits of cutthroat trout may be related to its larger mouth and well developed oral dentition. Differences in mouth size may be important in food segregation, as pointed out by Northcote (1954).

Evolutionary Significance of Life History and Ecological Traits of Coastal Cutthroat Trout

Continued surveys of northern California streams in summer, 1984, revealed that cutthroat trout occur predominantly in small coastal streams directly entering the ocean, and in small tributaries and upper reaches of larger drainages where they often occur above natural falls or log jams. Some of these trout appear to constitute resident, breeding populations (DeWitt 1954), although penetration of migratory cutthroat into these waters may occur (Michael 1983). Migratory cutthroat, represented by individuals >10 cm long, occur in relatively small numbers in the lower reaches of larger drainages during the summer months. DeWitt (1954) reported that cutthroat populations in California streams during summer and fall consist ordinarily of yearling and older trout, including mature fish that have spawned but have never gone to sea, and a few sea-run individuals trapped by receding water levels after spawning. These observations suggest that California stocks exhibit a variable life history pattern similar to that documented in Oregon (Nicholas 1978b; Tomasson 1978) and Washington (Fuss 1984) drainages.

Among migratory stocks, traits such as age at migration, run timing, and spawning time vary on a regional and local basis (Tomasson 1978; Campton 1981), reflecting adaptations to different environments and selective factors (Behnke 1979; Johnston 1981). These traits, however, are superimposed on a basic life history pattern common to stocks throughout the range. Unique aspects of this general pattern include the following: an extended rearing period in freshwater and estuarine waters prior to smolting (Giger 1972; Wydoski and Whitney 1979); restriction to estuaries and near shore areas in proximity to the home stream during summer residence in saltwater (Haig-Brown 1947; Giger 1972; Scott and Crossman 1973; Tomasson 1978); return of both mature and immature fish to freshwater every fall or winter with few overwintering in saltwater (Giger 1972; Johnston and Mercer 1976; Jones 1977); and selection of small streams for spawning and early rearing (Sumner 1948; Scott and Crossman 1973; Wydoski and Whitney 1979). Coastal cutthroat may thus be characterized by a relatively low degree of anadromy (Rounsefell 1958) and habitat affinities that appear to be largely complementary to that of anadromous steelhead trout. The apparent phyletic significance of these differences suggests that they formed a basis for ecological divergence and sympatric coexistence of these two closely related species.

The cutthroat trout, <u>Salmo clarki</u>, represented by two major lineages giving rise to coastal and interior forms, was the first salmonid to become established in western North America (Behnke 1979). In the upper Columbia basin, the formation of major falls originally isolated interior cutthroat trout (<u>S</u>. <u>c</u>. <u>lewisi</u>) and blocked the penetration of later invading trout of redband lineage (see Behnke (1979) for discussion of division of redband and coastal rainbow trout). Below the falls, interior cutthroat were largely replaced and now occur as sporadic, disjunct populations isolated above barriers. Based on comparisons of habitat utilization between allopatric populations of cutthroat and steelhead trout, and the results of laboratory stream experiments, Hanson (1977) suggested that the absence of sympatric populations in central Idaho streams was due to interaction for habitat. Hence, broad geographic segregation of interior cutthroat and redband steelhead trout appears to be the result of competitive exclusion of the former throughout much of its original range.

The maintenance of coexistence and species integrity of coastal cutthroat and steelhead trout throughout a broad geographic area represents a unique instance of sympatry among western trouts that may be traced to ecological and behavioral differences established incidentally in allopatry and later augmented by species interactions following initial contact. Following its divergence from an ancestral interior form and occupation of Pacific Coast regions, the coastal cutthroat trout retained a relatively strong tie to freshwater and a dependence on small stream and lake systems for spawning and rearing. This is reflected by the maintenance of isolated populations above barrier falls which apparently formed after cutthroat became established in upstream waters. In those systems associated with productive bodies of water (e.g., lakes, estuaries), migration became a significant feature of the life cycle. Anadromy, however, remained weakly developed. The appearance of the anadromous coastal rainbow trout was probably marked by rapid expansion of populations and domination of large stream systems and reaches with direct access to the ocean.

Hence, it seems likely that coastal cutthroat and steelhead trout achieved some degree of spatial segregation upon initial contact because of predisposed differences in spawning and rearing habitat. In zones of overlap (i.e., areas possessing habitat of intermediate character), interaction between species may have accentuated these differences through natural selection. The strong potential for spatial interaction during the early rearing period suggests that interaction for habitat may have been important in promoting further segregation of spawning and nursery areas. In addition, negative effects due to interbreeding may have reinforced traits leading to segregation. Because coastal cutthroat and steelhead trout presumably lack a significant barrier to hybridization, Behnke (1979) suggested that the maintenance of reproductive isolation is due to niche separation and specialization which places hybrids at a disadvantage and favors pure parental matings. Accordingly, the incidence of significant natural hybridization in some streams (Behnke 1979; Campton 1981) indicates a breakdown of ecological segregation resulting from the lack of environmental attributes favoring isolation. In this situation, hybrids may actually be favored.

MANAGEMENT RECOMMENDATIONS

From the foregoing it is evident that stable coexistence of sympatric populations of coastal cutthroat and steelhead trout depends on the maintenance of certain physical characteristics of stream environments that favor species segregation. Because of the dominance of steelhead trout in most accessible reaches possessing suitable spawning and rearing habitat, the integrity of small streams and physical barriers that limit steelhead distribution should be the focus of coastal cutthroat management in California. Of foremost importance is the identification of those streams that support resident populations and serve as spawning and nursery areas for migratory cutthroat. The latter will require correct identification of juvenile cutthroat and steelhead, as specimens less than 75 mm are often difficult to distinguish. It is possible that young cutthroat and steelhead from a particular locality may express distinctive traits that are easily discerned. Otherwise, more intensive techniques such as analysis of scale characteristics (Vernon and McMynn 1957) and electrophoresis (Campton 1981) will be necessary.

The limited extent and restricted distribution of stream habitat utilized by cutthroat trout coupled with the extreme sensitivity of small stream environments to watershed disturbance compounds the threat posed by widespread logging and related activities to resident and migratory populations in western coastal streams. In Oregon and Washington, studies of the immediate and long-term effects of logging on the physical and biological components of headwater stream environments have suggested that cutthroat trout are particularly sensitive to habitat alteration (Moring and Lantz 1975; Osborn 1981). Findings of these studies have emphasized the importance of buffer strips in providing shade and bank stability, as well as serving as a source of organic material to the stream. The availability of large forest debris in streamside zones following logging may be critical to long-term stability of headwater populations because of its role as cover and shelter for cutthroat trout, and as a stabilizing agent of small stream channels (Osborn 1981). Guidelines established in these studies for logging practices may be used as a basis for restoration of already damaged habitat.

The dependence of cutthroat trout also on estuarine waters demands that steps be taken to curb activities such as dredging, filling, and channelization in lower river reaches and tidewater areas. My surveys have indicated that a number of brackish and freshwater sloughs on the Smith River floodplain are important summer habitats for subadult and adult cutthroat.

Once adequate protection of critical habitat is ensured, efforts should be directed at assessing life history and population characteristics of migratory stocks. The Smith River would be an obvious choice for such a study. The operation of migrant traps or weirs at selected locations within the drainage would yield data on the timing and sizes of downstream and upstream runs, age-size composition of migrants, and estimates of growth and survival. A tagging and angler recovery program would help to determine migration patterns and levels of harvest. The information obtained may provide a basis for reevaluation and modification of existing angling regulations.

Hatchery supplementation of wild cutthroat stocks has proven successful in a number of Oregon coastal streams which currently support sizeable estuary fisheries (Giger 1972). The demand for such a fishery in California has not been strong evidently because cutthroat are usually not directly sought after nor readily recognized by the general angling public. Undoubtedly, the overwhelming popularity of salmon and steelhead has contributed to this situation. Comparative neglect in the past by biologists and managers alike has only recently begun to give way to increasing concern as a result of noticeable population declines in many state waters. The potential for development of a cutthroat fishery in California thus lies first in obtaining more comprehensive information on existing wild stocks so that natural production may be sustained and possibly enhanced in future years.

SUMMARY AND CONCLUSIONS

Diving surveys of the Smith River drainage, California, in summer, 1982-1983, revealed that juvenile coastal cutthroat trout and steelhead trout segregate broadly within the drainage and into different microhabitats along reaches where they occur sympatrically. In summer, 1983, a study was undertaken to quantitatively define and compare the physical microhabitats utilized by these species in natural sympatry and allopatry to assess the potential for spatial interaction. Data on trout distribution, collected in selected reaches by a diver using snorkeling gear, were related to depth, velocity, and substrate size characteristics measured over large stream areas and at individual fish locations. The major findings of the study were as follows:

1. Both in sympatry and local allopatry, juvenile steelhead exhibited a positive relationship between body size and the habitat variables, reflecting the general movement of young trout to areas of progressively deeper, swifter water and larger substrate with growth. A similar but less pronounced distribution pattern was observed among allopatric cutthroat in a small tributary above a falls.
2. Within their respective streams, allopatric cutthroat and sympatric steelhead <10 cm long (age 0+ and 1+ fish)

occupied the same type of habitat where they utilized similar current velocities, indicating a large potential for spatial interaction. Cutthroat within this size range, however, were found only in small tributaries above natural falls or log jams, and in upper reaches of the drainage above major concentrations of juvenile steelhead.

3. Sympatric cutthroat >10 cm (yearling and older fish) used slower, deeper water than sympatric steelhead of similar size, reflecting occupation by cutthroat of deeper pool areas near the bottom and association of steelhead with swift, surface currents in runs, rapids, and heads of pools.
4. Sympatric cutthroat generally occupied microhabitats comparable in velocity and depth characteristics to those occupied by equal-sized allopatric cutthroat, taking into account possible effects due to different stream sizes.

Microhabitat segregation of sympatric cutthroat and steelhead trout during summer is attributed to differential behavioral responses to cover and current velocity. Behavioral flexibility demonstrated by sympatric and allopatric cutthroat suggests that differences observed in sympatry may be due in part to interaction. Broad spatial segregation of coastal cutthroat and juvenile steelhead trout is attributed to differences in adult migratory behavior and spawning preferences. Segregation of adult spawners serves to maintain reproductive isolation and also to separate nursery areas, thus minimizing interaction between juveniles during the early rearing period when microhabitat requirements are most similar. Barriers or impediments to upstream migration undoubtedly play an important role. Stable coexistence of these closely related species thus appears to be a result of both selective and interactive segregation as defined by Brian (1956).

REFERENCES CITED

Armstrong, R. H. 1971. Age, food, and migration of sea-run cutthroat trout, Salmo clarki, at Eva Lake, southeastern Alaska. Trans. Amer. Fish. Soc. 100:302-306.

Behnke, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Bd. Canada 29:639-671.

_____. 1979. Monograph of the native trouts of the genus Salmo of western North America. Unpublished manuscript. 215 pp.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1981. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low stream flow. Pages 62-73 in N. B. Armantrout (ed.), Acquisition and utilization of aquatic habitat inventory information, Proc. Symp. Amer. Fish. Soc., Western Division.

Bisson, P. A., J. L. Nielsen, and J. W. Ward. 1982. Experimental release of coho salmon (Oncorhynchus kisutch) into a stream impacted by Mount Saint Helens volcano. Weyerhaeuser Co., Tacoma, Washington.

Brian, M. V. 1956. Segregation of species of the ant genus Myrmica. J. Animal Ecology 25:319-337.

Campton, D. E. 1981. Genetic structure of sea-run cutthroat trout (Salmo clarki clarki) populations in the Puget Sound area. M.S. Thesis, Univ. Washington, Seattle.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 in T. G. Northcote (ed.), Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver.

Connel, J. H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. M. Diamond (eds.), Ecology and evolution of communities. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

Cramer, F. K. 1940. Notes on the natural spawning of cutthroat trout (Salmo clarkii clarkii) in Oregon. Proc. Sixth Pacific Sci. Congress, Pacific Sci. Ass. 3:335-339.

DeWitt, J. W., Jr. 1954. A survey of the coast cutthroat trout, Salmo clarki clarki Richardson, in California. Calif. Fish and Game 40:329-335.

EDAW, Inc. 1980a. Smith River draft waterway management plan. Appendix one: Basin resources. 1725 Montgomery Street, San Francisco, CA 94111. Prepared for Calif. Dept. Fish and Game. 400 pp.

_____. 1980b. Smith River draft waterway management plan. Appendix six: Tributary description and inclusion alternatives. Prepared for Calif. Dept. Fish and Game. 1725 Montgomery Street, San Francisco, CA 94111. 209 pp.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Bd. Canada 29:91-100.

Fuss, H. J. 1984. Age, growth, and instream movement of Olympic Peninsula coastal cutthroat trout, Salmo clarki clarki. Pages 125-134 in J. M. Walton and D. B. Houston (eds.), Olympic wild fish conference. Proceedings of the Peninsula Coll. Fish. Tech. Program, Port Angeles, Washington.

Gause, G. F. 1964. The struggle for existence. Hafner Publ. Co., New York.

Giger, R. D. 1972. Ecology and management of coastal cutthroat trout in Oregon. Oregon State Game Comm., Fish. Res. Rep. 6, Corvallis, Oregon. 61 pp.

Glova, G. J. 1978. Pattern and mechanism of resource partitioning between stream populations of juvenile coho salmon (Oncorhynchus kisutch) and coastal cutthroat trout (Salmo clarki clarki). Ph.D. Thesis, Univ. Victoria, British Columbia.

Glova, G. J., and J. C. Mason. 1977. Comparison of coastal cutthroat trout populations in allopatry and those sympatric with coho salmon and sculpins in several small coastal streams on Vancouver Island, B.C. Fish. Mar. Serv. MS Rep. 1434: 35 pp.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. J. Fish. Res. Bd. Canada 29:265-273.

_____. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Trans. Amer. Fish. Soc. 103:440-447.

Haig-Brown, R. L. 1947. The western angler - An account of Pacific salmon and western trout in British Columbia. William Morrow and Co., New York.

Hanson, D. L. 1977. Habitat selection and spatial interaction in allopatric and sympatric populations of cutthroat and steelhead trout. Ph.D. Thesis, Univ. Idaho, Moscow.

Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 22:1035-1081.

Hartman, G. F., and C. A. Gill. 1968. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. J. Fish. Res. Bd. Canada 25:33-48.

Idyll, C. 1942. Food of rainbow, cutthroat and brown trout in the Cowichan River system, British Columbia. J. Fish. Res. Bd. Canada 5:448-458.

Iwatsubo, R. T., and D. S. Washabaugh. 1982. Water-quality assessment of the Smith River drainage basin, California and Oregon. U. S. Geological Survey, Water-Resources Investigations 81-82. 118 pp.

Johnston, J. M. 1981. Life histories of anadromous cutthroat with emphasis on migratory behavior. Pages 123-127 *in* E. L. Brannon and E. O. Salo (eds.), Proc. salmon and trout migratory behavior symposium. Univ. Washington, Seattle.

Johnston, J. M., and S. P. Mercer. 1976. Sea-run cutthroat in saltwater pens - Broodstock development and extended juvenile rearing (with life history compendium). Washington State Game Dept., Fish. Res. Rep., Project AFS-57-1, Olympia.

Jones, D. E. 1977. A study of cutthroat-steelhead in Alaska. Annual performance report and completion report, Vol. 18, Study AFS 42. Alaska Dept. Fish and Game, Juneau.

June, J. A. 1981. Life history and habitat utilization of cutthroat trout (Salmo clarki) in a headwater stream on the Olympic Peninsula, Washington. M.S. Thesis, Univ. Washington, Seattle.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). Rep. Inst. Freshwater Res. Drottningholm 39:55-98.

Klecka, W. R. 1975. Discriminant analysis. Pages 434-467 in N. H. Nie et al., Statistical package for the social sciences (SPSS), second edition. McGraw-Hill Book Co., New York.

_____. 1980. Discriminant analysis. Sage Publications, Beverly Hills and London.

Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Bd. Canada 13:327-342.

Lewis, S. L. 1969. Physical factors influencing fish populations in pools of a trout stream. Trans. Amer. Fish. Soc. 98:14-19.

Lindroth, A. 1957. Distribution, territorial behavior and movements of sea trout fry in the River Indalsalven. Rep. Inst. Freshwater Res. Drottningholm 36:104-119.

Lister, D. B., and H. S. Genoe. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Bd. Canada 27:1215-1224.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins Co., Baltimore.

Lowry, G. R. 1965. Movement of cutthroat trout, Salmo clarki clarki (Richardson) in three Oregon coastal streams. Trans. Amer. Fish. Soc. 94:334-338.

Michael, J. H., Jr. 1983. Contribution of cutthroat trout in headwater streams to the sea-run population. Calif. Fish and Game 69:68-76.

Moring, J. R., and R. L. Lantz. 1975. The Alsea watershed study: Effects of logging on the aquatic resources of three headwater streams of the Alsea river, Oregon. Part 1 - Biological studies. Oregon Dept. Fish and Wildlife, Fish. Res. Rep. 9, Corvallis. 66 pp.

Needham, P. R., and R. Gard. 1959. Rainbow trout in Mexico and California with notes on the cutthroat series. Univ. Calif. Publ. Zool. 67:1-124.

Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 29:64-81.

Nicholas, J. W. 1978a. Life history differences between sympatric populations of rainbow and cutthroat trouts in relation to fisheries management strategy. Pages 181-188 *in* J. R. Moring (ed.), Proceedings of the wild trout-catchable trout symposium. Oregon Dept. Fish and Wildlife, Corvallis.

______. 1978b. A review of literature and unpublished information on cutthroat trout (*Salmo clarki clarki*) of the Willamette watershed. Oregon Dept. Fish and Wildlife, Infor. Rep. Ser., Fish. 78-1. 22 pp.

Nilsson, N. -A. 1963. Interaction between trout and char in Scandinavia. Trans. Amer. Fish. Soc. 92:276-285.

______. 1965. Food segregation between salmonoid species in North Sweden. Rep. Inst. Freshwater Res. Drottningholm 46:58-78.

______. 1967. Interactive segregation between fish species. Pages 295-313 *in* S. D. Gerking (ed.), The biological basis of freshwater fish production. Blackwell Sci. Publ., Oxford and Edinburgh.

Nilsson, N. A., and T. G. Northcote. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. Can. J. Fish. Aquat. Sci. 38:1228-1246.

Northcote, T. G. 1954. Observations on the comparative ecology of two species of fish, *Cottus asper* and *Cottus rhotheus*, in British Columbia. Copeia 1954:25-28.

______. 1969. Patterns and mechanisms in the lakeward migratory behavior of juvenile trout. Pages 183-203 *in* T. G. Northcote (ed.), Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver.

Osborn, J. G. 1981. The effects of logging on cutthroat trout (Salmo clarki) in small headwater streams. Final Rep., FRI-UW-8113, Fish. Res. Inst., Univ. Washington, Seattle.

Pearlstone, P. S. M. 1976. Management implications of summer habitat characteristics of juvenile steelhead trout (Salmo gairdneri) in the Big Qualicum River. British Columbia Fish and Wildlife Branch, Fish. Management Rep. 67. 13 pp.

Ricker, W. E. 1941. The consumption of young sockeye salmon by predaceous fish. J. Fish Res. Bd. Canada 5:293-313.

Rounsefell, G. A. 1958. Anadromy in North American salmonidae. Fish. Bull. 131, 58:171-185.

Saunders, R. L., and J. H. Gee. 1964. Movements of young Atlantic salmon in a small stream. J. Fish. Res. Bd. Canada 21:27-36.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Bd. Canada, Bull. 184, Ottawa. 966 pp.

Six Rivers National Forest files. 1981-1982. Fox unit monitoring. Supervisors Office, Eureka, California.

Sumner, F. H. 1948. The coast cutthroat trout. Oregon State Game Comm. Bull. 3:1-8.

_____. 1962. Migration and growth of the coastal cutthroat trout in Tillamook County, Oregon. Trans. Amer. Fish. Soc. 91:77-83.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1:157-174.

Symons, P. E. K., and M. Heland. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (Salmo salar). J. Fish. Res. Bd. Canada 35:175-183.

Tomasson, T. 1978. Age and growth of cutthroat trout, Salmo clarki clarki Richardson, in the Rogue River, Oregon. M. S. Thesis, Oregon State Univ., Corvallis.

Vernon, E. H., and R. G. McMynn. 1957. Scale characteristics of yearling coastal cutthroat and steelhead trout. J. Fish. Res. Bd. Canada 14:203-212.

Volterra, V. 1926. Variations and fluctuations of the number of individuals of animal species living together. Pages 409-448 in R. N. Chapman (ed.), Animal ecology. McGraw-Hill Book Co., New York.

Withler, I. L. 1966. Variability in life history characteristics of steelhead trout (Salmo gairdneri) along the Pacific Coast of North American. J. Fish. Res. Bd. Canada 23:365-393.

Wydoski, R. S., and R. R. Whitney. 1979. Inland fishes of Washington. Univ. Washington Press, Seattle and London.

Appendix A. Results of Discriminant Analysis of Differences in Habitat Utilization between Steelhead (SH) and Cutthroat (CT) Trout Groups within Each of the Three Study Sites.

Site	Groups	Functions Derived	Percentage Contribution	Canonical Correlation	Wilks' Lambda	Chi-Square
Hurdygurdy Creek	SH<5 cm					
	SH 5-10 cm	1	90.63	0.44	0.78	24.90[a]
	SH>10 cm	2	9.37	0.16	0.98	2.55[c]
	SH<5 cm					
	CT>10 cm	1	100.00	0.38	0.86	8.14[b]
	SH 5-10 cm					
	CT>10 cm	1	100.00	0.56	0.68	14.38[a]
	SH>10 cm					
	CT>10 cm	1	100.00	0.80	0.36	11.73[a]
Middle Fork	SH<5 cm					
	SH 5-10 cm	1	58.44	0.30	0.85	7.98[c]
	SH>10 cm	2	41.56	0.25	0.94	3.34[c]
Little Jones Creek	CT<5 cm					
	CT 5-10 cm	1	75.73	0.37	0.82	8.29[c]
	CT>10 cm	2	24.27	0.22	0.95	2.09[c]

[a] Significant ($p<0.01$)

[b] Significant ($p<0.05$)

[c] Not significant ($p>0.05$)

Appendix B. Results of Discriminant Analysis of Differences in Habitat Composition among the Three Study Sites.

Study Sites	Functions Derived	Percentage Contribution	Canonical Correlation	Wilks' Lambda	Chi-Square
Hurdygurdy Creek					
Middle Fork	1	67.77	0.50	0.65	71.04[a]
Little Jones Creek	2	32.23	0.37	0.86	24.03[a]

[a] Significant ($p<0.01$)

Appendix C. Results of Discriminant Analysis of Differences in Habitat Utilization between Sympatric and Allopatric Steelhead (SH) and Cutthroat (CT) Trout Groups.

Trout Groups	Functions Derived	Percentage Contribution	Canonical Correlation	Wilks' Lambda	Chi-Square
Sympatric SH<5 cm Allopatric SH<5 cm	1	100.00	0.36	0.87	10.99[b]
Sympatric SH 5-10 cm Allopatric SH 5-10 cm	1	100.00	0.35	0.87	7.47[c]
Sympatric SH>10 cm Allopatric SH>10 cm	1	100.00	0.64	0.59	6.52[c]
Sympatric SH<5 cm Allopatric CT<5 cm	1	100.00	0.54	0.71	25.00[a]
Sympatric SH 5-10 cm Allopatric CT 5-10 cm	1	100.00	0.57	0.68	17.87[a]
Sympatric SH>10 cm Allopatric CT>10 cm	1	100.00	0.81	0.35	23.66[a]
Sympatric CT>10 cm Allopatric CT>10 cm	1	100.00	0.69	0.52	7.43[c]

[a] Significant ($p<0.01$)

[b] Significant ($p<0.05$)

[c] Not significant ($p>0.05$)

Appendix D. Results of Discriminant Analysis of Differences in Microhabitat Utilization between Sympatric and Allopatric Steelhead (SH) and Cutthroat (CT) Trout Groups.

Trout Groups	Functions Derived	Percentage Contribution	Canonical Correlation	Wilks' Lambda	Chi-Square
Sympatric SH<10 cm Sympatric SH>10 cm	1	100.00	0.61	0.62	15.09[b]
Sympatric SH<10 cm Sympatric CT>10 cm	1	100.00	0.73	0.47	25.16[a]
Sympatric SH>10 cm Sympatric CT>10 cm	1	100.00	0.76	0.43	32.46[a]
Allopatric CT<10 cm Allopatric CT>10 cm	1	100.00	0.59	0.65	14.40[b]
Sympatric SH<10 cm Allopatric CT<10 cm	1	100.00	0.67	0.56	17.55[a]
Sympatric SH>10 cm Allopatric CT>10 cm	1	100.00	0.67	0.56	20.53[a]
Sympatric CT>10 cm Allopatric CT>10 cm	1	100.00	0.75	0.44	29.62[a]

[a] Significant ($p<0.01$)

[b] Significant ($p<0.05$)

Appendix E. Sample Mean ($\bar{x}$), Standard Deviation (s), and Sample Size (n) of Microhabitat Measurements for Sympatric and Allopatric Steelhead (SH) and Cutthroat (CT) Trout of Different Size Classes.

Habitat Variable		Sympatric			Allopatric	
		SH<10	SH>10	CT>10	CT<10	CT>10
Substrate Size	$\bar{x}$	15.4	21.3	19.0	8.7	9.9
	s	8.8	13.8	16.9	6.8	11.1
	n	16.0	21.0	22.0	19.0	19.0
Total Depth	$\bar{x}$	57.3	73.5	124.4	39.1	62.2
	s	16.5	30.0	45.8	15.8	21.7
	n	16.0	22.0	24.0	21.0	19.0
Mean Velocity	$\bar{x}$	15.9	24.9	15.8	18.5	10.1
	s	7.7	14.9	11.7	12.2	13.1
	n	16.0	22.0	24.0	21.0	19.0
Surface Velocity	$\bar{x}$	22.2	33.6	27.1	21.3	16.8
	s	12.3	18.5	13.6	14.2	17.8
	n	16.0	22.0	24.0	21.0	19.0
Maximum Velocity	$\bar{x}$	35.0	39.3	34.6	33.7	29.7
	s	20.5	18.5	32.9	20.3	27.4
	n	11.0	21.0	20.0	21.0	19.0
Focal Point Velocity	$\bar{x}$	11.4	21.0	11.7	14.8	8.1
	s	6.3	12.6	7.9	9.8	11.0
	n	16.0	22.0	24.0	21.0	19.0
Distance From Bottom	$\bar{x}$	13.1	18.0	17.4	3.6	10.4
	s	14.4	15.7	12.0	2.4	8.0
	n	16.0	22.0	24.0	21.0	19.0

Appendix F. Results of T-Tests (T-Values) for Differences between Sample Means of Individual Microhabitat Variables Measured for Sympatric and Allopatric Steelhead (SH) and Cutthroat (CT) Trout Groups.

Test	Substrate Size	Total Depth	Velocity Mean	Velocity Surface	Velocity Maximum	Velocity Focal	Distance From Bottom
Symp. SH<10 Symp. SH>10	-1.51[c]	-1.95[c]	-2.19[b]	-2.14[b]	-0.60[c]	-2.78[a]	-1.00[c]
Symp. SH<10 Symp. CT>10	-0.78[c]	-5.60[a]	0.06[c]	-0.66[c]	0.04[c]	-0.10[c]	-1.02[c]
Symp. SH>10 Symp. CT>10	0.49[c]	-4.42[a]	2.32[b]	0.92[c]	0.57[c]	3.03[a]	0.16[c]
Allo. CT<10 Allo. CT>10	-0.39[c]	-3.86[a]	2.10[b]	0.90[c]	0.52[c]	2.05[b]	-3.71[a]
Allo. CT<10 Symp. SH<10	-2.51[b]	-3.39[a]	0.73[c]	-0.19[c]	-0.18[c]	1.19[c]	-2.97[a]
Allo. CT>10 Symp. SH>10	-2.87[a]	-1.36[c]	-3.35[a]	-2.95[a]	-1.31[c]	-3.47[a]	-1.93[c]
Allo. CT>10 Symp. CT>10	-2.00[c]	-5.45[a]	-1.50[c]	-1.39[c]	-0.50[c]	-1.26[c]	-2.18[b]

[a] Significant ($p<0.01$)

[b] Significant ($p<0.05$)

[c] Not significant ($p>0.05$)

Appendix G. Trout Density (Number of Fish/m^2) within Habitat Strata of Individual Habitat Variables during Morning (M) and Afternoon (A) Observation Periods, Hurdygurdy Creek Study Site. Ranks for Each Variable Appear in Parentheses.

Habitat Variable	Area (m^2)	Observation Period	Steelhead			Cutthroat
			<5 cm	5-10 cm	>10 cm	>10 cm
Substrate Size (cm)						
(1) <2	7	M	0.86	0.00	0.00	0.00
		A	0.00	0.00	0.00	0.14
(2) 2-5	42	M	0.79	0.05	0.00	0.00
		A	1.12	0.14	0.00	0.00
(3) 5-20	116	M	0.58	0.03	0.01	0.01
		A	0.73	0.09	0.00	0.00
(4) 20-40	144	M	0.41	0.22	0.08	0.00
		A	0.60	0.26	0.10	0.00
(5) >40	32	M	0.22	0.12	0.16	0.00
		A	0.16	0.09	0.03	0.00
Total Depth (cm)						
(1) <20	25	M	0.24	0.00	0.00	0.00
		A	0.36	0.24	0.00	0.00
(2) 20-40	82	M	0.82	0.10	0.00	0.00
		A	0.95	0.20	0.00	0.00
(3) 40-60	82	M	0.60	0.17	0.01	0.00
		A	0.83	0.09	0.00	0.00
(4) 60-80	60	M	0.47	0.18	0.03	0.00
		A	0.70	0.27	0.00	0.00
(5) 80-100	52	M	0.33	0.08	0.06	0.02
		A	0.35	0.08	0.04	0.02
(6) >100	40	M	0.12	0.10	0.28	0.00
		A	0.18	0.18	0.32	0.00

Appendix G. Trout Density (Number of Fish/m^2) within Habitat Strata of Individual Habitat Variables during Morning (M) and Afternoon (A) Observation Periods, Hurdygurdy Creek Study Site. Ranks for Each Variable Appear in Parentheses. (continued)

Habitat Variable		Area (m^2)	Observation Period	Steelhead <5 cm	Steelhead 5-10 cm	Steelhead >10 cm	Cutthroat >10 cm
Mean Velocity (cm/sec)							
(1)	<15	187	M	0.47	0.07	0.03	0.01
			A	0.68	0.12	0.03	0.00
(2)	15-30	104	M	0.55	0.20	0.08	0.00
			A	0.65	0.22	0.06	0.01
(3)	>30	50	M	0.54	0.12	0.08	0.00
			A	0.56	0.22	0.00	0.00

Appendix H. Trout Density (Number of Fish/m^2) within Habitat Strata of Individual Habitat Variables during Morning (M) and Afternoon (A) Observation Periods, Middle Fork Study Site. Ranks for Each Variable Appear in Parentheses.

Habitat Variable	Area (m^2)	Observation Period	Steelhead <5 cm	Steelhead 5-10 cm	Steelhead >10 cm
Substrate Size (cm)					
(1) <2	0	M	--	--	--
		A	--	--	--
(2) 2-5	15	M	0.47	0.07	0.07
		A	0.80	0.00	0.07
(3) 5-20	3	M	1.00	0.00	0.00
		A	0.00	0.67	0.00
(4) 20-40	67	M	0.22	0.21	0.01
		A	0.22	0.16	0.04
(5) >40	88	M	0.16	0.01	0.00
		A	0.15	0.03	0.00
Bedrock	3	M	0.33	0.00	0.00
		A	1.00	0.33	0.00
Total Depth (cm)					
(1) <20	34	M	0.18	0.00	0.00
		A	0.06	0.00	0.00
(2) 20-40	61	M	0.25	0.05	0.00
		A	0.36	0.07	0.00
(3) 40-60	58	M	0.26	0.07	0.02
		A	0.24	0.16	0.03
(4) 60-80	18	M	0.17	0.50	0.00
		A	0.28	0.17	0.00
(5) 80-100	5	M	0.20	0.00	0.20
		A	0.00	0.20	0.40
(6) >100	0	M	--	--	--
		A	--	--	--

Appendix H. Trout Density (Number of Fish/m^2) within Habitat Strata of Individual Habitat Variables during Morning (M) and Afternoon (A) Observation Periods, Middle Fork Study Site. Ranks for Each Variable Appear in Parentheses. (continued)

Habitat Variable	Area (m^2)	Observation Period	Steelhead <5 cm	Steelhead 5-10 cm	Steelhead >10 cm
Mean Velocity (cm/sec)					
(1) <15	113	M	0.29	0.09	0.01
		A	0.27	0.10	0.01
(2) 15-30	34	M	0.18	0.15	0.03
		A	0.24	0.12	0.06
(3) >30	29	M	0.03	0.03	0.00
		A	0.17	0.07	0.03

Appendix I. Trout Density (Number of Fish/m^2) within Habitat Strata of Individual Habitat Variables during Morning (M) and Afternoon (A) Observation Periods, Little Jones Creek Study Site. Ranks for Each Variable Appear in Parentheses.

Habitat Variable	Area (m^2)	Observation Period	Cutthroat		
			<5 cm	5-10 cm	>10 cm
Substrate Size (cm)					
(1) <2	8	M	0.25	0.00	0.00
		A	0.00	0.00	0.25
(2) 2-5	24	M	0.04	0.21	1.21
		A	0.29	0.21	0.83
(3) 5-20	68	M	0.25	0.09	0.04
		A	0.19	0.07	0.00
(4) 20-40	33	M	0.18	0.00	0.39
		A	0.27	0.06	0.33
(5) >40	0	M	--	--	--
		A	--	--	--
Total Depth (cm)					
(1) <20	18	M	0.22	0.00	0.00
		A	0.06	0.00	0.00
(2) 20-40	31	M	0.29	0.03	0.06
		A	0.13	0.00	0.10
(3) 40-60	42	M	0.21	0.07	0.07
		A	0.24	0.12	0.07
(4) 60-80	49	M	0.08	0.14	0.82
		A	0.29	0.14	0.55
(5) 80-100	10	M	0.10	0.00	0.00
		A	0.20	0.10	0.00
(6) >100	0	M	--	--	--
		A	--	--	--

Appendix I. Trout Density (Number of Fish/m^2) within Habitat Strata of Individual Habitat Variables during Morning (M) and Afternoon (A) Observation Periods, Little Jones Creek Study Site. Ranks for Each Variable Appear in Parentheses. (continued)

Habitat Variable	Area (m^2)	Observation Period	Cutthroat <5 cm	Cutthroat 5-10 cm	Cutthroat >10 cm
Mean Velocity (cm/sec)					
(1) <15	147	M	0.18	0.07	0.30
		A	0.21	0.09	0.22
(2) 15-30	3	M	0.33	0.00	0.33
		A	0.00	0.00	0.00
(3) >30	0	M	--	--	--
		A	--	--	--

Appendix J. Number of Steelhead and Cutthroat Trout of Different Size Classes Observed in Individual Habitat "Sets" within the Hurdygurdy Creek Study Site during Morning (M) and Afternoon (A) Observation Periods. Each Habitat "Set" Was Characterized by Three Habitat Variables which Were Scored with Integer Ranks Prior to Analysis (See Appendix G for Ranking).

				Steelhead						Cutthroat	
Set No	Substrate Size	Depth	Mean Velocity	<5cm		5-10cm		>10cm		>10 cm	
				M	A	M	A	M	A	M	A
1	3	2	3	15	17	1	1	0	0	0	0
2	4	2	3	0	1	1	0	0	0	0	0
3	2	2	3	2	2	0	4	0	0	0	0
4	4	2	3	2	2	0	1	0	0	0	0
5	2	2	3	1	0	0	0	0	0	0	0
6	4	2	2	4	2	0	0	0	0	0	0
7	4	2	3	4	6	2	1	0	0	0	0
8	4	1	3	2	0	0	1	0	0	0	0
9	4	1	2	1	4	0	3	0	0	0	0
10	3	2	2	1	0	0	2	0	0	0	0
11	4	2	2	11	14	2	5	0	0	0	0
12	2	2	2	8	10	2	0	0	0	0	0
13	4	2	1	5	6	0	0	0	0	0	0
14	3	2	1	1	3	0	0	0	0	0	0
15	2	2	1	4	7	0	0	0	0	0	0
16	3	2	2	2	1	0	0	0	0	0	0
17	3	3	2	0	4	0	0	0	0	0	0
18	4	3	2	4	4	9	5	0	0	0	0
19	5	3	2	0	0	1	1	0	0	0	0
20	2	3	2	4	6	0	0	0	0	0	0
21	2	3	1	4	8	0	0	0	0	0	0
22	3	3	1	3	4	0	0	0	0	0	0
23	3	1	1	2	7	0	2	0	0	0	0
24	3	2	1	7	6	0	2	0	0	0	0
25	3	3	1	12	7	1	1	1	0	0	0
26	4	3	1	1	2	1	0	0	0	0	0
27	4	3	1	3	2	2	0	0	0	0	0
28	4	4	2	5	4	1	1	0	0	0	0
29	4	4	1	7	13	1	7	1	0	0	0
30	5	4	2	3	2	0	0	0	0	0	0
31	2	4	2	2	6	0	0	0	0	0	0
32	2	4	1	7	6	0	2	0	0	0	0
33	3	4	1	12	20	1	0	0	0	0	0
34	2	5	1	0	0	0	0	0	0	0	0
35	2	5	2	0	2	0	0	0	0	0	0
36	4	5	2	1	5	0	0	1	0	0	0

Appendix J. Number of Steelhead and Cutthroat Trout of Different Size Classes Observed in Individual Habitat "Sets" within the Hurdygurdy Creek Study Site during Morning (M) and Afternoon (A) Observation Periods. Each Habitat "Set" Was Characterized by Three Habitat Variables which Were Scored with Integer Ranks Prior to Analysis (See Appendix G for Ranking). (continued)

				Steelhead						Cutthroat	
				<5cm		5-10cm		>10cm		>10 cm	
Set No	Substrate Size	Depth	Mean Velocity	M	A	M	A	M	A	M	A
37	4	5	1	2	0	0	1	0	0	0	0
38	1	5	2	6	0	0	0	0	0	0	1
39	5	5	2	0	0	1	0	1	0	0	0
40	5	5	1	0	1	0	0	0	0	0	0
41	4	6	1	0	0	0	1	0	0	0	0
42	3	5	1	3	5	1	2	0	0	1	0
43	4	5	1	1	0	0	0	0	0	0	0
44	4	5	1	0	1	1	0	0	0	0	0
45	4	4	1	4	6	0	0	0	0	0	0
46	4	6	2	1	0	0	0	2	2	0	0
47	4	6	1	0	4	1	3	3	6	0	1
48	5	6	2	0	0	0	2	1	1	0	0
49	4	6	2	1	0	2	0	2	2	0	0
50	5	6	2	3	2	1	0	0	0	0	0
51	4	6	3	0	0	0	0	1	1	0	0
52	5	6	2	0	0	0	1	1	0	0	0
53	5	6	3	0	0	0	0	1	0	0	0
54	5	5	1	2	0	0	0	0	0	0	0
55	4	5	3	1	0	0	1	1	2	0	0
56	4	4	3	0	0	2	2	1	0	0	0
57	4	4	2	1	0	0	1	0	0	0	0
58	4	3	3	0	0	0	3	0	0	0	0
59	4	3	2	0	2	1	1	0	0	0	0
60	4	3	1	4	10	4	1	0	0	0	0
61	4	4	1	2	3	0	1	0	0	0	0
62	4	5	1	0	2	1	0	0	0	0	0
63	3	5	1	1	1	0	0	0	0	0	0
64	5	5	1	0	2	0	0	0	0	0	0

Appendix K. Number of Steelhead Trout of Different Size Classes Observed in Individual Habitat "Sets" within the Middle Fork Site during Morning (M) and Afternoon (A) Observation Periods. Each Habitat "Set" Was Characterized by Three Habitat Variables which Were Scored with Integer Ranks Prior to Analysis (See Appendix H for Ranking).

				Steelhead					
Set No	Substrate Size	Depth	Mean Velocity	<5cm		5-10cm		>10cm	
				M	A	M	A	M	A
1	4	2	1	0	0	0	0	0	0
2	5	3	1	1	0	0	0	0	0
3	3	4	3	1	0	0	0	0	0
4	5	3	2	0	0	0	1	0	0
5	4	3	2	0	0	0	0	0	0
6	5	3	3	0	0	0	0	0	0
7	4	3	2	0	0	0	0	0	0
8	4	2	2	0	0	1	0	0	0
9	4	2	1	2	1	0	0	0	0
10	5	2	2	0	0	0	0	0	0
11	5	2	1	2	3	1	1	0	0
12	4	3	1	0	0	0	0	0	0
13	4	2	3	0	0	0	0	0	0
14	4	3	3	0	0	0	0	0	0
15	5	3	2	0	0	0	0	0	0
16	5	3	1	0	0	0	0	0	0
17	4	3	3	0	0	0	0	0	0
18	5	3	2	0	0	0	0	0	0
19	2	3	1	0	1	0	0	1	1
20	4	3	1	3	4	0	3	0	0
21	4	4	3	0	0	0	0	0	0
22	5	2	1	0	0	0	0	0	0
23	5	4	2	0	1	1	0	0	0
24	4	4	2	0	0	0	1	0	0
25	4	2	1	4	1	0	0	0	0
26	5	1	1	0	0	0	0	0	0
27	4	1	1	0	0	0	0	0	0
28	1	4	1	1	3	0	0	0	0
29	2	4	1	0	0	1	0	0	0
30	4	4	1	2	0	6	1	0	0
31	4	5	2	1	0	0	0	1	2
32	5	4	2	0	0	0	0	0	0
33	4	4	2	0	0	1	1	0	0
34	5	5	3	0	0	0	1	0	0
35	5	4	1	0	0	0	0	0	0

Appendix K. Number of Steelhead Trout of Different Size Classes Observed in Individual Habitat "Sets" within the Middle Fork Site during Morning (M) and Afternoon (A) Observation Periods. Each Habitat "Set" Was Characterized by Three Habitat Variables which Were Scored with Integer Ranks Prior to Analysis (See Appendix H for Ranking). (continued)

				Steelhead					
Set No	Substrate Size	Depth	Mean Velocity	<5cm		5-10cm		>10cm	
				M	A	M	A	M	A
36	5	4	3	0	0	0	0	0	0
37	4	4	3	0	1	0	0	0	0
38	4	3	2	2	4	1	0	0	0
39	4	2	2	0	1	0	1	0	0
40	2	2	1	0	0	0	0	0	0
41	5	1	1	2	0	0	0	0	0
42	3	3	1	3	0	0	1	0	0
43	3	3	1	0	0	0	0	0	0
44	5	3	3	0	0	0	0	0	0
45	4	3	3	0	1	0	0	0	0
46	4	1	1	0	0	0	0	0	0
47	4	2	3	1	1	1	1	0	0
48	5	2	2	0	0	0	0	0	0
49	5	2	1	2	2	0	1	0	0
50	2	3	1	2	0	0	0	0	0
51	4	3	1	1	1	1	1	0	0
52	4	3	2	0	0	1	0	0	0
53	3	3	3	0	0	0	0	0	0
54	4	3	3	0	0	0	0	0	0
55	2	3	3	0	2	0	0	0	0
56	4	2	3	0	0	0	0	0	0
57	4	2	2	0	0	0	0	0	0
58	4	2	1	0	1	0	0	0	0
59	5	2	1	0	3	0	0	0	0
60	3	2	1	1	2	0	1	0	0
61	2	2	1	0	1	0	0	0	0
62	4	3	1	1	1	0	1	0	0
63	3	2	1	0	1	0	1	0	0
64	2	3	1	1	1	0	0	0	0
65	2	3	2	2	2	0	0	0	0
66	2	2	1	3	3	0	0	0	0
67	5	1	1	4	2	0	0	0	0

Appendix L. Number of Cutthroat Trout of Different Size Classes Observed in Individual Habitat "Sets" within the Little Jones Creek Study Site during Morning (M) and Afternoon (A) Observation Periods. Each Habitat "Set" Was Characterized by Three Habitat Variables which Were Scored with Integer Ranks Prior to Analysis (See Appendix I for Ranking).

				Cutthroat					
				<5cm		5-10cm		>10cm	
Set No	Substrate Size	Depth	Mean Velocity	M	A	M	A	M	A
1	3	2	1	5	1	1	0	0	0
2	3	3	1	0	0	0	0	0	0
3	3	2	1	1	1	0	0	0	0
4	3	3	1	3	4	2	0	0	0
5	2	4	1	0	1	0	0	1	0
6	1	3	1	0	0	0	0	0	0
7	3	4	1	2	2	2	3	3	0
8	3	3	1	0	2	1	1	1	1
9	2	4	1	0	4	0	1	2	1
10	2	5	1	1	2	4	1	2	0
11	3	4	1	2	3	0	0	0	0
12	3	3	1	1	0	0	1	0	0
13	3	2	1	0	1	0	0	0	0
14	3	1	1	0	0	0	0	0	0
15	1	2	1	0	0	0	0	0	0
16	2	2	1	0	0	0	0	0	0
17	4	4	1	1	2	0	0	0	0
18	2	3	1	0	0	0	0	0	0
19	4	3	1	1	1	0	0	0	0
20	1	2	1	1	0	0	0	0	0
21	2	4	1	0	1	0	0	0	0
22	4	3	1	1	2	0	0	0	0
23	3	3	1	0	0	0	1	0	0
24	3	2	1	2	1	0	0	0	0
25	3	1	1	0	0	0	0	0	0
26	4	4	1	1	2	0	3	13	11
27	2	4	1	0	0	1	2	16	11
28	2	2	1	0	0	0	0	2	0
29	4	3	1	0	0	0	0	2	3
30	1	3	1	0	0	0	0	2	1
31	2	1	1	1	0	0	0	0	0
32	1	1	1	1	0	0	0	0	0
33	1	2	1	0	0	0	0	0	2
34	4	2	1	0	0	0	0	0	0
35	4	2	2	0	0	0	0	1	0
36	4	1	2	2	0	0	0	0	0
37	4	1	1	0	1	0	0	0	0
38	4	3	2	0	0	0	0	0	1

Appendix M. Microhabitat Measurements for Sympatric Steelhead and Cutthroat Trout.

Trout Group	Substrate[a] Size (cm)	Total Depth (cm)	Velocity (cm/sec)				Distance (cm)		
			Mean	Surface	Maximum	Focal	From Bottom	From Cover	From Nearest Fish
Sympatric Steelhead <5 cm	6	40	11	17	--	11	10	90	10
	11	47	18	20	--	13	8	270	24
	11	78	10	13	17	14	58	670	39
	1	45	13	23	--	11	2	--	22
	6	33	26	33	34	13	3	--	50
	19	63	15	35	40	14	16	--	40
	11	37	20	23	30	4	5	--	18
	26	54	17	25	35	2	4	--	40
	26	85	3	2	12	2	5	--	21
Sympatric Steelhead 5-10 cm	26	38	17	11	79	15	5	--	114
	19	81	24	34	43	13	16	--	40
	26	67	12	17	--	10	10	430	34
	19	66	15	19	--	11	22	180	33
	19	52	31	31	33	23	0	--	52
	19	70	21	49	56	23	15	60	70
	1	60	2	3	6	4	30	180	60
Sympatric Steelhead >10 cm	19	40	21	30	60	13	5	--	40
	19	42	37	62	62	33	5	--	21
	26	57	20	29	47	31	9	--	57
	19	92	7	15	26	12	31	90	58
	19	63	27	46	48	20	10	60	63
	26	65	29	49	56	12	8	30	32
	6	50	48	74	--	29	9	80	50
	19	65	41	44	62	27	10	100	50

Appendix M. Microhabitat Measurements for Sympatric Steelhead and Cutthroat Trout. (continued)

Trout Group	Substrate[a] Size (cm)	Total Depth (cm)	Velocity (cm/sec) Mean	Velocity (cm/sec) Surface	Velocity (cm/sec) Maximum	Velocity (cm/sec) Focal	Distance (cm) From Bottom	Distance (cm) From Cover	Distance (cm) From Nearest Fish
Sympatric	45	124	14	13	14	11	62	--	62
Steelhead	11	83	9	16	16	5	20	490	21
>10 cm	45	58	27	40	38	23	14	210	58
	19	105	21	35	35	16	52	90	--
	19	54	43	46	48	44	11	60	108
	BR	160	14	34	23	9	30	90	--
	19	60	8	20	48	16	10	50	120
	4	110	7	12	14	4	15	550	110
	<1	83	0	0	0	0	42	0	42
	11	87	36	32	44	31	10	180	--
	26	50	19	10	24	22	5	90	12
	6	47	49	55	59	47	13	30	94
	45	50	22	32	45	22	13	180	38
	45	71	48	45	56	35	13	150	71
Sympatric	26	122	9	4	21	16	13	60	61
Cutthroat	19	134	5	8	11	7	23	2380	90
>10 cm	1	68	30	33	--	17	5	30	50
	11	108	19	23	29	11	10	--	40
	45	134	19	31	27	23	20	--	34
	4	118	0	0	0	0	39	370	39
	45	107	3	7	10	2	10	300	54
	11	76	45	129	129	2	5	--	76
	1	88	29	63	82	14	8	--	88

Appendix M. Microhabitat Measurements for Sympatric Steelhead and Cutthroat Trout. (continued)

Trout Group	Substrate[a] Size (cm)	Total Depth (cm)	Velocity (cm/sec)				Distance (cm)		
			Mean	Surface	Maximum	Focal	From Bottom	From Cover	From Nearest Fish
Sympatric	45	89	26	35	37	16	3	15	44
Cutthroat	45	112	13	13	22	9	23	--	28
>10 cm	19	69	36	62	92	25	5	60	69
	26	153	19	29	--	22	15	110	134
	<1	60	9	33	65	9	13	0	15
	<1	170	0	2	--	3	41	--	--
	4	131	10	13	17	10	15	2670	90
	BR	132	13	10	21	19	15	1370	33
	BR	107	23	54	47	17	15	150	27
	26	124	5	7	11	2	18	610	18
	4	131	10	13	17	10	15	2670	90
	4	264	13	19	--	18	23	180	132
	26	213	8	12	12	2	53	0	53
	45	160	8	25	16	3	15	150	40
	11	116	26	25	26	23	15	90	--

[a] BR = bedrock

Appendix N. Microhabitat Measurements for Allopatric Cutthroat Trout.

Trout Group	Substrate[a] Size (cm)	Total Depth (cm)	Velocity (cm/sec)				Distance (cm)		
			Mean	Surface	Maximum	Focal	From Bottom	From Cover	From Nearest Fish
Allopatric	6	42	19	19	25	15	1	90	10
Cutthroat	1	47	4	4	24	7	3	200	--
<5 cm	11	31	13	20	28	8	3	100	31
	11	32	19	15	24	17	3	0	16
	6	23	23	41	65	12	1	50	69
	BR	33	36	40	43	30	3	0	50
	1	74	1	0	1	1	4	450	37
	11	29	30	31	34	22	1	0	--
	1	34	8	13	32	1	4	0	--
	19	14	26	27	84	23	3	--	
Allopatric	6	39	45	53	61	17	3	20	122
Cutthroat	1	28	12	23	29	17	3	120	7
5-10 cm	11	36	10	20	26	6	5	40	72
	19	55	14	15	15	11	5	180	165
	19	29	25	25	48	26	3	300	14
	1	77	0	0	0	0	13	60	19
	1	47	4	4	24	7	3	200	--
	11	32	19	15	24	17	3	0	16
	BR	33	36	40	43	30	3	0	50
	11	28	26	29	54	32	5	60	112
	19	58	18	14	23	11	3	0	--
Allopatric	1	77	0	0	0	0	13	60	19
Cutthroat	1	78	3	2	9	4	13	200	20
>10 cm	11	60	11	14	21	4	3	0	60

Appendix N. Microhabitat Measurements for Allopatric Cutthroat Trout. (continued)

Trout Group	Substrate[a] Size (cm)	Total Depth (cm)	Velocity (cm/sec)				Distance (cm)		
			Mean	Surface	Maximum	Focal	From Bottom	From Cover	From Nearest Fish
Allopatric	1	46	2	16	32	3	8	0	92
Cutthroat	19	86	1	1	6	2	20	350	22
>10 cm	1	34	8	13	32	1	4	0	--
	11	31	13	27	29	14	3	0	--
	11	31	16	64	103	14	5	0	62
	19	34	4	7	74	6	5	30	8
	19	38	29	39	58	8	1	--	76
	1	66	3	14	17	10	5	240	16
	1	78	0	0	0	0	20	250	78
	1	78	3	2	9	4	13	200	20
	11	60	11	14	21	4	3	0	60
	11	43	54	39	49	49	3	0	32
	19	86	1	1	6	2	20	350	22
	4	89	9	37	37	9	15	60	89
	1	78	3	2	9	4	13	200	20
	45	88	20	27	52	15	30	180	22

[a] BR = bedrock