AN ABSTRACT OF THE THESIS OF

Jon Benjamin Grunbaum for the degree of Master of Science in Fisheries Science presented on February 20, 1996.

Title: Geographical and Seasonal Variation in Diel Habitat Use by Juvenile (age 1+) Steelhead Trout (Oncorhynchus mykiss) in Coastal and Inland Oregon Streams

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Abstract approved: ______________________
Gordon Reeves

Juvenile (1+) steelhead trout (Oncorhynchus mykiss) observed in coastal and inland Oregon streams exhibited marked seasonal and geographic differences in diel behavior and microhabitat use. During summer day observations in pools, fish held positions elevated above the stream bottom and were in positions where mean focal and surface water velocities were 11 $cm{\cdot}s^{-1}$ and 22 $cm{\cdot}s^{-1}$, and 4 $cm{\cdot}s^{-1}$ and 14 $cm{\cdot}s^{-1}$, for coastal and inland fish, respectively. On summer nights, however, coastal and inland trout in pools were observed close to the stream substrate in areas where mean focal and surface water velocities were 3 $cm{\cdot}s^{-1}$ and 13 $cm{\cdot}s^{-1}$, and 1 $cm{\cdot}s^{-1}$ and 8 $cm{\cdot}s^{1}$, respectively. Compared to day use, coastal trout on summer nights were positioned primarily over smaller-sized substrate (silt and detritus, sand, and small gravel at night versus sand, small, medium, and large gravel, and cobble during the day) and were located in wider areas of the pools (5.3 m day mean versus 5.9 m night mean).

In winter, geographic variations in diel activity patterns became apparent. Diel shifts in microhabitat use by trout in coastal streams were similar to those exhibited in summer but inland trout became entirely nocturnal, apparently

concealing themselves in cover during the day but emerging from concealment at night to occupy microhabitats similar to those occupied during summer nights. Diel trends in microhabitat use by coastal and inland juvenile trout in riffle habitats were similar in character to those displayed by trout in pools, although much less pronounced.

Day versus night counts of coastal and inland trout did not show diel movement between adjacent pool and riffle study units, which suggested that the same populations of fish were being observed in diel observations. In both regions, fish numbers were generally greater at night than during the day, especially in the inland region where no 1+ juvenile trout were observed on winter days. .

In laboratory stream aquaria experiments, trout were never observed to be associated with cover at night, regardless of water temperature, but during simulated daylight, use of cover for concealment by both coastal and inland trout was negatively correlated with water temperature. The cover-seeking response to water temperature changes was significantly greater for inland versus coastal trout. Field and aquaria observations of diel habitat use support the hypothesis that coastal and inland trout may have different adaptive strategies for survival in winter.

Geograhical and Seasonal Variation in Diel Habitat Use by Juvenile (age 1+) Steelhead Trout (Oncorhynchus mykiss) in Oregon Coastal and Inland Streams

by

Jon Benjamin Grunbaum

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented February 20, 1996
Commencement June 1996

Master of Science thesis of Jon Benjamin Grunbaum presented on February 20, 1996

APPROVED:

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Major Professor, representing Fisheries Science

Redacted for Privacy

Chair of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

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ACKNOWLEDGMENTS

I would like to thank Dr. Gordon Reeves , Dr. Dede Olson, Dr. Hiram Li, and Dr. Robert Beschta for their guidance and support. I also thank and am deeply grateful to the following people whose enthusiasm, interest and cooperation made this study possible: Alex Atkins, Barb Campbell, Charlie Dewberry, Debbie Haapala, Bruce Hansen, Deian Moore, Frank Vassar, Dave Price, and Jon Zieidler. Special thanks go to my parents, Ben and Jean Grunbaum, for their continuing encouragement and support over the years.

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INTRODUCTION

Rhythmicity in the behavior of animals is a common adaptation to life in environments in which physical conditions continually change in seasonal and diel cycles (Thorpe, 1978). Long distance annual migrations of bird and whale populations, the winter hibernation of mammals, and the strictly nocturnal activities of bats are familiar examples of repetitive behavior patterns that coincide with annual or diel periodicity. Through rhythmic behavior, animals are able to avoid or tolerate harsh environmental regimes and exploit shelter or food resources at the most opportune time and place. Knowledge of repetitive behavior that occurs in seasonal and diel cycles and the external and internal factors that stimulate and influence it are intrinsic to an ecological understanding of a species.

Problem Statement

Although many variables in the life histories of fishes have been shown to be rhythmic (Thorpe, 1978; Spieler and Kendall, 1984), much of our current knowledge of the behavior of salmonids residing in lotic habitats is founded upon field studies that have taken place predominately during the daylight hours of summer months (e.g., Fausch and White, 1981; Morantz et al., 1987). The relatively limited information available concerning the behavior and habitat requirements of salmonids during seasons other than summer coupled with a paucity of information on circadian rhythms and nocturnal activity has limited our view of salmonid ecology. A complete understanding of the temporal range of the activities of salmonids in streams is essential for derivation of accurate and unbiased stream habitat suitability criteria and for identification of factors limiting salmonid production (Nickelson et al. 1992). Wise management decisions regarding the habitat requirements of each species and stock of indigenous fish require specialized knowledge of diel, seasonal, regional and phenological influences on habitat use.

This study was designed to further our knowledge of the ecology of age 1+ juvenile steelhead trout. The specific objectives of the study were: (1) to examine the diel habitat use of age 1+ steelhead trout in coastal and interior Oregon streams in summer and winter, and (2) to examine the response of each group to declining water temperatures in laboratory streams.

Hypotheses

Hypotheses addressed in this study are as follows:

(1) Juvenile steelhead trout exhibit diel shifts in their use of stream habitats;

(2) The character or magnitude of these diel shifts can differ between summer and winter seasons;

(3) The character of these diel shifts can differ between coastal and inland populations;

(4) Water temperature is a phenological factor that directly influences diel use of cover.

Operational Terms

Observations and measurements made at the stream study sites were designed to provide information about microhabitat use, and microhabitat availability. Microhabitat use relates to a trout population's pattern of association with measured microhabitat variables within the geographic study unit at a given season and time of day. Four microhabitat variables, surface water velocity, bottom water velocity, total depth, and types of substrate, were used as the parameters for establishing microhabitat availability in each of the study sites. If there were no observable patterns of association in microhabitat use, a fish population would be expected to be either randomly distributed or be distributed in direct proportion to the available habitat.

REVIEW OF LITERATURE

Seasonal shifts in habitat use and behavior of juvenile salmonids rearing in streams have been reported for coho salmon (Oncorhynchus kisutch) and steelhead trout (O. mykiss), (Hartman, 1965; Bustard and Narver, 1975), rainbow trout (O. mykiss) (Baltz et al., 1991), Atlantic salmon (Salmo salar) (Rimmer et al., 1984; Metcalfe et al., 1986; Cunjak, 1988a), brown trout (Salmo trutta) (Heggennes and Saltveit, 1990), and Arctic charr (Salvelinus alpinus) (Naslund, 1990). Investigators have related seasonal shifts in habitat use and behavior as a response to specific phenological factors such as changes in water temperature (Taylor, 1988), current velocity (Gibson, 1978; McMahon and Hartman, 1989), day length (Northcote, 1958), or to a combination of phenological factors (Hartman, 1963). Seasonal fluctuation in water temperature is the phenological factor most frequently cited as stimulating seasonal shifts in habitat selection and behavior of young salmonids.

Many researchers have described diurnal habitat use and behavior of juvenile salmonids rearing in streams, but there are relatively few studies of nocturnal habits and activities. Eriksson (1978), discussed the flexibility of circadian rhythms and warned that it is not possible to generalize on the activity and behavior of fish because of a high degree of adjustability to environmental conditions. Nocturnal studies have primarily been concerned with diel feeding chronologies. Jenkins (1969), Tanaka (1970), Bisson (1978), and Riehle and Griffith (1993) have reported nocturnal feeding in rainbow trout, although Tippets and Moyle (1978), Johnson and Johnson (1981), and Angradi and Griffith (1990) have concluded that feeding in this species is mostly diurnal. Less attention has been given to diel patterns of habitat use in stream salmonids. In the few studies that have been conducted, differences in habitat use have been detected between day and night periods. Brown trout have been observed exhibiting diel shifts from active feeding positions during the day to shallower, slower water at night (Harris et al., 1990), or to hiding places in the substrate (Heggenes, 1988). Brook charr (S. fontinalis) in subarctic streams have been observed to be active and feeding during the day but quiescent, closer to the substrate and nearer the stream edge at night (Walsh et al., 1988).

Diel shifts that appear to be seasonally moderated have been noted by several researchers. Adams et al. (1988) observed that in the summer Arctic char were active primarily at night and reclusive during the day, but as summer progressed into autumn, these trout became increasingly active during the day and increased their association with larger substrates. Heggenes (1988) observed that brown trout become nocturnal in winter. Edmundson et al. (1968) and Campbell and Neuner (1985) reported that in summer juvenile steelhead and rainbow trout moved from active feeding positions during the day to resting positions in shallow, near-shore, low velocity areas at night, but in winter the fish apparently hid in the substrate during the day and became more active at night. Similarly, Riehle and Griffith (1993) found seasonally moderated diel shifts in use of microhabitats and feeding chronologies in juvenile steelhead trout.

Murphy et al. (1986) have proposed that cover is more important in winter than summer to trout parr. As water temperatures decrease from autumn to winter, the availability of adequate cover may become the main habitat factor limiting fish population density of a stream or stream reach in winter (Chapman and Bjornn, 1969). Insufficient or inadequate cover in winter may motivate salmonids to migrate to another location (Bjornn, 1971; Rimmer et al., 1983; Hillman et al., 1987). Juvenile steelhead/rainbow trout reportedly seek out cover for concealment during winter days (Everest, 1969) or at low water temperatures (Hartman, 1965). However, the temperature required to stimulate this response varies widely among studies and, in some cases, the response was not observed even at near-freezing water temperatures (Needham and Jones, 1959; Maciolek and Needham, 1951). The generality of this behavioral response in steelhead/rainbow trout remains unclear.

Researchers have suggested that regional variability (Swales et al., 1986) may exist in the natural history patterns of salmonids. This variability may have genetic as well environmental components. DeGraaf and Bain (1986), and Bozek and Rahel (1992) found site differences in habitat use by Atlantic salmon and cutthroat trout (O. clarki), respectively, that could be only partially attributable to differences in habitat availability. Kelso et. al. (1981) observed different rheotactic responses by rainbow trout fry from progenies of inlet and outlet spawning populations of two British Columbia lakes and concluded that genetic as well as environmental factors contributed to observed differences. Coastal and inland populations of salmonids may have localized adaptations allowing them to better cope with the drastically different regional climatic regimes of coastal and inland streams (Swales et. al., 1986). Riddell and Leggett (1981) related stock differences in body morphology of Atlantic salmon to large differences in distance between the rearing streams of each population to the ocean. Similarly, Taylor and McPhail (1985a,b) found that coho salmon from coastal populations were morphologically more robust and able to attain greater initial velocities, but had less stamina, than coho from inland populations. Parkinson (1984) theorized that the genetic variation he observed between populations of steelhead trout in British Columbia reflects the potential of this species to evolve adaptations to local stream conditions.

MATERIALS AND METHODS: FIELD

Study Design

Juvenile (1+) steelhead trout populations in coastal and inland basins were selected for this study on the assumption that regional environmental and physiographical differences (distance from the ocean, elevation, climatic regime, etc.) would result in local adaptations in habitat use. Diel counts were made in selected pool and riffle units in four coastal streams (Cummins, Tenmile, Big, and Cape Creeks) and four inland streams (Copeland, Calf, Steelhead, and Canton Creeks) of western Oregon (Fig. 1) to determine if there were day or night patterns in the use of cover for concealment by trout and to determine if largescale diel movements between riffles and pools was occurring. Physiographic and environmental characteristics of study streams are presented in Table 1. A detailed survey of diel microhabitat use was then made in the study units of Cummins and Tenmile Creeks (coastal) and Copeland and Calf Creeks (inland). Summer and winter observations were made on the coast between 8-13 August 1990 and between 11-25 February 1991, respectively. In the inland streams they were made between 30 August and 5 September 1990 and between 20-26 January 1991, respectively.

Paired day and night observation sessions were conducted by divers with snorkeling gear between the hours of 1000 to 1500 and 2200 to 0200, respectively. Diurnal observations preceded nocturnal observations, and both dive sessions were completed in the same 24h period. Waterproof dive lights

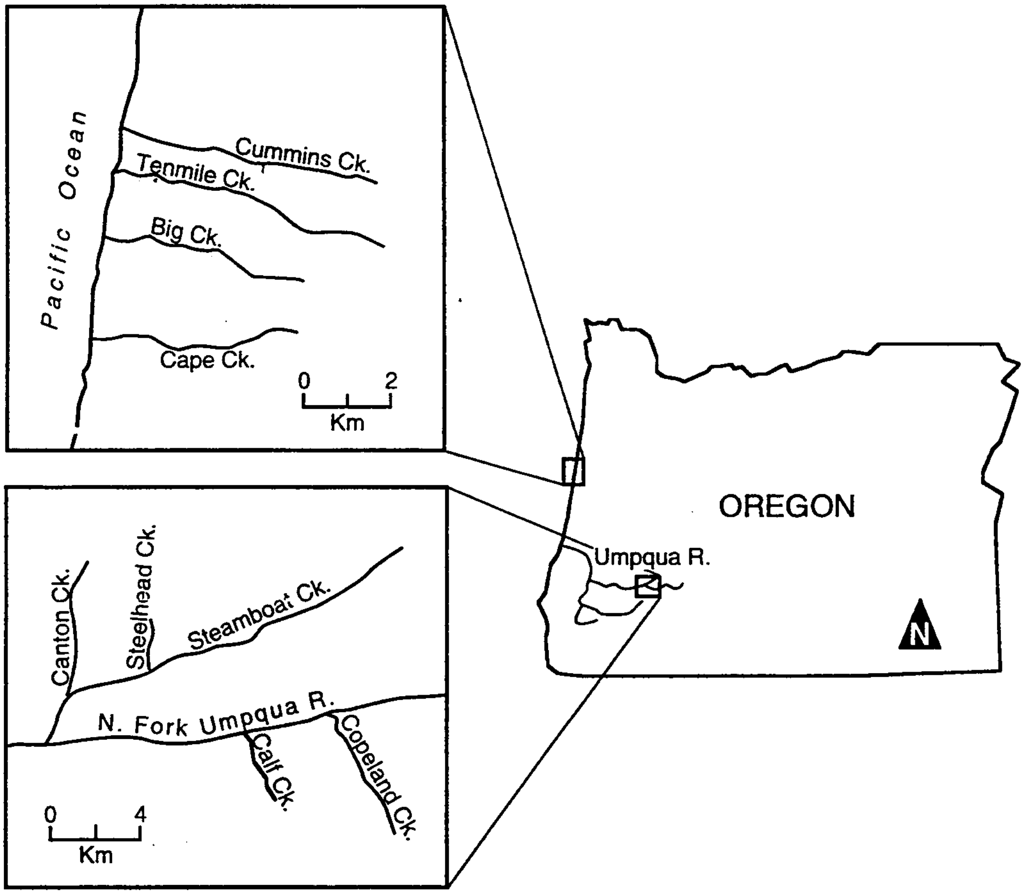

Figure 1. Locations of coastal and inland streams where diel habitat use by 1+ juvenile steelhead trout was examined.

Table 1. Physical features of study sites in coastal and inland streams.

Feature	Coastal Streams	Inland Streams
Approximate Coordinates	124.07 W 44.10 N	122.40 W 43.20 N
Stream Order[a]	3	3/4
Elevation	~10 to ~70 m	~350 to ~600 m
Gradient of Study Reaches	~2 to ~5 %	~3 to ~7 %
Average Bankfull Channel Widths	~12 m (Cummins) ~12 m (Tenmile) ~13 m (Big) ~15 m (Cape)	~10m (Steelhead) ~12 m (Calf) ~16 m (Copeland) ~17 m (Canton)
Channel Unit Control Elements	large wood or or bedrock	large boulder or bedrock
Average Summer Water Temperature Range	8 - 16 °C	12 - 20 °C
Average Winter Water Temperature Range	5 - 12 °C	0 - 8 °C
Geology	basalt	basalt

[a] Stream order is rated according to Strahler (1957)

were used to make night-time observations. Underwater visibility of ≥ 3 m was required for a dive. Several winter survey attempts on the coast were aborted due to excessive turbidity in the coastal streams.

Study Sites

Study sites in each stream were located starting at the first access point upstream from the confluence of a coastal stream with the Pacific Ocean or an inland stream with a larger order river. Starting at these points and working upstream, the stream channel was classified into pool and riffle habitat units (Bisson et al., 1982) until eight pool-riffle sequences were identified. Three pool-riffle sequences were randomly chosen from the eight pool-riffle sequences that were identified. Habitat use data from observations of juvenile trout habitat use in riffles and pools was analyzed separately.

Water temperatures were taken with hand held thermometers in the eight study streams immediately prior to observational dives. Absolute water temperatures between streams within regions closely paralleled one another. Stream flow rates were measured with a Marsh-McBirney Model 201 current meter according to Platts et al. (1987) in the two streams per region in which diel microhabitat use was observed. Temperatures and discharge rates are shown on Table 2.

All species of fish inhabiting the study sites were noted during dives. Coastal streams contained, in order of observed abundance, steelhead trout, coho salmon, sculpin (Cottus spp.), and cutthroat trout. The inland stream population of fish, in order of observed abundance, included steelhead trout, sculpin, dace (Rhinichthys spp.) and chinook salmon (O. tshawytscha).

Table 2. Snorkeling survey dates, water temperatures and stream discharge in coastal and inland sites.

Summer Survey, 1990

Coastal Streams	Survey Dates Day / Night	Temperature (^0C) Day	Temperature (^0C) Night	Discharge ($m^3 \cdot s^{-1}$)
Cummins	Aug. 8-9	16.0	14.5	0.174
Tenmile	Aug. 9-10	16.0	14.0	0.452
Big Creek	Aug. 10-11	14.5	11.5	
Cape	Aug. 8-9	15.0	12.0	
Inland Streams				
Copeland	Aug. 30-31	16.5	14.0	0.222
Calf	Aug. 30-31	17.0	14.0	0.049
Steelhead	Aug. 30-31	16.0	14.0	
Canton	Aug. 30-31	17.0	15.0	

Winter Survey, 1991

Coastal Streams	Survey Dates Day / Night	Temperature (^0C) Day	Temperature (^0C) Night	Discharge ($m^3 \cdot s^{-1}$)
Cummins	Feb. 24-25	8.5	8.0	1.43
Tenmile	Feb. 23-24	9.0	8.0	2.76
Big Creek	Feb. 25-26	8.5	8.5	
Cape	Feb. 11-12	8.5	7.5	
Inland Streams				
Copeland	Jan. 20-21	4.5	4.0	2.34
Calf	Jan. 21-22	2.0	1.0	1.27
Steelhead	Jan. 24-25	2.5	2.5	
Canton	Jan. 24-25	2.0	2.0	

Note: Stream discharge was measured only in streams where microhabitat utilization was observed and quantified.

Data Collection

Diel Counts

Paired day and night counts of juvenile steelhead trout were made within each specific pool and riffle unit in all streams in each region and season. Counts were made by divers who entered the water at the downstream end of each pool-riffle study unit and slowly crawled or swam upstream while counting all 1+ steelhead trout.. These counts were made to determine whether a net diel movement into concealment was occurring. Other possibilities for a diel fluctuation in fish numbers in the study units could include mass diel migrations up or down the streams out of the study reach or schooling behavior resulting in patchy distribution. Snorkeling observations were conducted to investigate the possibility of largescale diel movement of fish. In observations made during pre-dusk and dusk hours very few fish were observed to pass through, leave, or enter a habitat unit. The possibility that diel differences in fish numbers could be due to patchy distribution seems highly unlikely because this was not observed in any of the six habitat units per stream that were monitored and because in any given region and season diel trends in fish numbers were similar between habitat units within streams and between streams.

Diel Microhabitat Use

Diel microhabitat use was observed and recorded in Cummins and Tenmile Creeks on the coast, and Copeland and Calf creeks in the inland region. During observation sessions, divers entered the water at the downstream end of each pool-riffle study unit and slowly crawled or swam upstream while thoroughly searching the entire wetted area of the unit for 1+ Steelhead trout. A sighted trout was observed for 1-2 minutes. If the trout appeared to be holding a focal position (Kalleberg 1958), or otherwise occupying a particular station (Edmundson et al., 1968), and did not appear alarmed or displaced, the diver first estimated its' size by comparing fish length with incremental marks on a Plexiglas data slate or by comparing it to substrate particles which could then be directly measured. The trout was classified as class 1 (90 to 125 mm in total length) or class 2 (>125 mm in total length). The diver next measured the focal elevation of the fish (i.e. the vertical distance of the fish above the substrate to the nearest centimeter) with a meter stick or tape, and then marked the focal position or station of the fish with a brightly colored numbered stone placed on the substrate. This procedure was repeated for all undisturbed trout within each pool or riffle study unit.

On the day following diurnal and nocturnal dives, divers returned to the stream to measure eight additional microhabitat characteristics (other than focal elevation) that were also associated with the position of each observed trout. These additional microhabitat parameters were as follows:

1) focal water velocity (current velocity measured at the position or station of each fish);
2) surface velocity (current velocity measured 5 cm below water surface directly above each fish's position or station);
3) bottom velocity (current velocity measured 5 cm above substrate directly below each fish's position);
4) total depth to the nearest cm of the water column in which the fish was observed;

5) distance to nearest cover object (any physical object or broken water surface that could provide a hiding place large enough to conceal a fish when viewed from above);
6) stream width at focal position;
7) shore distance (lateral distance from each fish's location to the nearest shore) to the nearest 0.1m;
8) dominant substrate size beneath fish.

In addition, two derived variables: relative elevation and relative shore distance, were calculated after the dives were completed. Relative elevation which is useful in comparing the vertical positioning of the fish in the water column while adjusting for water depth, was determined by dividing the focal elevation of the trout by total depth of the water column. A value of near 1.00 indicates a position high in the water column while a value close to zero indicates a position close to the stream bottom. Relative shore distance provides some index of relative proximity of each fish to the stream margin while adjusting for stream width. A value close to 0.50 indicates a position near mid-channel while a value close to zero indicates a position close to shore.

All variables except substrate size were continuous. Substrate size was linearly transformed from a categorical variable to discrete values to simplify analyses after data collection by assigning values one through eight based on particle size (from small to large). Substrate categories were as follows: 1 = silt and detritus, 2 = sand (<3 mm), 3 = small gravel (3 mm to 25 mm), 4 = medium gravel (>25 mm to 75 mm), 5 = large gravel (>75 mm to 150 mm), 6 = cobble (>150 mm to 300 mm), 7 = boulder (>300 mm), and 8 = bedrock. All water velocities were measured to the nearest $cm \cdot s^{-1}$ with a Marsh-McBirney Model 201 current meter.

Microhabitat Availability

Immediately following observations of microhabitat use by individual fish, available habitat in each of the study pools was quantified in order to examine diel habitat use in relation to the total range of available habitat. A subset of four parameters (surface velocity, bottom velocity, total depth, and substrate) were chosen for examining proportional use of available habitat because these habitat attributes did not require the presence of individual fish. Microhabitat availability was determined by measuring each parameter value at stations positioned along horizontal transects superimposed over the study units. Grid spacing was generally 2m on horizontal transects and along the unit length. However, actual spacing of transects and transect stations depended on the spatial homogeneity of the four habitat parameters. Closer spacing was necessary to characterize microhabitats in areas of great heterogeneity and grid spacing was increased in homogenous stream areas. Stream stage was monitored as habitat availability measurements were being made to ensure that measured habitat availability reflected the actual available habitat at the time trout habitat use was being observed.

Data Analysis

Paired sample t-tests (Zar, 1984) were used in analysis of field data in recognition of the fact that each habitat unit has unique physical conditions and different available habitats to which fish might respond differently. In this approach to data analysis, each pool or riffle was considered an observational unit. Using paired t-tests to compare day and night obervations of habitat use within specific pools or riffles increased the accuracy of diel comparisons by taking into account inherent differences that exist between pools or riffles.

Diel Fish Counts. Observational pairs of day and night count data in riffles and pools were grouped within region and by season and then compared. Paired-sample t-tests (Zar 1984) were used to determine if there were statistically significant ($P \leq 0.05$) diel differences in the number of fish counted in pools and riffles.

Diel Microhabitat Use. Regional and seasonal observational data were first combined according to different habitat types (i.e. pool and riffle). Pool and riffle microhabitat use data were then segregated into four groups by region and season (coast-summer, inland-summer, coast-winter, and inland-winter) in order to test for diel shifts in habitat use and compare diel habitat use between regions and seasons. Paired sample t-tests (Zar, 1984) were used to determine if there were significant ($P \leq 0.05$) diel shifts in microhabitat use or significant ($P \leq 0.05$) differences in habitat use between fish of the two size classes. Geographic and seasonal trends in diel habitat use were subjectively compared.

Microhabitat Availability. The proportion of habitat available in relation to microhabitat parameters were calculated for each pool habitat unit. Proportions of day and night use in defined ranges of the microhabitat parameters was similarly calculated per habitat unit. The resultant day, night, and availability proportions were summed across all pool observational units within region and season, then standardized to 100 percent. Day and night use and availability proportions were then graphically displayed in histograms for each of the sample groups.

RESULTS: FIELD

Diel Counts

Mean numbers of 1+ juvenile steelhead trout counted in pools and riffles of coastal and inland streams in winter and pools of inland streams in summer tended to be greater at night than during the day. This trend was statistically significant ($P< 0.05$) in winter in pools on the coast and in riffles and pools inland - where no fish were seen in the study units during the day but numerous trout were seen in the same units at night (Table 3). Diel counts were approximately the same in pools of coastal streams and riffles of inland streams in summer. The only instance in which average number of trout were greater in a habitat type during the day ($P < 0.01$) occurred in riffle units of coastal streams in summer.

In winter, observations made in ancillary dives performed during dusk discounted the possibility that juvenile steelhead were making diel migrations up or down the streams or other movements that could result in patchy distribution not detected three pool and riffle sample sites per stream. As daylight diminished, fish density increased slowly and no fish were observed to pass through, enter, or leave a specific habitat unit. It appeared that any discrepancies between day and night fish numbers were due to fish using nearby cover more during the day than at night.

Diel Microhabitat Use

Some differences were detected in habitat use between fish of the two size classes in pools of all streams except the inland streams in winter. In general, larger fish were associated with faster surface velocities and coarser substrates, and were located in deeper water, further from the stream bottom, and higher in the water column (Appendics A, B, C, D). Size-related differences were small in magnitude and statistically significant in very few cases (Table 4). In most instances, the proportions of small and large fish observed for microhabitat use in each stream were comparable day to night (Table 4). Trends in diel habitat use between fish of different size classes were always the same and microhabitat use data from both size classes of fish were combined for subsequent analyses. Pooling of data for diel comparisons was justified because trends in diel habitat use were identical between size classes of fish, and differences in magnitude of microhabitat use by fish of the two size classes (Appendices A,B,C,D) were small in comparison to the magnitude of diel shifts (Appendices E, F) in habitat variables that were found significant in analyses with both size classes combined.

Within region and season, the number of variables in which diel shifts were detected and the magnitude of these shifts were considerably less for riffles than pools. Statistical analyses of diel microhabitat use in riffles beyond the basic data summaries presented in Table 5 was not possible due to low numbers of fish commonly encountered in this habitat type. Observations from a total of at least 30 trout were desired for statistical comparisons in the paired t-tests.

Table 3. Diel comparisons of total numbers, mean numbers, and mean differences in numbers of 1+ juvenile steelhead trout in pool and riffle study units .

	Fish Counts		Mean Difference
Site / Season	Day (mean)	Night (mean)	(Day - Night)
Coast / Summer			
Pool (n = 12)	144 (12)	149 (12.4)	- 0.4
Riffle (n = 12)	37 (3.1)	9 (0.8)	2.3*
Total	181	158	
Coast / Winter			
Pool (n = 12)	101 (8.4)	215 (17.9)	- 9.5*
Riffle (n = 10)	16 (1.6)	63 (6.3)	- 4.7
Total	117	278	
Inland / Summer			
Pool (n = 10)	73 (7.3)	120 (12)	- 4.7
Riffle (n = 10)	32 (3.2)	39 (3.9)	- 0.7
Total	105	159	
Inland / Winter			
Pool (n = 12)	0	128 (10.7)	- 10.7*
Riffle (n = 12)	0	75 (6.3)	- 6.3*
Total	0	203	

* $P < 0.05$

In summer, 1+ juvenile trout in coastal and inland streams exhibited similar diel shifts in microhabitat use in pools (Table 6). Compared to day use, trout at night used slower focal water velocities, were associated with slower surface currents, were positioned lower in the water column and were closer to (or resting upon) the stream bottom. Significant ($P < 0.05$) diel shifts in use of pool microhabitats were found for focal velocity, surface velocity, focal elevation, and relative elevation in the water column. Also, trout in pools of coastal streams were located in significantly ($P < 0.05$) wider areas of the pools and over smaller substrates at night compared to day.

Distribution of coastal trout in pools in winter appeared to be spatially limited by high discharge rates and current velocities to small eddies and backwater areas. Diel shifts in microhabitat use in pools were nevertheless evident (Table 6). During the day the trout remained concentrated in these slow-water pockets and did not attempt to defend particular focal positions as in summer. Compared to day use, trout at night occupied slower focal and surface velocities, shallower water, smaller substrates, and were positioned lower in the water column and closer to (or resting upon) the stream bottom. Significant ($P < 0.05$) diel shifts in use of pool microhabitats were detected for focal velocity, surface velocity, focal elevation, total depth, relative elevation in the water column, and substrate size (Table 6).

Dramatic diel shifts were observed in microhabitat utilized by inland trout in winter. No fish were observed during day although many were in view at night. I presumed that they were concealed within the substrate during the day so the range of use in the microhabitat parameters could not be assessed. At night, trout occupied microhabitats similar to those occupied by trout during summer nights. They were close to or in fin contact with the stream bottom and were located in areas that provided for relatively slow focal, surface, and bottom

Table 4. Numbers and percentages of small and large 1+ juvenile steelhead trout in streams where differences in use of pool microhabitat(s) was related to fish size. Significant ($P < 0.05$) differences in microhabitat use is indicated by lowercase letters.

Stream	Season	Time	Size Class 1	Size Class 2	Size Class % 1	Size Class % 2	Focal Elev.	Total Depth	Relative Elev.	Cover Dist.	Shore Dist.	Substrate Type
Cummins	Summer	Day	8	18	30	70	--	--	--	--	--	--
Cummins	Summer	Night	10	24	30	70	--	b	--	--	e	--
Tenmile	Summer	Day	8	11	42	58	--	--	--	--	--	--
Tenmile	Summer	Night	12	16	43	57	--	--	--	--	--	--
Calf	Summer	Day	14	16	47	53	a	b	c	--	--	--
Calf	Summer	Night	8	14	36	64	--	--	--	d	--	--
Copeland	Summer	Day	10	6	62	38	--	--	--	--	--	--
Copeland	Summer	Night	21	32	40	60	--	--	--	--	--	--
Cummins	Winter	Day	6	15	29	71	--	--	--	--	--	f
Cummins	Winter	Night	10	8	55	45	--	--	--	--	--	--
Tenmile	Winter	Day	10	18	36	64	--	--	--	--	--	--
Tenmile	Winter	Night	12	17	41	59	--	--	--	--	e	--
Calf	Winter	Night	11	7	61	39	--	--	--	--	--	f
Copeland	Winter	Night	30	24	55	45	--	--	c	--	--	--

a - Larger fish higher above stream bottom
b - Larger fish in deeper water
c - Larger fish relatively higher in water column
d - Larger fish closer to cover
e - Larger fish further from shore
f - Larger fish over courser substrate

Table 5. Means and standard deviations (in parentheses) of microhabitat use by 1+ juvenile steelhead trout in riffles. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat	Coast Summer		Coast Winter		Inland Summer		Inland Winter[a]
Variable	Day [n=21]	Night [n=4]	Day [n=8]	Night [n=9]	Day [n=26]	Night [n=30]	Night [n=46]
Focal velocity ($cm \cdot s^{-1}$)	20.8 (14.7)	5.2 (10.5)	13.2 (9.3)	8.4 (8 8)	13.6 (14.5)	2.8 (3.1)	4.4 (3.2)
Surface velocity ($cm \cdot s^{-1}$)	42.3 (25.3)	13.5 (27.0)	65.4 (36.6)	22.1 (20.7)	26.8 (20.7)	16.7 (23.8)	13.5 (9.1)
Bottom velocity ($cm \cdot s^{-1}$)	8.7 (11.2)	0.5 (1.0)	8.6 (7.9)	8.6 (9.0)	2.4 (3.0)	2.6 (3.0)	3.6 (1.7)
Focal elevation (cm)	6.6 (2.6)	1.3 (2.5)	14.1 (12.9)	7.3 (3.7)	10.0 (5.4)	0.7 (1.5)	5.9 (3.0)
Total depth (cm)	31.2 (7.7)	30.8 (5.6)	61.0 (14.0)	46.3 (19.6)	43.8 (14.9)	34.8 (12.7)	45.5 (13.7)
Rel.elevation	0.22 (0.09)	0.05 (0.10)	0.24 (0.19)	0.18 (0.11)	0.23 (0.09)	0.02 (0.04)	0.11 (0.06)
Cover distance (m)	0.8 (0.4)	0.3 (0.5)	1.4 (0.8)	1.4 (0.6)	0.6 (0.3)	0.4 (0.3)	0.5 (0.4)
Shore distance (m)	1.4 (0.8)	0.8 (0.1)	1.9 (0.9)	1.8 (1.0)	1.6 (1.0)	1.6 (1.5)	2.1 (0.7)
Stream width (m)	4.2 (1.7)	3.4 (0.6)	6.5 (2.8)	8.1 (1.3)	8.2 (3.7)	9.1 (4.1)	11.0 (3.0)
Rel. shore distance	0.35 (0.09)	0.23 (0.12)	0.29 (0.08)	0.23 (0.14)	0.2 (0.1)	0.18 (0.12)	0.19 (0.06)
Substrate size	5.1 (0.9)	4.0 (1.8)	3.6 (1.1)	4.0 (0.7)	5.2 (1.2)	5.1 (1.6)	3.6 (0.5)

a No fish were observed during daylight

Table 6. Means of microhabitat use by 1+ juvenile steelhead trout in pools and results of paired t-test comparisons of diel habitat use. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Coast Summer		Coast Winter		Inland Summer		Inland Winter[a]	
	Day [n=45]	Night [n=62]	Day [n=49]	Night [n=47]	Day [n=46]	Night [n=75]	Night [n=72]	Day
Focal velocity ($cm \cdot s^{-1}$)	10.6	2.6*	21.3	7.1*	4.2	1.3*	4.0	*
Surface velocity ($cm \cdot s^{-1}$)	21.7	12.7*	34.7	13.0*	13.8	7.6*	14.0	*
Bottom velocity ($cm \cdot s^{-1}$)	2.6	2.0	16.1	6.5	1.4	1.1	3.0	*
Focal elevation (cm)	18.4	2.0*	17.2	4.0*	17.2	1.6*	6.0	*
Total depth (cm)	66.5	69.1	83.5	58.2*	61.8	65.3	65.0	*
Rel.elevation	0.27	0.03*	0.20	0.07*	0.26	0.03*	0.08	*
Cover distance (m)	0.94	1.12	1.60	1.39	0.74	1.34	0.59	*
Shore distance (m)	2.11	2.0	2.78	2.47	1.95	2.21	2.31	*
Stream width (m)	5.31	5.92*	8.79	8.92	6.07	7.94	10.43	*
Rel. shore distance	0.39	0.34	0.33	0.29	0.32	0.29	0.24	*
Substrate size	4.0	2.9*	4.7	2.6*	5.7	5.9	4.5	*

*$P < 0.05$

[a] No fish were observed during daylight.

water velocities and moderate water depth (Table 6). An intensive daytime search revealed the locations of only two age 0+ steelhead trout in a pool-riffle sequence where over 100 - 1+ steelhead trout had been observed the previous night. Every stone large enough to conceal a trout but small enough to be moved (~0.75m diameter) was overturned in the search, suggesting that if the trout were still in these study units, they must have been concealed in the interstitial spaces of very large substrates or cracks in bedrock.

Diel Microhabitat Association

The percentage of fish using habitat within specific ranges of a quantified habitat variable was often disproportionate to the percentages of area available within those ranges and diel shifts in association with available pool microhabitats occurred frequently (Figs. 2-5). Substrate association by coastal trout appeared dependent on time of day during summer (Figures 2) and winter (Fig. 3). Day association with substrate was approximately proportional to availability in the assigned categories in summer. During winter days, fish were associated with medium and large gravel far in excess of the proportional area available in these categories. At night in summer and winter, coastal fish were associated with smaller substrates (small gravel, sand, or silt and detritus) more than would be expected, and larger substrates (medium and large gravel, and cobble) less than would be expected, based on the proportional available areas in these categories.

Trout in inland streams in summer were associated with substrate types approximately in proportion to the area available in each category during the day but at night were associated with the smaller-sized substrates (medium and small gravel, and sand) slightly more, and larger substrates (large gravel, cobble, and boulder) slightly less, than would be expected based on the proportional areas of availability in the assigned ranges (Figure 4). However, during winter nights, inland trout were associated with the four smallest substrate types (medium and small gravels, sand, silt and detritus) far in excess of the proportional area that was available in these categories (Figure 5).

With the exception of inland trout on winter days, fish always used deeper pool areas in excess of the proportionate area of availability of deeper water regardless of time of day, region, or season and generally were not observed in water that was less than 20 cm deep (Figures 2, 3, 4, and 5).

At night, trout in both regions and seasons tended to be associated with pool areas having slow bottom currents, usually less than 10 $cm \cdot s^{-1}$, much more than would be expected based on the proportionate areas available in the slowest water categories (Figures 2, 3, 4, 5). In coastal pools during summer and winter days, and inland pools on summer days, fish use of bottom currents was more evenly distributed proportionate to availability, although areas with the highest bottom water velocity were not utilized.

During summer days in the inland region, and on the coast in both seasons, use in the assigned ranges of surface velocity was generally proportionate to the areas of availability, although the slowest category (<5 $cm \cdot s^{-1}$) was used less than would be expected based on availability. At night in winter, trout in both regions mainly used pool areas having the slowest ranges of surface currents more than what was of proportionately availability (Figs. 3, 5). These ranges included surface currents of less than 10 $cm \cdot s^{-1}$ in the coastal region and less than 15 $cm \cdot s^{-1}$ inland. On summer nights, use of surface currents was distributed roughly in proportion to availability although there was slightly more use of slower water areas at night versus day (Figs. 2, 4).

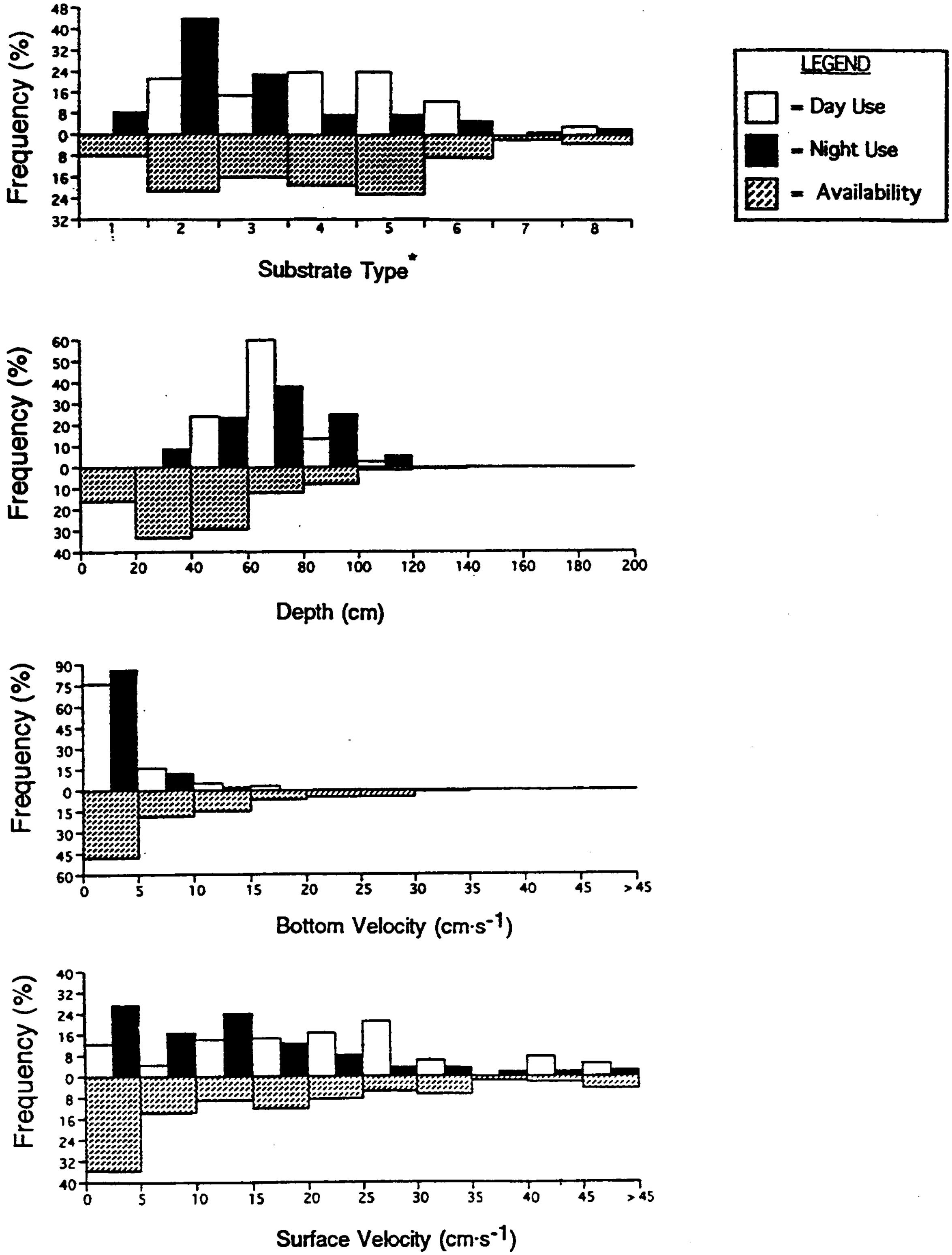

Figure 2. Comparison of diel habitat use by 1+ juvenile steelhead trout to habitat availability in pools of coastal streams in summer. * See text for size classes.

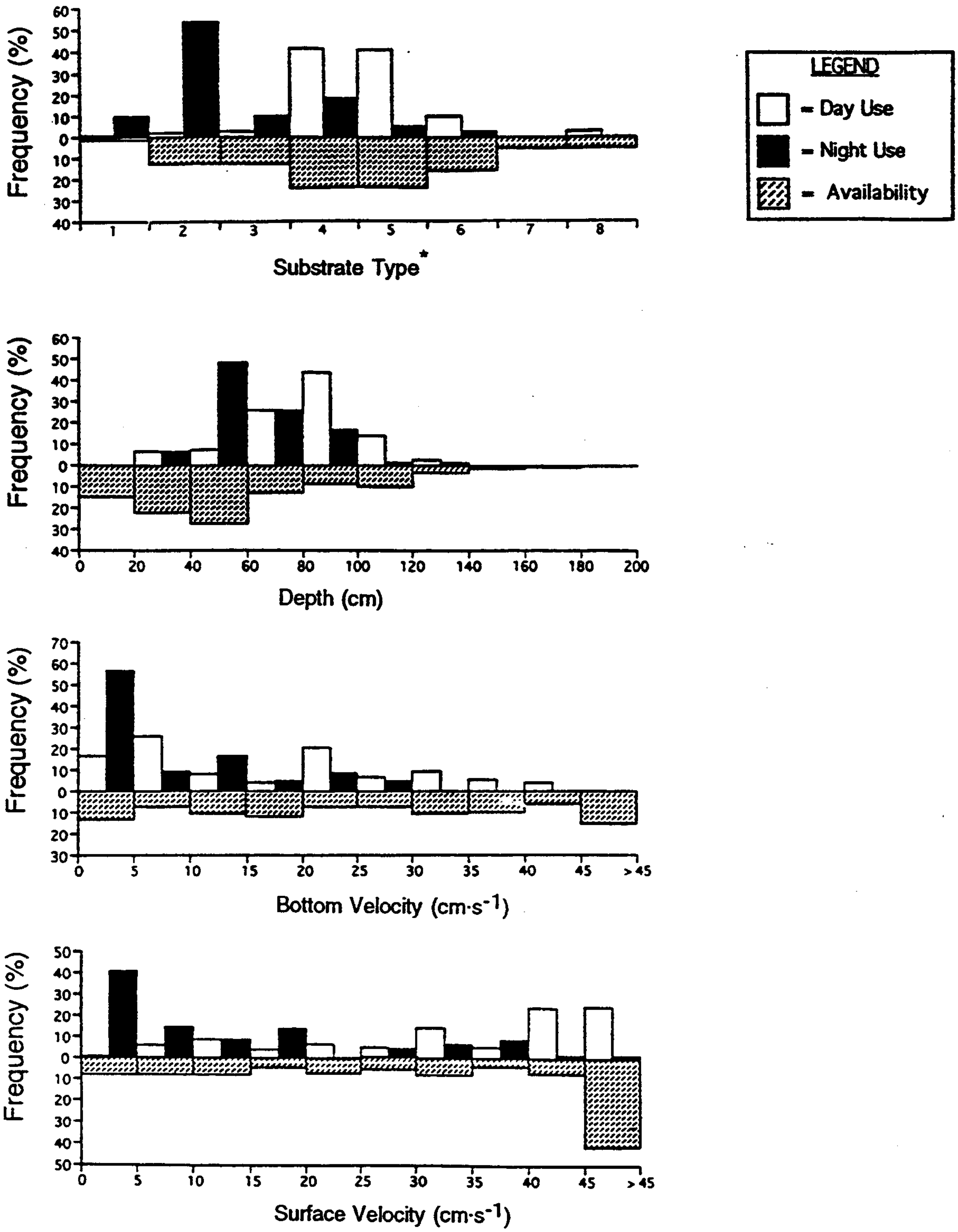

Figure 3. Comparison of diel habitat use by 1+ juvenile steelhead trout to habitat availability in pools of coastal streams in winter. * See text for size classes.

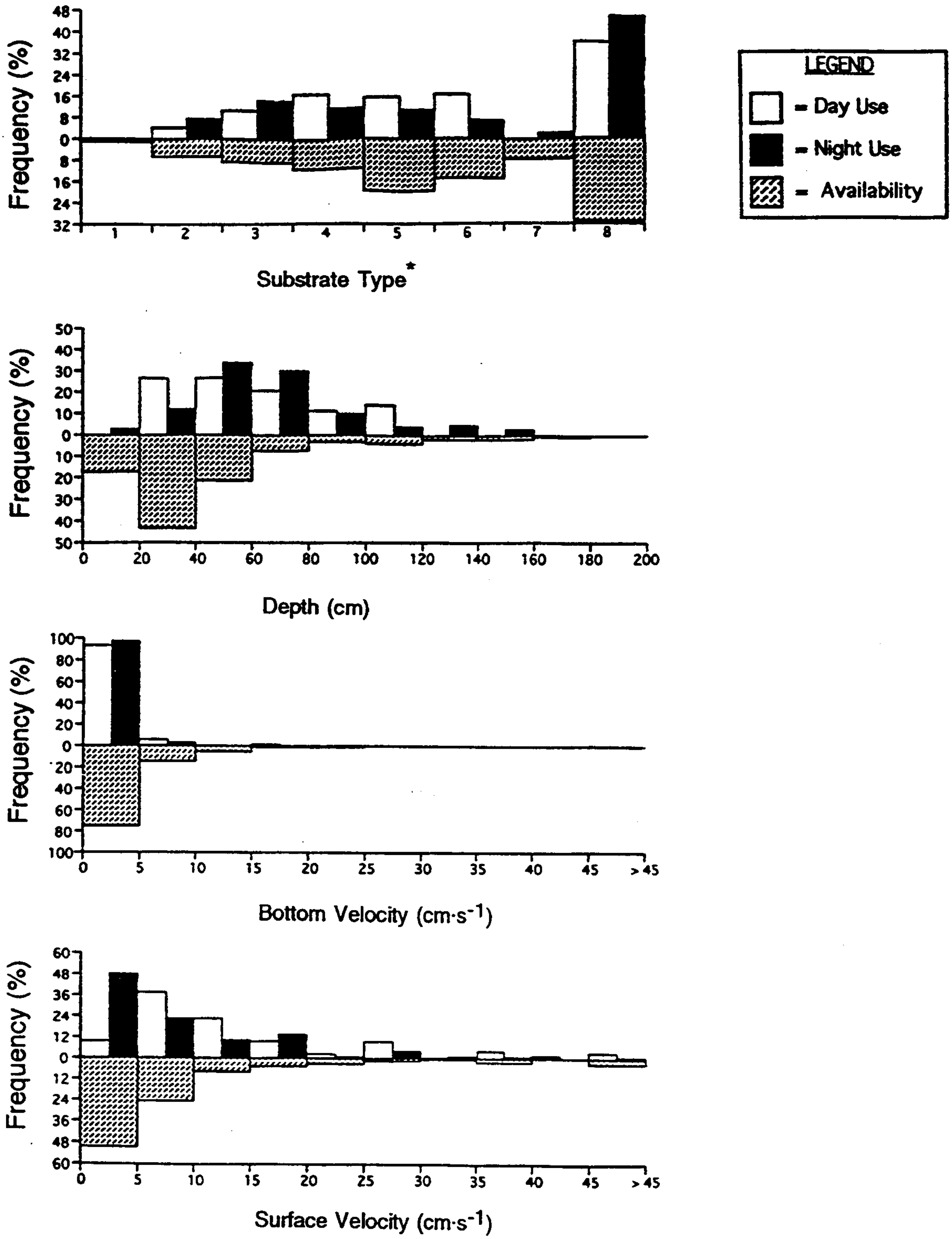

Figure 4. Comparison of diel habitat use by 1+ juvenile steelhead trout to habitat availability in pools of inland streams in summer. * See text for size classes.

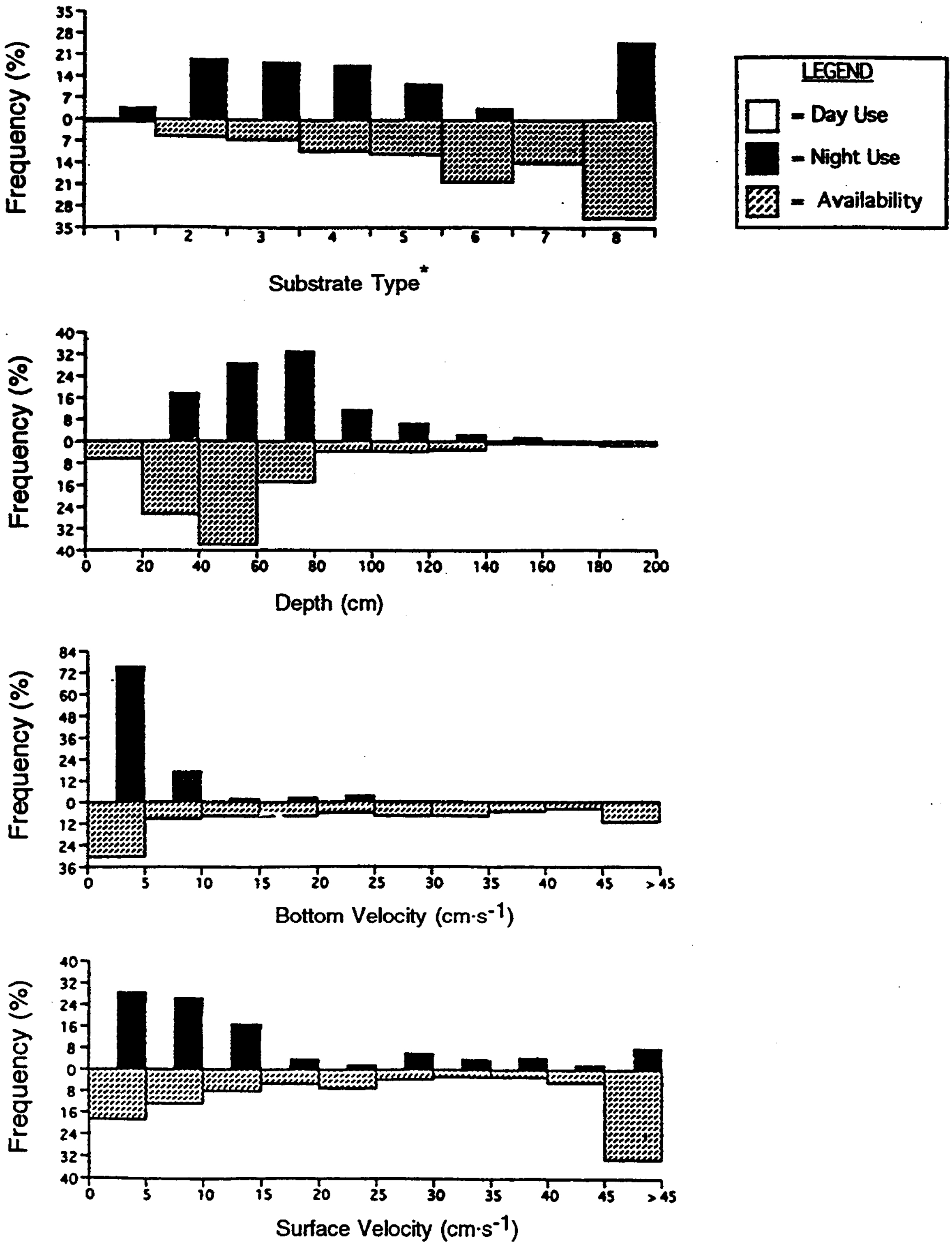

Figure 5. Comparison of diel habitat use by age 1+ steelhead trout to habitat availability in pools of inland streams in winter. Note: No fish were observed during the day in winter. * See text for size classes.

MATERIALS AND METHODS: LABORATORY

Experimental Design

Age 1+ steelhead trout from a coastal stream (Tenmile Creek) and an inland stream (Canton Creek) were observed in two stream aquaria (Reeves et al. 1983, 1987) to examine the effect of water temperature on diel behavior. The stream channel in each of the two aquaria was divided into two equal sections by a screened partition. Each section had two pool and two riffle areas with surface substrate consisting entirely of gravel <1 cm in diameter. Five round terra-cotta drainage tiles, 311 mm long by 136 mm in diameter, provided the only cover for trout in each section. In each section, three tiles were placed in riffle areas and two in pool areas. Tiles were almost completely buried within the substrate and had wood caps fastened by epoxy to both ends to prevent filling by substrate but to allow entry by trout through semicircular openings (Fig. 6). Sides of the tiles were cut away longitudinally and these cut surfaces were placed flush against the Plexiglas viewing walls of the channels to allow easy verification of cover use (Fig. 7).

Artificial daylight was provided by nine 60-W incandescent bulbs suspended at equal intervals over each aquarium. Winter photoperiod was simulated by use of a timer and cam that controlled light intensity (Everest and Rogers 1982), providing cycles of 12 hours of light followed by 12 hours of darkness. The light phase consisted of a 1.5 hour "dawn" where light intensity gradually increased from zero to full intensity, 9 hours of full light intensity, and a 1.5 hour "dusk" where full light intensity gradually dimmed to zero.

Steelhead trout used in the experiments were captured by electroshocking (Smith-Root Model 12A DC Backpack Electrofisher - settings

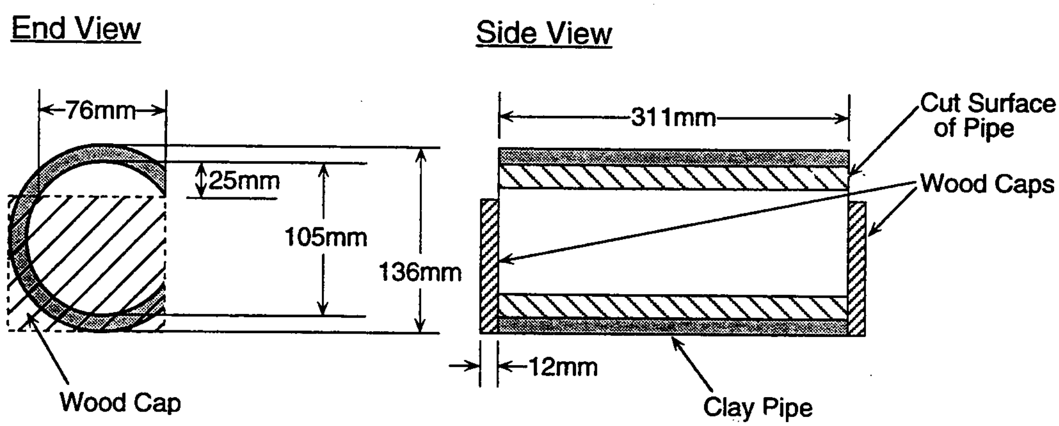

Figure 6. Dimensions of terra cotta pipe structure used in laboratory streams to provide cover for juvenile steelhead trout.

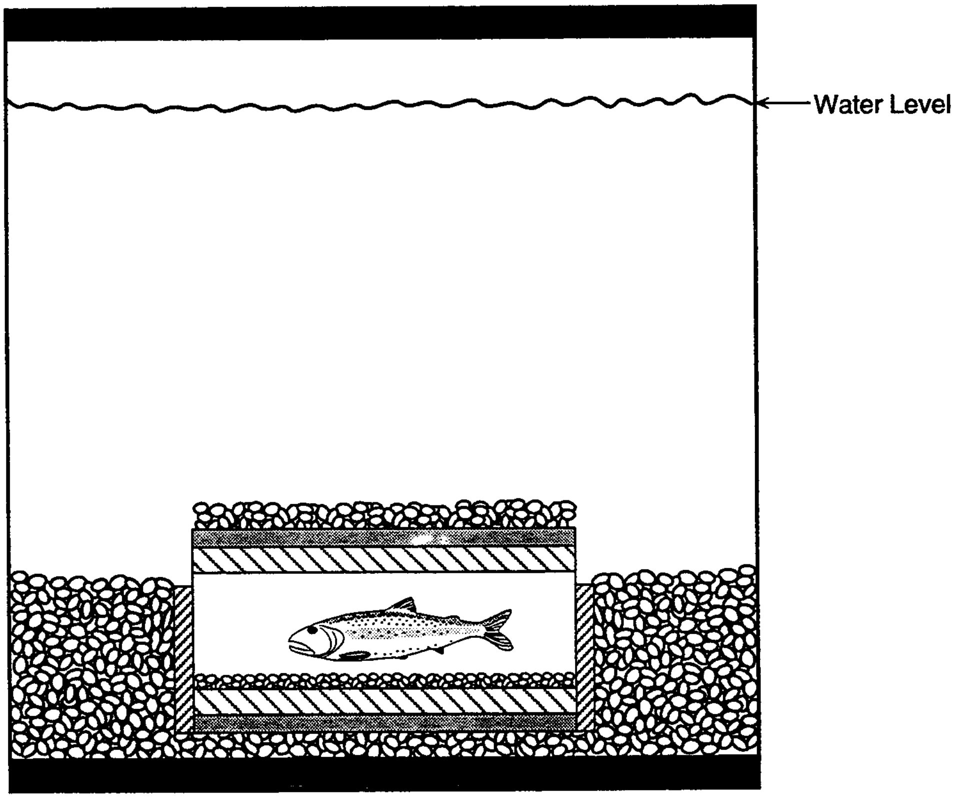

Figure 7. Placement of cover structure within the laboratory stream.

60HZ; 400V) from Canton Creek in the inland region on 8 December 1990 and from Tenmile Creek in the coastal region on 15 January 1991. Prior to their introduction into the experimental channels, fish were held for one month in 122 cm diameter circular fiberglass tanks fed by well water on a flow-through design. Water temperature in holding tanks fluctuated between 12°C and 14°C. Fish were fed to satiation once daily with thawed frozen brine shrimp (Artemia spp.) and bi-weekly with meal worms (Tenebrio spp.). Great care was taken to ensure that fish were not startled or disturbed during the holding period.

Before placement in the stream aquaria, individual fish were weighed to the nearest 0.1 g and measured to the nearest 1.0 mm (fork length) then given fin-clips to facilitate individual identification. Mean (±1 SD) length, weight, and condition factor (K) (Anderson and Gutreuter, 1985) of trout in the two experiments were 149.2 mm (39.7), 37.1 g (13.4), and 1.10 K (0.12) for coastal trout, and 130.2 mm (14.2), 24.1 g (7.9), and 1.06 K (0.06) for inland trout. Four trout from a single region were placed in each stream aquaria section for a total sample size of 16 fish. One coastal fish became ensnared and suffocated in a net designed to prevent fish from jumping out of the experimental channel so that one of the four sections in the experiment had three rather than four fish. Trout density in both experiments was slightly less than one trout per m^2 in all other sections.

Data Collection

The trout were allowed one week to habituate to the stream aquariums. During this period water temperature in the stream aquaria was slowly raised to 16^{o}C starting from the temperature of the water in the circular holding tank from which the trout had been retrieved. Adjustment to aquaria and 16^{o}C water was confirmed by ensuring that variation in tail beat rate and breathing rate became constant over time. All fish appeared acclimated to stream channel well before the end of one week.

During observations in the laboratory channels, fish were fed thawed frozen brine shrimp via a food delivery system described in Reeves et al. (1983). Daily rations were equal to 10% of the total wet weight of trout in each aquaria as measured at the start of the experiment and were provided in two equal rations — once in the morning after 1 hour of full light intensity and again 1 hour before initiation of dusk. Daily rations were intentionally small to motivate fish to maintain feeding positions out of cover (see Wilzbach, 1985).

"Day" and "night" observations of fish use of the cover structures were made as water temperature was decreased from 16^{o}C to 2^{o}C, then increased again to 16^{o}C, at a rate of 1^{o}C per day. Trout from coastal and inland populations were tested separately in trials that each lasted 28 days. Temperature changes were made at night after the last observation session for each 1^{o}C temperature plateau. Diel use of cover structures was recorded five times each day: three times during full "daylight," and twice during the hours of darkness. Daylight observations were made just prior to morning feedings, at midday, and just prior to the pre-dusk feeding. Times for the two nighttime observations were randomly chosen each day; the only criterion being that observations must be made at least 1 h after onset of total darkness and at least

1 h before initiation of dawn. An observation session consisted of noting the location of individual fish within a channel.

Data Analysis

Analyses of day and night cover use at temperatures ranging between $2^{o}C$ and $16^{o}C$ were performed separately. The effect of water temperature on cover use by the entire sample of coastal (n=15) and inland (n=16) trout was plotted and described by logistic regression. Lowest and highest cover use proportions observed in each replicate were standardized to values approaching zero and 100%, respectively, then linearly transformed by natural logarithm for use in the logistic regressions. The form of the logistic equation used in the regressions was: $Y_i = B_0+B_1T_i$ where Y_i = natural logarithm of the standardized and transformed cover use proportions, and T_i = water temperature In addition, the response of coastal and inland trout to water temperature changes in each of the four aquaria sections was similarly calculated. The daytime cover seeking responses of coastal and inland fish to changes in water temperature were statistically compared using paired t-tests. Trials for coastal and inland fishes were paired by aquaria partition. Slopes of the logistic equations that described use of cover versus water temperature by coastal and inland fish in each of the four partitions were used as response indicators in the paired t-tests.

RESULTS: LABORATORY

In the controlled environment of the laboratory streams, juvenile steelhead from coastal and inland streams used cover during the day depending on water temperature (Fig.8A) but were never observed in the cover structures at night, regardless of temperature (Fig. 8B). During simulated daylight, the number of trout utilizing the cover structures in each partition was negatively correlated with water temperature in experiments with coastal and inland trout . More trout remained out of cover during the day when the water temperature was nearer 16^{0}C than when water temperature was decreased towards 2^{0}C.

The degree of cover use by coastal or inland trout at any given water temperature was similar irregardless of whether water temperature was being decreased or increased. Logistic equations were calculated to describe the relationship of water temperature to day use of cover for each replicate in the experiments (Table 7). The response of inland trout to changes in water temperature was significantly stronger than the response of coastal trout (paired t-test, $P<0.01$). At any given water temperature between 16^{0}C and 2^{0}C a higher proportion of inland trout versus coastal trout used cover, however, the differences became most apparent at temperatures below 12^{0}C (Fig. 8A).

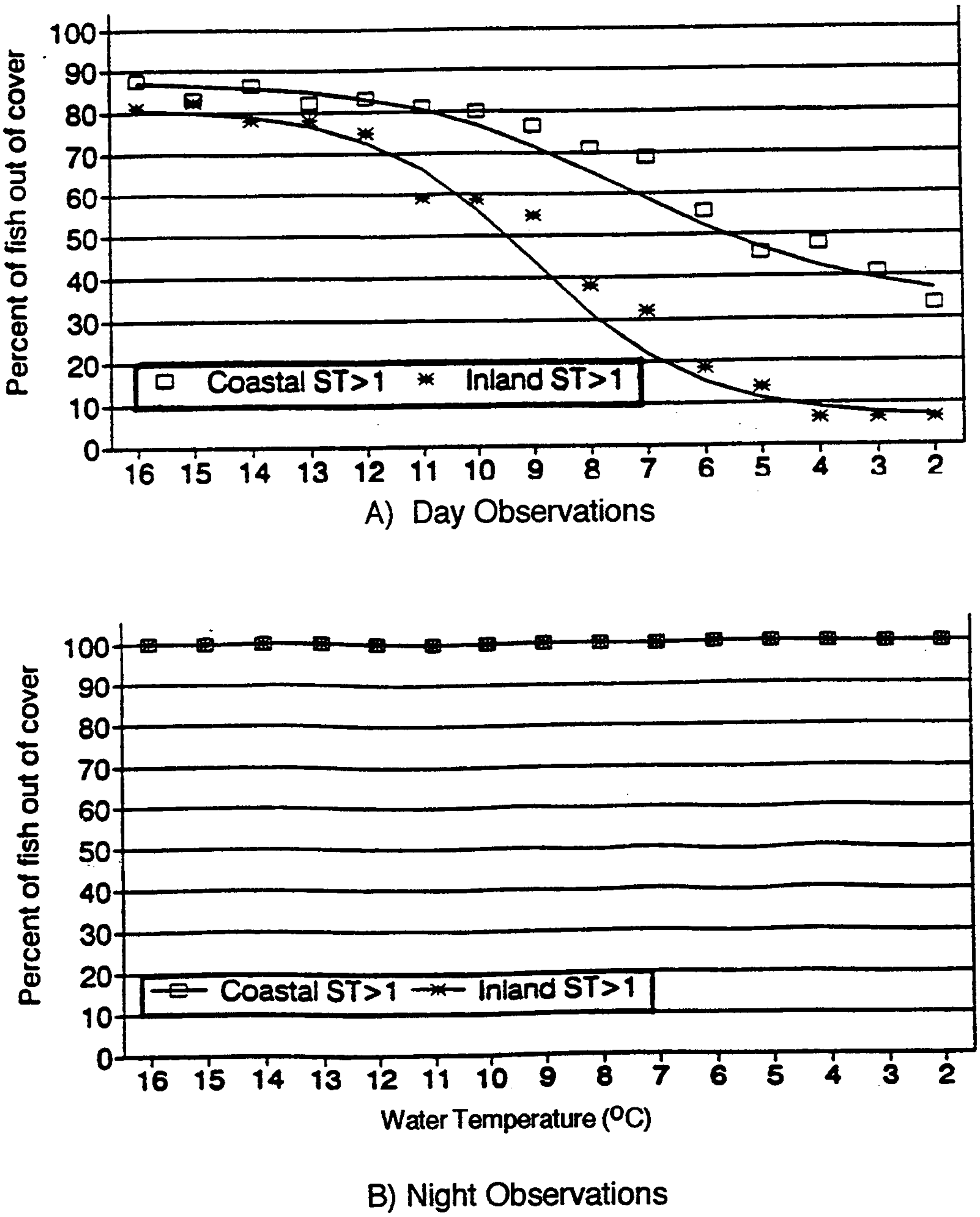

Figure 8. Relationship between water temperature and diel use of cover structures for concealment by coastal and inland 1+ juvenile steelhead trout in laboratory streams: A) Day, B) Night. Logistic curves are fitted to the data points for daytime cover use.

Table 7. Parameter values of logistic equations describing day cover use versus water temperature by coastal and inland 1+ juvenile steelhead trout in partitions of laboratory streams and for each population overall.

	Coastal Trout (n = 15)			Inland Trout (n = 16)		
Partition	Intercept	Slope	R^2	Intercept	Slope	R^2
I	- 1.95	0.452	60%	- 6.20	0.668	93%
II	- 4.72	0.546	88%	- 6.63	0.675	93%
III	- 4.36	0.466	69%	-5.91	0.660	95%
IV	-2.84	0.373	55%	- 5.90	0.658	93%
Overall	- 3.62	0.499	89%	- 6.12	0.682	97%

DISCUSSION

Inland populations of salmonids in streams may exhibit ecological and behavioral characteristics that differ from those of coastal populations (Swales et al., 1986). Results of this study suggest that coastal and inland 1+ juvenile steelhead trout have different behavioral strategies to survive in winter. Diel activity patterns in summer were characteristically similar between regions with most variation appearing to be a reflection of regional differences in habitat availability. In winter, diel activity patterns differed greatly between regions. Although more fish were counted in the pool and riffle study units of coastal streams at night compared to day, fish in the inland region became entirely nocturnal. This difference in diel behavior and microhabitat use is likely adaptation to the drastically different physical conditions characteristic of the coastal and inland regions in winter, particularly water temperature. The range of water temperatures in coastal study streams are greatly moderated by oceanic influences. Study streams in the inland region, out of the zone of oceanic influence and at a higher elevation, experience wider annual and diel temperature ranges with water temperatures that get much warmer in the summer and much colder, and for longer periods of time, in winter. Inland fish must be able to withstand prolonged periods of low temperatures in winter, but fish on the coast where water temperatures are generally much warmer do not. Fish in coastal streams in winter have to withstand only brief periods of extemely cold water temperatures and be constantly prepared for return of mild winter water temperatures due to maritime influences and resultant increases in metabolic rate and energy demands.

Day concealment in winter may be more adaptive for trout in inland regions than on the coast. Riehle and Griffith (1993) observed that subyearling steelhead trout rearing in Silver Creek, Idaho became increasingly nocturnal with the onset of winter. Campbell and Nuener (1985) also reported that in winter juvenile and adult resident rainbow trout concealed themselves during the day but occupied positions out of cover at night. Heggenes et al. (1993) hypothesized that the winter shift in strategy to day concealment and night-time activity displayed by brown trout in two Norwegian streams is an ecologically adaptive homeostatic response that helps to ameliorate the effects of large-scale environmental changes and harsh conditions in winter. In the inland region where winters are characterized by cold water temperatures and high flows, survival may be maximized by remaining concealed in the substrate during the day rather than trying to defend feeding territories as in summer. However, on the coast where winter water temperatures are moderated by the ocean, an active existence and the same foraging strategy all year round may be most adaptive for survival. In Oregon coastal streams seasonal shifts in behavioral survival strategies necessitated by severe winter conditions are probably unnecessary and would likely be ecologically disadvantageous because of the high metabolic costs of largescale acclimations to seasonal decreases or increases in water temperature (Cunjak, 1987; Maciolek, 1951).

Daytime concealment behavior of 1+ steelhead trout at low water temperatures has been well documented in the literature but the actual water temperature reported to bring about this response varies widely. Contrary to an absolute water temperature threshold for initiation of this response, as reported in many studies (Bustard and Narver, 1975; Rimmer et al. 1984; Johnson and Kucera, 1985; Contor, 1989;) data from the aquaria experiments of this study and observations of other researchers (Chapman and Bjornn, 1969; Bjornn, 1971; Rielhle and Griffith, 1993) suggest that day concealment behavior in stream salmonids may operate on a continuum with changes in water temperature. Fausch and White (1981) have proposed that selection of microhabitat depends on a balance between energy gain and the energetic cost of obtaining it, which in turn can be directly influenced by water temperature (Smith and Li, 1983). As energy demands decrease with water temperature and the energetic cost of obtaining food increases, trout may spend increasing amounts of time conserving energy by concealing themselves in cover rather than expending energy defending feeding positions. Gardiner (1984) warns that visual counts of salmonids in streams may underestimate the actual number of fish when water temperatures are below 13°C. Juvenile steelhead trout in the laboratory streams were concealed a small percentage of the time even in temperatures as high as 16°C. Trout in streams may be concealed in cover even in relatively warm water as long as their appetite is satiated. Wilzbach et al., (1986) found that cutthroat trout used cover a greater percentage of the time during periods of high food abundance than during periods of low food abundance.

The strategy of concealment within cover during the day but emerging from cover at night might confer ecological advantages to inland trout in winter for several reasons. Attempting to maintain feeding activities in the cold water of winter may not be cost efficient or metabolically possible. Swimming performance and the ability to capture prey is significantly reduced at low water temperature and disproportionally costly (Webb 1978), especially in high currents (Metcalf et al., 1986). In the inland regions where winter water temperatures are low trout may save energy by remaining in cover during the day but may emerge from cover at night and feed opportunistically when little energy will be wasted on defending territories, although Cunjak et al. (1987)

found that the maintenance metabolism of brown trout in winter could not be offset by energy intake. Because metabolic activity is greatly decreased at cold temperatures starvation of salmonids in streams is unlikely and healthy trout should be able to survive several months of fasting (Griffith 1993). Elliot (1972) found that the rate of gastric evacuation in brown trout exceeded the rate of digestion rate at temperatures below 5^0C. In rainbow trout, Windell et al. (1976) reported that an increase of 5^0C at the low end of the temperature range allowed a much greater absolute percentage of food to be digested before being evacuated than a similar increase in temperature at the high end of the range. This may partially explain why coastal fish remain active during the day in winter and are more hesitant to use cover at low water temperatures than inland fish.

Overwintering mortality of salmonids in streams is high and largely caused by physical injury in stream reaches where snow bridging does not occur (Griffith 1993). In regions with harsh winter conditions spatial stream conditions can change daily. Safe shelter in the stream environment is transitory due to changes in physical factors such as flow regime, freezing and thawing, and ice and bedload movements. Moving out of cover at night might provide opportunities for trout to re-assess day cover locations thereby avoiding many environmental hazards inherent in streams subject to fridgid winters such as becoming stranded because of stream de-watering due to changes in streamflow, entrapment or habitat exclusion by ice, and being crushed by movements of ice and substrates mobilized by high flows. Becoming nocturnal would also facilitate predator avoidance during conditions in which fish are physiologically least able to escape capture attempts.

During summer days, coastal and inland trout maintained elevated feeding positions in near proximity to moving water but at night became relatively inactive in areas with slow water currents. These findings are in agreement with Hoar (1953), Edmundson et al., (1968), Campbell and Neuner (1985), and Riehle and Griffith (1993) who have reported similar diel shifts in habitat use by juvenile steelhead trout. These researchers also reported that fish moved into to shallower water and closer to the stream margin at night. These other diel shifts were not observed in this study except for in the coastal region in winter when shallower areas of the pools were utilized more frequently at night. Coastal and inland trout observed in this study utilized moderate to deep areas of the pools and remained approximately the same distance away from the stream margin, regardless of whether it was night or day.

Seasonal fluctuations in water temperature (Gibson 1978) and water velocity (Taylor 1988) have been suggested as primary environmental factors influencing social behavior and habitat selection in salmonids. Chapman (1966) hypothesized that space rather than food is the primary density regulating mechanism for salmonids in streams in winter. Coastal trout in winter exhibited diel shifts in microhabitat use but their overall distribution was tightly confined by high water velocity to small pockets of slow water refugia in backwater eddies. Instead of defending well-spaced feeding positions as in summer, trout occurred in aggregations. Kawanabe (1969) observed that Ayu (Plecoglossus altivelis) are strongly territorial until a certain threshold of population density is exceeded, beyond which increased crowding causes the initiation of schooling behavior. Kawanabe suggests that this aspect of their social structure influences their own production. Absence of territorial behavior by coastal trout on winter days may be a similar behavioral mechanism triggered by forced crowding. Adoption of gregorious behavior by trout may play an important role by allowing many fish to temporarily share small areas of the stream during freshets and other times of extreme high flows, thereby decreasing both mortality and downstream displacement and allowing the population to maintain its numbers until water velocity diminishes.

Experimental results of this study offer no explanation for the differences in diel concealment behavior between fish populations that were drawn from different geographical regions but were subjected to identical experimental conditions. The question of whether this variation is the result of regional adaptations to geographic differences in phenologic regimes or is due merely to a high degree of flexibility of the circadian clock to environmental conditions, as suggested by Muller (1978), remains unanswered. Geographic and seasonal variation in behavioral patterns and ability to utilize stream habitat could be inherited in steelhead trout. In an analysis of genetic variation of steelhead trout Parkinson (1984), speculated that this species exists as a collection of semi-isolated populations each having the potential to evolve adaptations to local environmental conditions. Differences in the rheotactic response of rainbow trout fry progeny from populations spawning in inlet and outlet streams of lakes have been attributed to an interplay of genetic and environmental factors (Kelso et al., 1981). Winter decreases in metabolic rate and swimming ability of rainbow trout have been observed to occur in the absence of changes in water temperature in laboratory experiments (Facey and Grossman, 1990). These types of adaptive functions could be achieved through rhythmic endocrine control (Thorpe 1978).

The notable diel, seasonal, geographical, and phenological variation in habitat utilization exhibited by trout brings into question the validity of applying suitability models beyond the spatial and temporal realm, or apart from similar physical conditions in which they were developed. Moyle and Baltz (1985) recommend that instream flows should be based on microhabitat use and availability data collected on site and even these data should be used cautiously because of changes in a stream's physical characteristics, especially temperature regime. In a comparison of empirical habitat models designed to predict stream carrying capacity, Hogan and Church (1989) concluded that the models were only regionally valid at best because different aspects of habitat become the critical, limiting elements for a particular species in different regions. Also, suitability models developed in one season may not be valid in another. Grossman and Freeman (1987) attributed most seasonal changes in microhabitat use by rainbow trout to variations in microhabitat availability. Results of this study indicate that the complete chronology of habitat use, both diel and annual, and the effect of water temperature on these chronologies must be known and included in derivation of habitat suitability criteria and that these criteria should not be used to predict fish habitat availability in regions beyond those in which they were derived. Habitat management programs for juvenile steelhead trout based only on summer daytime observations or made within a single season are likely to be misleading.

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APPENDICES

APPENDIX A

Means of microhabitat use by 1+ juvenile steelhead trout of small and large size classes in pools of coastal and inland streams on summer days. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Tenmile Creek		Cummins Creek		Calf Creek		Copeland Creek	
	Small [n=8]	Large [n=11]	Small [n=8]	Large [n=18]	Small [n=14]	Large [n=16]	Small [n=10]	Large [n=6]
Focal velocity ($cm \cdot s^{-1}$)	9	15	8	8	3	4	5	4
Surface velocity ($cm \cdot s^{-1}$)	17	27	14	20	14	14	14	17
Bottom velocity ($cm \cdot s^{-1}$)	3	2	2	4	1	1	2	1
Focal elevation (cm)	16	24	16	18	7	21*	20	27
Total depth (cm)	60	69	65	68	37	70*	69	82
Rel.elevation	0.23	0.33	0.26	0.24	0.19	0.29*	0.28	0.31
Cover distance (m)	0.87	1.05	0.76	0.83	0.95	0.46	0.98	0.65
Shore distance (m)	2.73	2.30	1.96	1.84	1.86	1.52	2.20	1.66
Stream width (m)	6.5	5.9	5.0	4.8	6.1	5.4	6.7	5.7
Rel. shore distance	0.40	0.40	0.39	0.38	0.30	0.28	0.32	0.31
Substrate size	4.0	3.91	4.6	4.8	5.7	6.9	4.5	6.3

* $P < 0.05$

APPENDIX B

Means of microhabitat use by 1+ juvenile steelhead trout of small and large size classes in pools of coastal and inland streams on summer nights. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Tenmile Creek		Cummins Creek		Calf Creek		Copeland Creek	
	Small [n=12]	Large [n=16]	Small [n=10]	Large [n=24]	Small [n=8]	Large [n=14]	Small [n=21]	Large [n=32]
Focal velocity ($cm \cdot s^{-1}$)	3.	2	2	2	1	0	2	2
Surface velocity ($cm \cdot s^{-1}$)	12	14	10	12	7	7	7	12
Bottom velocity ($cm \cdot s^{-1}$)	3	2	2	2	0	0	2	2
Focal elevation (cm)	2	2	2	2	2	3	0	1
Total depth (cm)	61	73	59	74*	47	69	71	78
Rel.elevation	0.03	0.03	0.03	0.02	0.05	0.05	0.01	0.01
Cover distance (m)	0.79	0.89	1.68	1.43	2.78	0.89*	1.06	1.08
Shore distance (m)	2.15	2.01	2.38	1.82*	1.91	2.08	2.52	2.58
Stream width (m)	7.1	6.1	5.9	5.4	7.3	6.6	8.3	9.3
Rel. shore distance	0.33	0.32	0.40	0.34	0.27	0.30	0.30	0.29
Substrate size	2.5	2.9	2.4	3.3	6.5	6.6	4.5	6.0*

* $P < 0.05$

APPENDIX C

Means of microhabitat use by 1+ juvenile steelhead trout of small and large size classes in pools of coastal and inland streams on winter days. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Tenmile Creek		Cummins Creek		Calf Creek		Copeland Creek	
	Small [n=10]	Large [n=18]	Small [n=6]	Large [n=15]	Small [n=0]	Large [n=0]	Small [n=0]	Large [n=0]
Focal velocity ($cm \cdot s^{-1}$)	9	11	30	36				
Surface velocity ($cm \cdot s^{-1}$)	20	22	51	42				
Bottom velocity ($cm \cdot s^{-1}$)	7	7	26	25				
Focal elevation (cm)	25	24	9	12				
Total depth (cm)	90	94	56	75				
Rel.elevation	27	25	0.15	0.16				
Cover distance (m)	0.72	0.82	1.98	2.30				
Shore distance (m)	2.83	2.81	2.22	2.54				
Stream width (m)	11.3	11.4	7.8	7.5				
Rel. shore distance	0.25	0.25	0.28	0.34				
Substrate size	5.0	4.6	4.5	4.5				

* $P < 0.05$

APPENDIX D

Means of microhabitat use by 1+ juvenile steelhead trout of small and large size classes in pools of coastal and inland streams on winter nights. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Tenmile Creek		Cummins Creek		Calf Creek		Copeland Creek	
	Small [n=12]	Large [n=17]	Small [n=10]	Large [n=8]	Small [n=11]	Large [n=7]	Small [n=30]	Large [n=24]
Focal velocity ($cm \cdot s^{-1}$)	5	7	4	11	5	3	3	3
Surface velocity ($cm \cdot s^{-1}$)	17	21	9	15	12	13	18	12
Bottom velocity ($cm \cdot s^{-1}$)	5	7	5	9	5	1	3	3
Focal elevation (cm)	3	5	2	4	4	5	5	7
Total depth (cm)	58	68	49	57	62	58	75	66
Rel.elevation	0.05	0.08	0.03	0.06	0.07	0.08	0.06	0.13*
Cover distance (m)	1.4	1.5	1.1	1.0	0.4	0.3	0.7	0.6
Shore distance (m)	2.4	3.1*	1.6	1.7	2.6	2.4	2.3	2.2
Stream width (m)	10.4	11.0	8.3	7.7	9.1	8.7	11.6	11.9
Rel. shore distance	0.25	0.29	0.22	0.24	0.28	0.28	0.20	0.19
Substrate size	3.0	3.4	1.8	2.5*	5.0	4.3	4.3	4.4

* $P < 0.05$

APPENDIX E

Means of day and night microhabitat use by 1+ juvenile steelhead trout of small and large size classes combined in pools of coastal and inland streams in summer. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Tenmile Creek		Cummins Creek		Calf Creek		Copeland Creek	
	Day [n=19]	Night [n=28]	Day [n=26]	Night [n=34]	Day [n=30]	Night [n=22]	Day [n=16]	Night [n=53]
Focal velocity ($cm \cdot s^{-1}$)	12	3	9	2	4	0	5	2
Surface velocity ($cm \cdot s^{-1}$)	24	13	19	13	14	7	13	8
Bottom velocity ($cm \cdot s^{-1}$)	2	2	3	2	1	0	2	2
Focal elevation (cm)	22	2	18	2	13	2	21	0
Total depth (cm)	66	68	67	70	50	57	73	74
Rel.elevation	0.27	0.03	0.26	0.03	0.23	0.05	0.28	0.00
Cover distance (m)	1.0	1.1	0.9	1.4	0.8	1.7	0.7	1.0
Shore distance (m)	2.2	2.0	2.1	2.0	1.7	2.0	2.2	2.43
Stream width (m)	5.5	6.4	5.1	5.4	5.9	6.7	6.2	9.2
Rel. shore distance	0.37	0.32	0.40	0.36	0.29	0.30	0.34	0.27
Substrate size	3.6	2.7	4.4	3.2	6.2	6.5	5.2	5.2

APPENDIX F

Means of day and night microhabitat use by 1+ juvenile steelhead trout of small and large size classes combined in pools of coastal and inland streams in winter. Numbers of fish upon which summary statistics are calculated appear in brackets.

Microhabitat Variable	Tenmile Creek		Cummins Creek		Calf Creek		Copeland Creek	
	Day [n=28]	Night [n=29]	Day [n=21]	Night [n=20]	Day [n=0]	Night [n=18]	Day [n=0]	Night [n=62]
Focal velocity ($cm \cdot s^{-1}$)	11	5	35	11		4		4
Surface velocity ($cm \cdot s^{-1}$)	29	14	43	11		13		16
Bottom velocity ($cm \cdot s^{-1}$)	8	5	25	9		3		4
Focal elevation (cm)	22	4	10	4		2		6
Total depth (cm)	92	58	72	60		59		70
Rel.elevation	0.23	0.06	0.16	0.07		0.07		0.09
Cover distance (m)	1.2	1.4	2.3	1.4		0.4		0.8
Shore distance (m)	3.0	2.8	2.5	2.0		2.5		2.2
Stream width (m)	9.8	9.4	7.5	7.7		9.0		11.9
Rel. shore distance	0.32	0.30	0.33	0.27		0.28		0.19
Substrate size	4.8	2.9	4.4	2.3		4.9		4.1