

AN ABSTRACT OF THE THESIS OF

Deborah J. Walks for the degree of Master of Science in Fisheries Science presented on March 11, 1997. Title: Discharge and its Consequences to Physical Habitat and Trout Populations in the Deschutes River of Central Oregon.

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The severely reduced summer flows (98% discharge diverted for irrigation) in the Upper Deschutes River of Central Oregon creates habitat conditions, such as water temperatures of up to 29°C, which are harmful to resident trout populations. An increase in discharge is currently under consideration, but will this increase trout numbers? Standard approaches to determining a recommended instream flow —Instream flow incremental methodology (IFIM), Weighted usable area (WUA), and the Tennant method— are inadequate to predict the response of trout to an increase in discharge, especially as none of them include water temperature within their model. We examined the influence of discharge on physical habitat and on trout populations at a habitat unit level with an empirical determination of the relationships between discharge and physical habitat, trout density and discharge, trout density and temperature, and discharge and

water temperature. Aerial habitat inventory at different river stages complemented our research on physical habitat. Habitat size was found to be correlated with discharge, especially as channel width increases; however, habitat unit distribution varied non-linearly with changes in discharge. The percentage of cascade/rapid habitat increased with discharge more quickly in higher gradient reaches than in the lower gradient reaches. Percentage of pools and riffles did not fluctuate in a predictable manner with changes in discharge, but there was a general trend towards less pool habitat with higher discharges.

We found a direct relationship between discharge and water temperature, where irrigation canals, with 3 to 10 times higher discharge than the main river, uniformly had lower water temperatures. Regression analysis showed that at just over twice the current summer discharge, the maximum water temperature in the main river might decrease by up to 3°C.

Rainbow trout populations were significantly lower in a habitat unit when maximum water temperature was above 24°C or below 14°C ($p < 0.0005$), whereas brown trout populations did not change significantly with water temperature ($p = 0.1175$). Increases in discharge were related to higher brown trout populations ($p < 0.0613$), but were associated with no change in rainbow trout abundance ($p = 0.1752$) but an increase in rainbow trout density (abundance/m³) ($p = 0.0001$). We concluded that rainbow trout are probably more limited than brown trout by the high water temperatures found within the Deschutes River, and an increase in discharge will both lower water temperatures and increase habitat size.

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**Discharge and its Consequences to Physical Habitat and Trout Populations in the
Deschutes River of Central Oregon.**

by

Deborah J. Walks

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Deborah J. Walks, Author

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It took hundreds of millions of years to produce the life that now inhabits the earth — eons of time in which that developing and evolving and diversifying life reached a state of adjustment and balance with its surroundings. The environment, rigorously shaping and directing the life it supported, contained elements that were hostile as well as supporting. ... Given time — time not in years but in millennia — life adjusts, and a balance has been reached. For time is the essential ingredient; but in the modern world there is no time.

Rachel Carson, 1962

Discharge and its Consequences to Physical Habitat and Trout Populations in the Deschutes River of Central Oregon.

INTRODUCTION

In the Upper Deschutes River of Central Oregon, changes in public attitudes towards traditional western water appropriation practices, and in water use, have opened up discussion about the potential for trout habitat restoration. The Upper Deschutes River currently experiences extremely low summer flows due to irrigation withdrawals removing 98% of the regulated flow. Downstream from the irrigation canals, water temperature increases over the next 50 km, reaching up to 29°C—well above the upper incipient lethal temperature for trout (recorded summer 1994, Oregon Department of Fisheries and Wildlife (ODFW), unpublished data). One restorative measure that has been suggested in order to improve water quality and trout habitat in the upper river is to increase summer low flows by decreasing the amount of water diverted for irrigation. Will this increase trout populations? There is some debate concerning flow requirements for the trout within the river system. However, the additional discharge could both improve water quality and increase habitat quantity.

The purpose of our research was to examine the relationships between discharge, physical habitat, and trout populations: first, to establish whether such relationships exist within the specific context of the Upper Deschutes River, and second, to determine the nature of these relationships with particular consideration being given to the potential

effects of an increase in discharge. Therefore, we broke our research into two components: the influence of discharge on the physical habitat, and the overall effect of discharge and physical habitat on trout populations.

We felt that traditional methodologies available to predict changes in trout populations due to changes in discharge were not adequate for this system as many important factors, such as water temperature, are not included within these methods. Instream flow methodologies are not universally applicable, and often do not meet tests of their validity (see Fausch et al. 1988, Scott and Shirvell 1987, Mathur et al. 1985, Mosley 1985, and Annear and Conder 1984 for reviews). The instream-flow-incremental-methodology (IFIM) (Estes and Osborn 1986, Bovee 1982, Bovee and Milhous 1978, Bovee and Cochnaur 1977) bases its estimate of minimum flow requirements primarily on PHABSIM (physical habitat simulation), which uses microhabitat preference curves for the species of fish in question to determine their habitat needs. The reliance on preference curves means that frequently many species of fish, and life history stages of fishes, are not accounted for in the calculations (Annear and Conder 1984). Determining these preference curves can be costly and time consuming. The WUA (weighted useable area), based on cross-sectional area, water depth, and water velocity preferences (Newcombe 1981), generally assumes that increases in WUA will correspond with fish habitat requirements. However, this technique has sometimes been demonstrated to have a very low correlation with trout standing crop, especially when habitat features such as water temperature are potentially

limiting (Conder and Annear 1987). The Tennant method (Tennant 1976) tends to ignore to a large degree the biological component to river systems, and is based solely on the percent of average flow, where 30 % is the recommended flow required to maintain a viable fishery, and 10% is recommended as a minimum short-term flow. It has been suggested that it might be a good starting point for examining instream flow requirements (Annear and Conder 1984). The effects of its flow recommendations could affect different river systems very differently because it does not take into account any biological or ecological data specific to the river in question.

Many physical habitat features may influence trout populations (Table 1), and discharge has been shown to exert control over a number of these features, including habitat unit morphology (Leopold et al. 1964, Leopold and Wolman 1957, Leopold and Maddock 1953, Newcombe 1981). Both adult brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) prefer deeper pool habitat units rather than shallower, swifter riffles, although their preferences vary and depend on many factors (Gowan et al. 1994, Decker and Erman 1992, Gelwick 1990, Bisson et al. 1988, Bowlby and Roff 1986, Fausch 1984, Scott and Crossman 1973).

Water temperature, also influenced by discharge (Li et al. 1994, Adams et al. 1993, Voelz and Ward 1990, Ward and Stanford 1982, Ward 1974), is a limiting factor in the distribution and abundance of many fish species (Imhof et al. 1990, Magnuson et al. 1979). Brown trout and rainbow trout have similar water temperature preferences: between about 11°C to 19°C (Diana 1995). Optimum water temperature for brown trout

is approximately 13°C, with growth occurring at water temperatures from 4°C to 19°C; their upper incipient lethal temperature is around 25°C (Weatherley et al. 1991, Jensen 1990, Elliot 1990, 1988, 1985, 1981, 1975a, 1975b, Preall and Rigler 1989, Edwards et al. 1979). The upper incipient lethal for rainbow trout is around 26°C (Elliot 1994), and optimum water temperature for rainbow trout is between 11°C and 17°C (Filbert and Hawkins 1995, Papoutsoglou and Papapaskeva-Papoutsoglou 1978, Sperber et al. 1977). Therefore, the response of trout to an increase in discharge would depend, in part, on concurrent changes in water temperature and physical habitat.

Table 1: Summary of research on the relationship between physical habitat factors and trout populations (abundance, standing crop, etc.).

Abiotic Factor	Researcher	Results
Habitat space	Greenberg (1994)	-found juvenile brown trout moved out of pool habitats when predators were present and a decrease in discharge caused a decrease in the amount of available escape habitat.
Velocity	Rimmer (1985) Fausch (1984)	-higher water velocities require increased energy to forage than at lower velocities. -found a strong biotic-interaction component where dominant trout are able to stake out optimal velocity territory selected to maximize food resources and minimize their energy expenditure.

Table 1, Continued

Abiotic Factor	Researcher	Results
Substrate	Bozek and Rahel (1991a)	-presence of juvenile rainbow and brown trout related to gravel substrates. -spawning gravel related to presence of juvenile brown and rainbow trout. -juvenile trout also showed little dispersion from spawning gravel.
	Beard and Carline (1991)	
	Cargill (1980)	
Large woody debris (LWD) and instream cover	Crispin et al. (1993)	-addition of LWD effective for increasing salmon abundance and improving salmon habitat. -LWD created new plunge-pool habitat and more instream cover. -Increases in surface area and water volumes with more LWD. -relationship between salmon smolt abundance and LWD and debris jams. -instream cover used by juvenile rainbow trout to escape predation.
	McMahon and Holtby (1992)	
	Tabor and Wurtsbaugh (1991)	
Out-of-stream cover and increased solar radiation	Li et al. (1994)	-trout abundance highly negatively correlated to stream temperature and solar radiation.
	Tait et al. (1994)	
Water temperature	Filbert and Hawkins (1995)	-microhabitat selection in juvenile rainbow trout. -community composition (presence/absence of trout) related to water temperature. -behavioral temperature preferences. -decrease in trout populations with high (>21.4°C) maximum water temperature.
	Tait et al. (1994)	
	Li et al. (1994)	
	Baltz et al. (1991)	
	Rahel and Hubert (1991)	
	Christie and Regier (1988)	
	Baltz et al. (1987)	
	Cross (1987)	
	Bowlby and Roff (1986)	
	Magnuson et al. (1979)	
	Binns and Eiserman (1979)	

Table 1, Continued

Abiotic Factor	Researcher	Results
Dissolved oxygen concentration (DO)	Mundahl (1990)	-As temperature increases, DO decreases.
	Coble (1982)	-reduced fish abundance corresponding to sites with low DO in the absence of a temperature effect.
	Vannote and Ball (1972)	
	US Dept. of Health, Education and Welfare (1958)	

We performed our study on trout populations within the Deschutes River Basin at a habitat unit level. Habitat units are an acceptable level for studying trout efficiently (e.g. Hankin and Reeves 1988), and trout biomass has been found to be highly correlated with the surface area of pool habitat units (Bowlby and Roff 1986). Quantifying the relationship between trout and discharge based on changes in habitat units, as well as broaching the issue of changes in water temperature and its relationship with discharge, gave us an ecologically-based approach to understanding the influence of discharge on trout. In addition, it allowed us to examine a large study area quickly and efficiently.

METHODS

Study Area

The Deschutes River flows north through Central Oregon, ending at the Columbia River, and drains most of the eastern flank of the Central Cascade Mountains (Fig. 1). Its drainage area is approximately 27,200 km², making it the second largest watershed in Oregon (U.S. Bureau of Reclamation, 1993). It flows through a semi-arid region with some of its tributaries entering from more arid land (e.g. Crooked River, Little Deschutes River) and others entering from the Cascades (e.g. Tumalo Creek, Squaw Creek, Metolius River). In the Upper Deschutes River, impoundments and irrigation withdrawals significantly modify the river. Flow of the main stem is controlled by dams at two reservoirs upstream of Bend (Crane Prairie, and Wickiup).

Hydrographs dated from 1966 to 1994 for the regulated section of river downstream of Bend show higher winter and spring discharges and lower summer flows (Fig. 2a). Upstream of Bend, hydrographs are reversed from historical flows, with summer flows higher than winter flows (Fig. 2b). These highly regulated flows create relatively stable discharge in the Deschutes River study area mid-April through to October. Upstream of Bend, OR, after the confluence with the warm water river, Little Deschutes, the summer discharge of the Deschutes is approximately 51.0 m³/sec with a

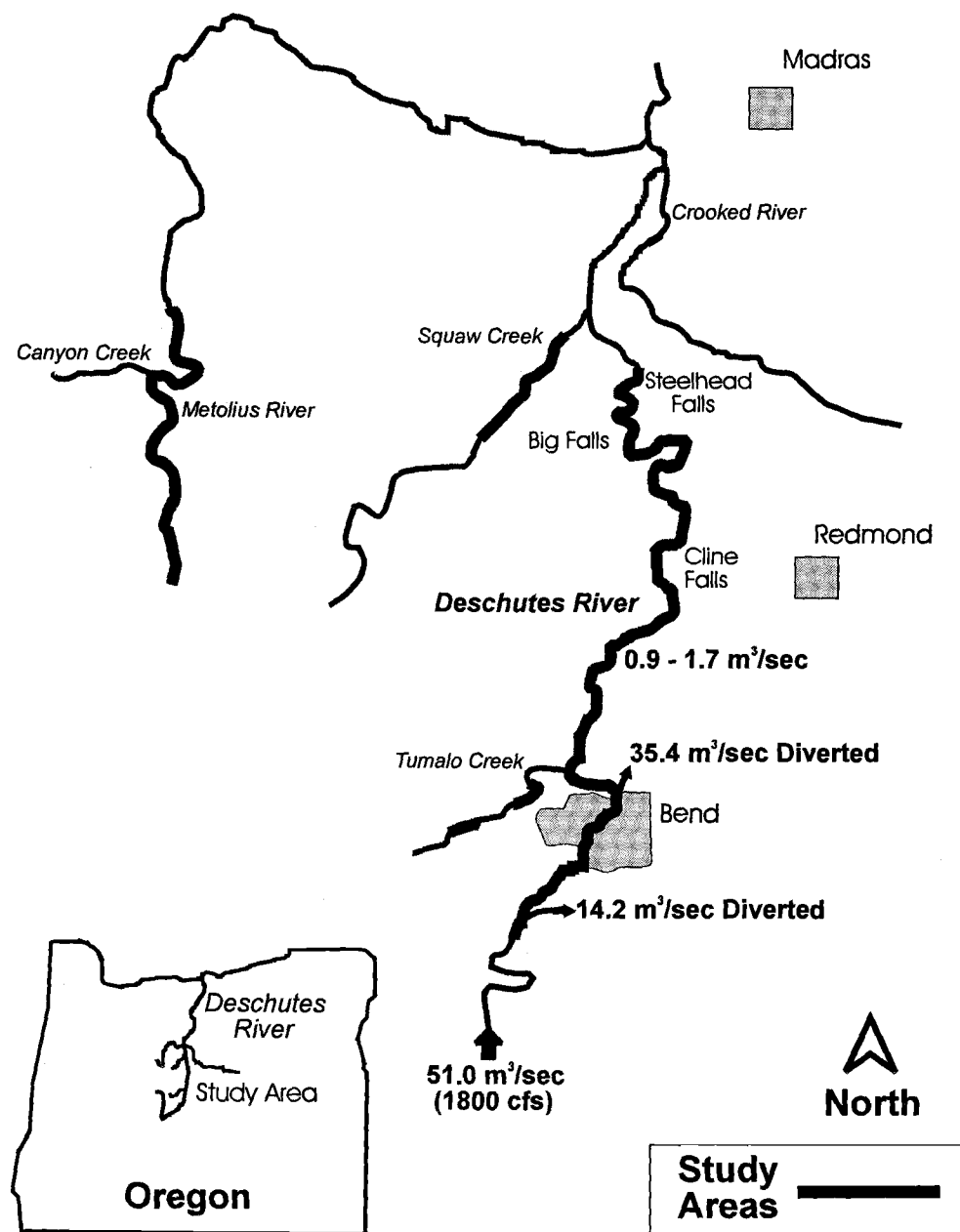


Figure 1: Map showing study area in the Deschutes River Basin, in Central Oregon. Deschutes River discharge is shown for upstream and downstream of irrigation diversions. Summer average irrigation diversion discharges are also shown.

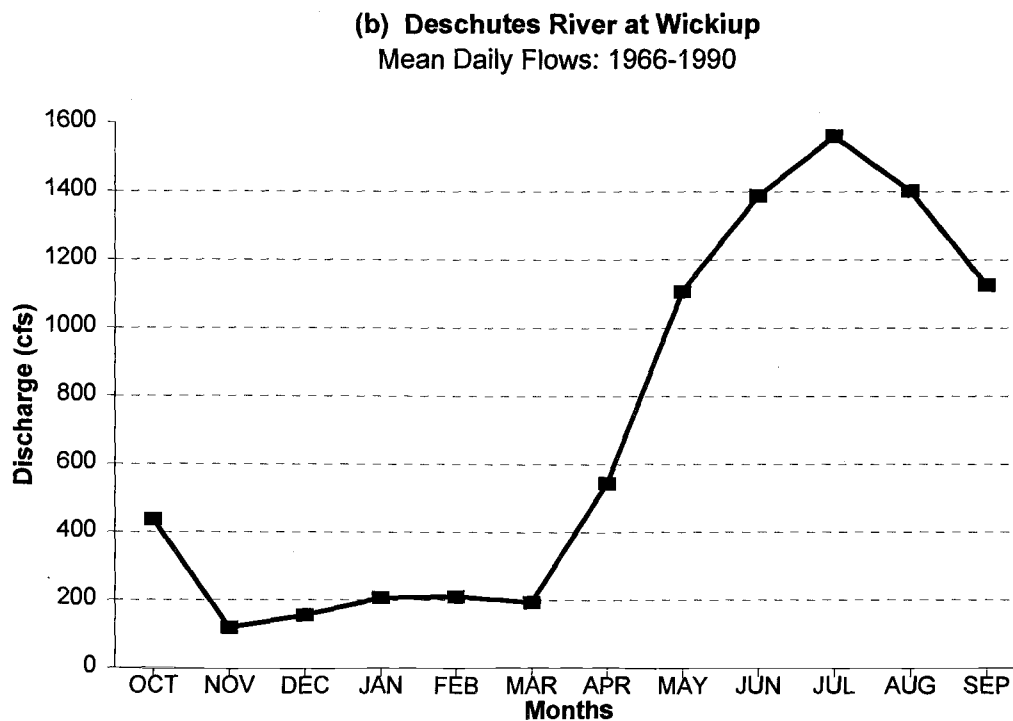
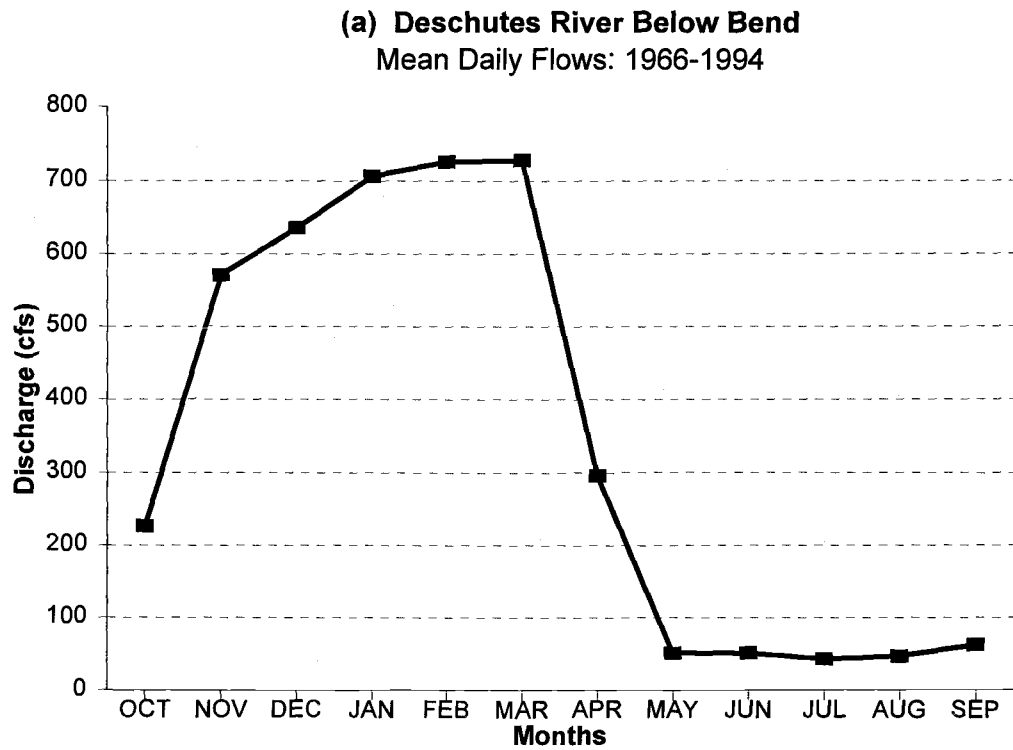


Figure 2: Hydrographs for the Deschutes River (a) Downstream, and (b) Upstream of main irrigation diversions. The upstream hydrograph shows peak flows in the summer months, opposite of natural river flows in this region.

summer near-surface mean water temperature of 16°C (Fig. 1). In passing through Bend, almost all water is diverted into irrigation canals, leaving 0.9 - 1.7 m³/sec in the channel. Approximately 50 km downstream there is a marked increase in flow from underground aquifers, and this increase in discharge coincides with a decrease in temperature from over 29°C to around 12°C.

Historically, this section of the Deschutes was home to bull trout (*Salvelinus confluentus*), rainbow trout, and mountain whitefish (*Prosopium williamsoni*). The upper limit of steelhead trout (*Oncorhynchus mykiss*) was Big Falls (Fig. 1) (Nehlsen 1995). Currently, this section of the Deschutes contains several introduced species including brown trout, tui chub (*Gila bicolor*), three-spine stickleback (*Gasterosteus aculeatus*), brown bullhead (*Ameiurus nebulosus*), largescale sucker (*Catostomus macrocheilus*), smallmouth bass (*Micropterus dolomieu*), as well as the native rainbow trout and mountain whitefish; bull trout are no longer present in the Upper Deschutes Basin above Steelhead Falls. Present day trout numbers are much reduced from historical abundances (Nehlsen 1995). There has been no trout stocking in the main river since 1977 (ODFW 1993). Tumalo Creek, a colder tributary of the Deschutes which enters close to Bend (Fig. 1), contains excellent spawning gravel used by brown trout in the fall (ODFW 1993). Tumalo Creek also contains bull trout and introduced brook trout (*Salvelinus fontinalis*) in addition to rainbow trout.

Influence of Discharge on Physical Habitat

Aerial Videography

Effect of discharge on the quantity and distribution of physical habitat was examined using remote sensing. Four different river stages were filmed using a sony Hi8 Handycam video recorder mounted vertically on a helicopter: (1) Feb. 15—28.3 m³/sec; 2) April 17—17.0 m³/sec, May 16—7.0 m³/sec, July 30—1.3 m³/sec). Flow records and water diversion schedules were examined in order to plan the flight dates. These stages were chosen to provide a broad range of discharge conditions, and to include the target flow of 7.0 m³/sec as recommended for this section of the Deschutes River by the Oregon Department of Fish and Wildlife (ODFW 1993).

Use of a helicopter, and its associated maneuverability, allowed the camera to remain vertically positioned over the river as the pilot followed the meandering flight line. It also allowed us to fly relatively slowly, and at a low altitude in order to obtain clearer images. Vertical positioning of the camera is required in order to measure depicted objects accurately on the video (Avery and Berlin 1992). Flights were scheduled for mid-day to decrease shadowing in the image. The Hi8 handycam was set to manual focus at infinity with a shutter speed of 1/4000. During the flight, altitude was monitored and adjusted by consulting topographic maps, so that the camera remained approximately 360 m above the water surface. This produced visible images at

an approximate scale of 1:800. At this scale, pixel resolution is approximately 0.5 m^2 ground area. This means that an object would need to be a minimum of 0.5 m^2 in size to be detectable on the videos.

A differentially-corrected global positioning system (GPS) was present in the helicopter during the flights, which allowed us to know our accurate UTM coordinate position. At regular intervals, UTM coordinates were read aloud and recorded onto the audio track of both video tapes. This provided differentially-corrected reference points on the video tapes so that we did not have to rely on the presence of landmarks.

Ground Truthing

Measurements made on the visible video images were ground truthed in summer 1996 in order to assess the accuracy of the video image. Ground measurements were made at each of the bridges crossing the river. These measurements included bridge width, channel width at the bridge, and bridge length from abutment to abutment. Other objects such as culverts passing under bridges, pipes crossing the river, and structures in or around the river were also measured. This allowed for both a determination of scale, and calibration of other river measurements. In addition, these ground locations were recorded onto a GPS system to coordinate video analysis. Selected channel units were also delineated and measured on the ground in order to assess the accuracy of the video delineation and measurements.

Video Analysis

Habitat delineations were done hierarchically (e.g. Bisson and Montgomery 1996, Rosgen 1994, Hawkins et al. 1993, and Bisson et al. 1982). Kershner and Snider (1992) discuss the importance of delineating habitat units versus smaller or larger designations, because they have functional significance to fish habitat use and life-history requirements. Habitat units were delineated as riffles, pools, or rapids/cascades according to their surface-water smoothness and velocity, as well as their apparent shallowness. Analysis of the videos was assisted by the use of a Targa 2000 digitizing board. The Targa allowed an individual frame from the video to be examined and measured with reasonable accuracy. Features that distinguish channel units were sometimes easier to see with a moving frame than on a still, so both were used in the delineation process. Apparent shallowness was also used to delineate riffles from pools, especially for the low-flow condition where less whitewater was noted in riffle units which nonetheless had numerous rocks protruding from the surface of the water.

The 60 km study area was broken into reaches based on geomorphic features (Fig. 3). Stream segment breaks were first determined from topographic maps showing gradient, terrace morphology and valley slope, waterfalls, and tributary inflows following methods used by Rosgen (1994), and from reach survey data from ODFW (unpublished). We then checked our reach breaks during fly-over, and recorded major reach features directly onto the audio track of the videotapes during the flight.

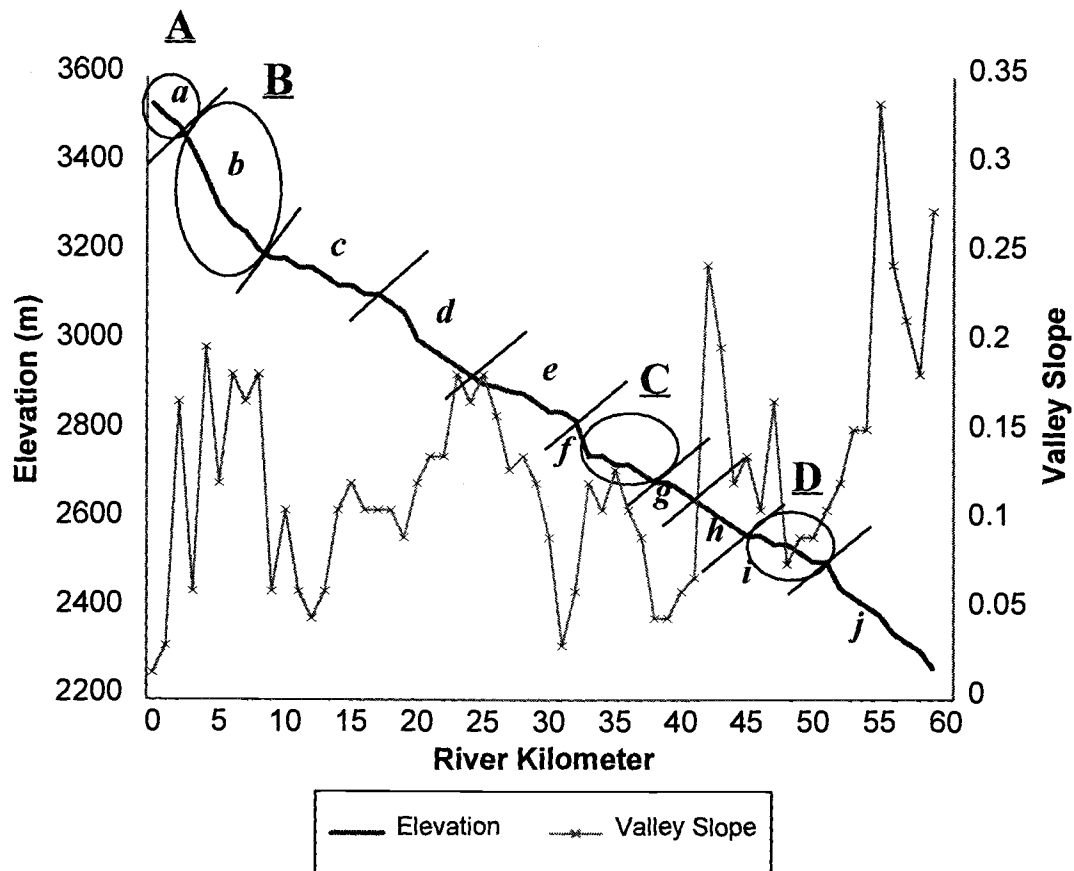


Figure 3: Longitudinal profile of the Deschutes River study area, showing changes in elevation and valley slope by river kilometer, with numbers ascending in a downstream direction. Underlined letters label the subsections we delineated on the videos, and italicized letters label individual reaches.

Three distinctive reach types were present among the 10 reaches found in the study area; represented by low (type I), medium (type II), and high (type III) gradients (relative to this study) of approximately 0.4 %, 0.7 %, and >0.95 %, respectively (see Fig. 3). Gradients were determined from elevation changes in the river. The changes in valley slope were not very consistent throughout the any of the reaches (Fig. 3). We did

not measure the entire section of river, but rather selected four subsections which characterized the three different reach types described above. The same segments were delineated and measured on each video in order to obtain a representative sample from each of the available reach types (Type I, II, and III; see Table 2). Using this method, approximately 26% of the entire study area was delineated and measured for each discharge level.

Table 2: Characterization of reaches along the Deschutes River study area. Reach type I, II, and III represent low, medium, and high gradient reaches, respectively. A subsection of the study area was selected based on a representative sample from these reach types.

Reach Label	Length (m)	Gradient (%)	Reach Type Category
<i>a</i>	2,350	0.85	II
<i>b</i>	5,150	1.43	III
<i>c</i>	10,000	0.40	I
<i>d</i>	7,000	0.78	II
<i>e</i>	7,500	0.41	I
<i>f</i>	4,800	0.73	II
<i>g</i>	2,700	0.34	I
<i>h</i>	4,500	0.58	II
<i>i</i>	6,500	0.38	I
<i>j</i>	8,000	0.86	III

Measurements made from the four videos were corrected for scale using the ground-truthed measurements. A natural log transformation was then applied to the channel unit width, length, and surface area data to normalize measurements and equalize variances. Measurements for each reach type, from each video, were compared using multiple sample t-tests, and regression analysis was used to determine how channel unit width and surface area were related to discharge for each river section.

We compiled all of our regression equations for width, length, and surface area and weighted them according to the percentage of the river represented by each reach type in order to interpolate the overall change in the river. For example, we took the regression equation for habitat unit width derived for reach type I (see Table 5, p. XX), and multiplied that equation by 0.456, which represents the percentage of the study area characterized by type I conditions. Likewise, the equation for type II width changes with discharge was multiplied by 0.316, where type II conditions are present in 31.6% of the river. And finally, the reach type III regression equation was weighted by 0.228, where type III conditions are present in roughly 22.8% of the study area. Summing these three weighted equations we get an overall regression equation which relates to the overall change in channel width for the entire river

Initially, measurements were made on a digitized image; however, this proved very time consuming and required almost a megabyte of computer storage space per video frame digitized. Coarse measurements of habitat unit surface area were obtained using the video monitor screen for display; and then corrected to the appropriate scale

based on our ground truthing. This method of measurement could introduce bias due to a slight horizontal compression of the image on the monitor screen. Since the flights followed the river fairly accurately however, the image was typically vertical on the monitor screen. Therefore, the distortion would be roughly the same for all images. Additionally, due to the nature of vertical aerial photography, there is a radial distortion outwards from the true centre of the image (Avery and Berlin 1992). Therefore measurements were made as close as possible to the centre of the image. The distortion error was approximately the same for all images, so physical habitat changes for each of the flight videos could be compared.

Exact measurement of habitat units by digitizing each image frame would have had its own biases, and would have required far more computer memory and time. The digitized image's resolution is the same as on the monitor screen, and would still have radial distortion. In addition, we found that watching the video as a moving image improved our ability to delineate habitats, whereas digitizing the image removes the possibility to view the river animated.

Water Temperature Response to Discharge Changes

Effect of discharge on water temperature was tested by comparing summer water temperatures in the main study area (flows between 0.9 - 1.7 m³/sec), and upstream of the main study area (34.0-51.0 m³/sec), with water temperatures in the irrigation canals

(flows ranging from 3.1 - 19.8 m³/sec). All sites were fairly similar except that the canals generally have less or no riparian zone so there is less shading of the water.

Twenty-six stowaway water temperature data loggers were placed in the Deschutes River and in the canals (Fig. 4). All stowaways and thermometers were calibrated with each other using an ice water bath. Stowaways were placed upstream from each irrigation diversion, at each diversion, and then periodically at public access along the river and the canals downstream from the diversions. These stowaways were placed in the water in the second week of June and removed the last week of August, 1996. Each was checked on a regular basis to ensure it was still appropriately placed in the water.

All 26 stowaways were fixed by string to an object near the bank and were positioned in a relatively shade-covered area near to the water surface. In locations where there was no bankside vegetation or other object to provide shade, we attempted to block direct sunlight from reaching the stowaway by constructing a shield with rocks. Four additional recording thermographs were used to test the difference in water temperature between the surface and the bottom of deep pools. Two deep pools were selected and the stowaways were affixed near the surface and at depths of approximately 2.5 m and 3 m.

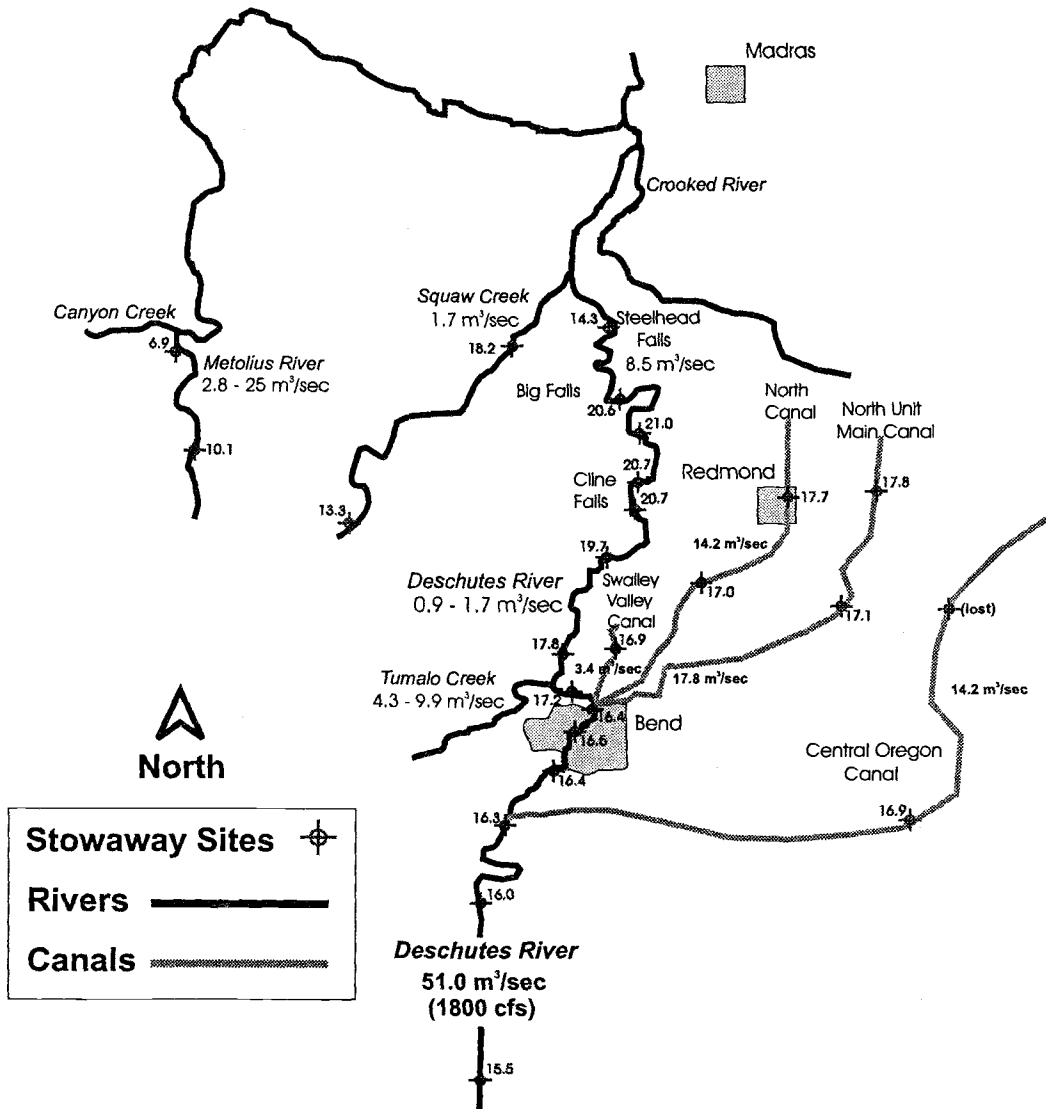


Figure 4: Map of Deschutes River study area, showing the location of Stowaway™ thermographs in the rivers, and in four of the irrigation canals. Average water temperature for each site is given.

Influence of Discharge on Trout Populations

Study Design

Because we felt that water temperature might be an integral part of the system responding to discharge changes, we tested the separate effects of discharge and water temperature on trout populations. Sites with a variety of water temperature and discharge regimes, but otherwise similar physical habitat features were located in the Deschutes and parts of Tumalo Creek, Squaw Creek, and the Metolius River (Fig. 5). Other rivers and streams were considered, such as the Crooked River (Fig. 1), but they had different water quality or other features that would have been confounding to our study design.

In total we examined 126 habitat units distributed among 23 different site areas which had public access. We grouped sites into two categories each with three levels of water temperature and discharge (Table 3), based on physical survey data for discharge and seasonal water temperature data from the recording thermographs. Due to the absence of low/low and high/high blocks (Table 3), category effects were compared using one-way analysis of variance (ANOVA), the first comparing water temperatures at medium discharge, and the second compared discharge for medium water temperatures. Therefore, the separate effects of water temperature and discharge could be examined.

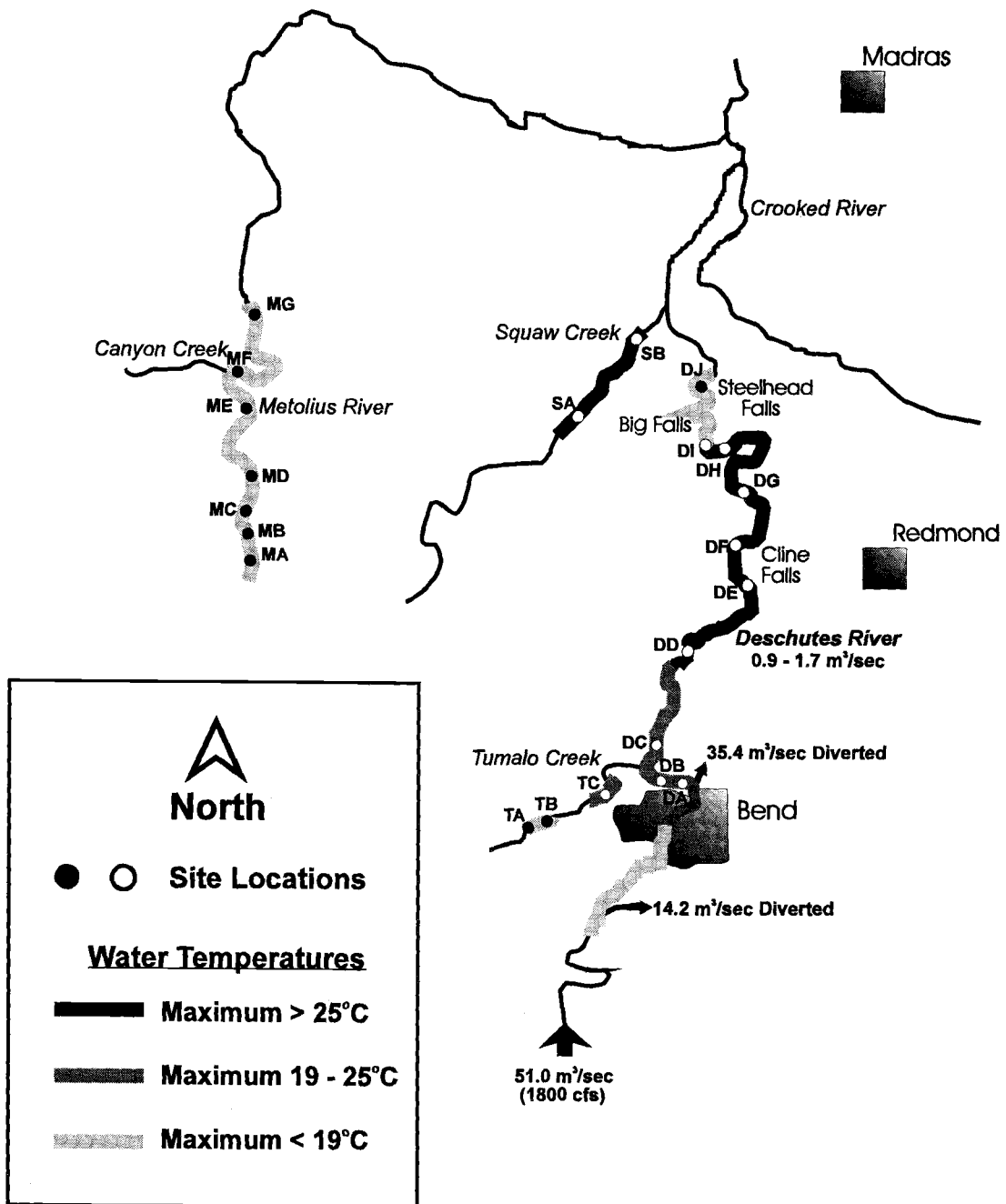


Figure 5: Map showing trout survey sites located on the Deschutes River, the Metolius River, Squaw Creek, and Tumalo Creek. Maximum water temperatures as recorded Summer, 1996, are displayed for the study areas.

A power analysis found that a minimum of 20 samples were required from each category to adequately compare means.

Table 3: Characterization of sampling sites in the Deschutes River Basin.

Water Temperature (°C) Level		Discharge (m ³ /sec)		
		Low (< 1.7) (43 sites)	Medium (1.7 - 3.4) (44 sites)	High (> 3.4) (39 sites)
Low (mean <10 max <14)	(28)	no sites were found	TB (4) MA (7)	TA (11) ME (4) MF (1) MG (1)
Medium (mean 10-19 max 14 - 24)	(50)	DA (4) DB (6)	DC (2) TC (15) MB (1)	DJ (13) MC (2) MD (7)
High (mean >19 max >24)	(48)	DD (4) DE (6) DF (14) SB (9)	DG (2) DH (1) DI (1) SA (11)	no sites were found

D= Deschutes Sites (A-J), T= Tumalo Sites (A-C), M= Metolius Sites (A-G), S= Squaw Sites (A-B)
Numbers within () indicate the number of habitat units examined within the site location.

Ten study sections along the Deschutes (*DA* through *DJ*) (Fig. 5), had discharges mainly in the low and medium categories, and temperatures in the medium to high categories. Three sections were located in Tumalo Creek (*TA*, *TB*, *TC*), a cold water system with water temperatures ranging from 4.5°C to 14.5°C. Site *TA* had a mean

water temperature of 6.2°C and a discharge of approximately 5.0 m³/sec; therefore, it was placed in the low temperature/high discharge category (Table 3). Sections *TB* and *TC* both had medium discharges and different water temperatures and therefore fell into different categories in our study design (Table 3). Squaw Creek had a discharge ranging between 0.5 m³/sec to 2.0 m³/sec. Mean summer water temperatures were 18.2°C, with a range from 9.2°C To 28.5°C. Three sections were located on Squaw Creek. These all had high temperatures, but fell into different discharge categories. The Metolius River study sections were located within the first 9 km of the river (Fig. 5). The Metolius River derives much of its flow from numerous underground springs which quickly increase the discharge in a short length of river. Discharge within our study sites on the Metolius ranged from 1.4 m³/sec to 29.4 m³/sec. Water temperatures averaged between 6.9°C and 10.1°C in the study area.

Fish Surveys and Physical Habitat Data Collection

Fish surveys were conducted in the summers of 1995 and 1996. Sites were selected along the Deschutes River, Squaw Creek, Tumalo Creek, and the Metolius River as detailed above. At each site we examined all of the pool units within one water temperature and discharge regime that were accessible without crossing private property boundaries. Mostly pools were surveyed within a site, however, we also incorporated one or two of the adjoining riffle habitat units where possible. At each site, for each channel unit, we made both physical habitat measurements and conducted fish surveys.

Snorkel-surveys were used to count all species of fish. We separated trout into five size classes, and enumerated each group. Size class 0 included young-of-the-year trout less than one finger in length (3 - 10 cm, mean length approximately 7 cm). Size class 1 trout were less than a hand-length (10 - 16 cm, mean length 14 cm). Size class 3 trout were larger than a hand-length, and smaller than half-way from finger-tip to elbow in length (16 - 25 cm, mean length of 20 cm). Size class 4 were trout were smaller than finger-tip to elbow, with a mean length of 30 cm (25 - 35 cm), and size class 5 were any trout larger than half an arm length (>35 cm, mean length 40 cm). Non-trout species were not differentiated by size.

Each survey was conducted by a team of 2-3 people equipped with a roughened plastic slate and pencil. A minimum of two thorough longitudinal searches through the study site were conducted. In typical units with a width of less than 20-30 m, one person counted the left half of the habitat unit by swimming side to side through that segment and one the right half. When the river was especially wide, or visibility low, three divers divided up the river with one in the center. We found that counts often were different when going upstream versus downstream, therefore we always made at least one count while swimming upstream and one while going downstream. The highest count was used in all cases.

Snorkel-surveys have been shown to provide an accurate count of trout (Hillman et al. 1992, Bozek and Rahel 1991b, Northcote and Wilkie 1963); however, we were very cautious when fish were abundant or water was turbid. In sites where fish

abundance was high, we double-checked our individual counts as follows. Several passes were made until we felt comfortable with our counts. In a final count of all the fish we did not separate them into size classes or species. This allowed us to double-check the total number of fish against the tally of species and size classes. Because we were unable to locate or accurately count fish in turbid waters, habitat units thus affected were left out of our analysis. Electrofishing was not used because fish populations in much of the study area are already severely affected by low flows and high water temperatures (Nehlsen 1995, ODFW 1993).

Trout populations were quantified by three variables: abundance (total number of trout), density (number per unit volume), and an index of relative biomass (IRB). IRB was determined using mean length-weight relationships (Table 4) as given in Carlander (1969), based on trout counts multiplied by the mean lengths of each size class. We expressed this in two forms: IRB, and IRB per unit volume ($\text{cm} \cdot \text{m}^{-3}$); based on the area and volume of the habitat unit being surveyed.

This index (IRB) was used because we questioned whether a numerical abundance of trout would necessarily reflect more suitable habitat. Total number of trout may be low for a site, but at the same time this site could be controlled by a few larger, dominant fish who control the better habitat. In addition, our calculated trout IRB by volume measurements help to equalize the differences in volume found among the sampled habitat units.

Table 4: Trout length (mm) - weight (g) relationships from Carlander (1969). Bull/Brook equation is derived by averaging coefficients from each species.

Trout Species	Length - Weight Regression Equation
Rainbow Trout	$\log(\text{weight}) = -4.817 + 2.965 \cdot \log(\text{length})$
Brown Trout	$\log(\text{weight}) = -4.734 + 3.030 \cdot \log(\text{length})$
Bull/Brook Trout	$\log(\text{weight}) = -4.968 + 3.000 \cdot \log(\text{length})$

Physical habitat variables that we measured quantitatively included water temperature, discharge, and channel unit width, depth, and length. Surface water temperature was measured at each site in shade created by the observer. We recorded temperature at the center, and near the right and left banks. In addition, 26 recording thermographs were placed throughout the study area for the period beginning the first week in June until the last week in August, 1996, as described above (Fig. 4).

Discharge was measured immediately upstream or downstream from a sampled habitat unit using a Swoffer™ digital flow meter in all sites. A suitable location was determined based on both of the discharge calculation assumptions: of uniform flow across each cross-section area; and with generally sub-critical flow at the surface. In some locations a suitable place could not be found due to the swiftness of the river and at these sites discharge was estimated from surface velocity coupled with depth and width measurements.

Channel unit measurements (width and length) were made by visual estimates and with a measuring tape. Average width of the channel unit was estimated, or determined by an average of several transects. Visual estimates were calibrated by measuring roughly every three to four sites. Repeatedly, visual measurements were accurate to 95-100% of actual measurement. Depth, both mean and maximum, were recorded for each pool. Maximum depth in deep channel units was measured with a telescoping surveyor's rod and in shallower channel units measured with other available measuring devices. Mean depth was determined from the average of four depth measurements made in different sections of the pool. These measurements were done at a points halfway between the deepest part of the pool unit and the boundary edge of the pool unit (Fig. 6). This measurement technique assumes a conical shape to a pool unit, and if there are no plateaus with deeper sections beyond them, should quickly and accurately estimate mean depth. In riffles, a number of measurements, spaced throughout the habitat unit were averaged to determine mean depth.

Qualitatively measured variables included turbidity, instream cover, embeddedness, and substrate. An estimate of mean turbidity for each site was ranked on a 3-point scale from low-med-high: greater than 5 m visibility, approximately 3-5 m visibility, and less than 2 m visibility, respectively. An estimate of high turbidity meant the fish count was unlikely to be very accurate and could also have additional effects on the trout populations which we did not have the means to quantify. In this case, we did not continue to survey at this site unless water conditions changed on a subsequent visit.

Instream cover was rated on a 5-point scale from low to high. This was qualitatively estimated based on our knowledge of the other sites sampled. We did this primarily to determine whether instream cover affected fish counts. Large woody debris was not specifically quantified at each site, because our sites typically had none, or the few sites that did had such an abundance that we would not have been able to count it accurately in a reasonable length of time. Therefore, we quantified the contribution of the large woody debris to in-stream cover and recorded its abundance qualitatively (none, few, high abundance).

Dominant and subdominant substrates were identified for each channel unit at each site by visual estimation after fish counts were completed. Dominant substrate was the most common substrate found within the habitat unit, and subdominant was the second most common. We separated substrates into ten size classes based on a modified Wentworth scale (Hynes 1970): 1) silt; 2) sand; 3) gravel; 4) large gravel; 5) cobble; 6) rubble; 7) boulder; 8) large boulder; 9) bedrock; and 10) basalt (lava rock - typically of particle size similar to bedrock).

We estimated the proportion of large substrate particles (size class 5 and up) covered with fine substrate particles (size class 1 or 2). This was rated on a 5-point scale (5 categorized the most substrate surface showing) where low embeddedness (5) meant that larger substrate was mostly uncovered (less than 5% of surface), followed by:

4) 5-25%, 3) 25%-50%, 2) 50%-75%, and high embeddedness (1) where over 75% of the surface of a large substrate particle was buried in fine sediments (Hamilton and Bergersen, no date).

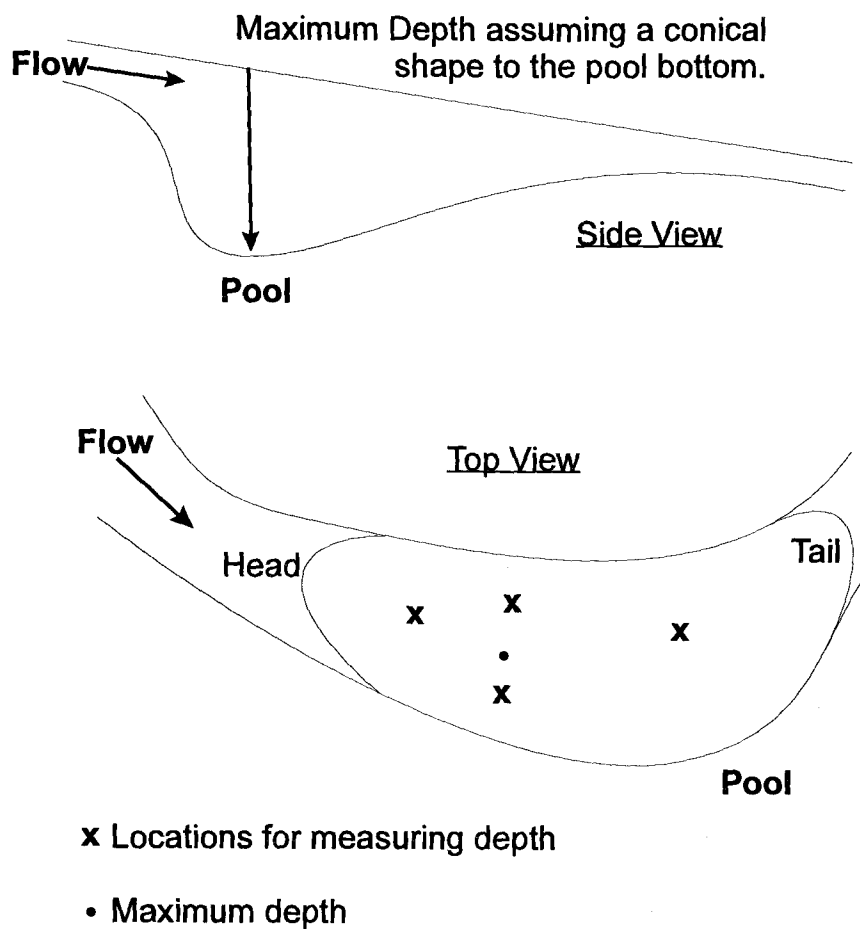


Figure 6: The measurement of average depth within a pool habitat unit. Both a top view, and a side view of the pool are depicted.

Analysis of Trout Population Data

Because sites which had both low discharge and low water temperature and sites which had both high discharge and high water temperature were not found we used one-way analysis of variance (ANOVA) to examine variance of trout populations due to water temperature and discharge. In both cases either discharge or water temperature was held constant (using the sites which fell into the medium-level category); thus, we established replication of habitat conditions in order to generate means and variances for each site-group. This allowed us to get an overall picture of how discharge and temperature influence trout populations over a stream-reach.

We then examined the relationship, using multiple linear regression analysis, between physical habitat and trout populations. This allowed us to observe how physical habitat unit differences affect trout abundance, density, and an index of relative biomass (IRB). All fish variables were transformed using either a logarithm or square-root transformation, to normalize the data and equalize variances.

We used cluster analysis, based on nearest neighbor euclidean distance, to compare the similarity between habitat units. We included all physical habitat variables except water temperature and discharge, as well as the total abundance of non-trout fishes in order to examine the similarity in trout habitat between all habitat units surveyed. This analysis examined how other habitat variables were potentially confounding the influence of water temperature and discharge on trout populations.

RESULTS

Influence of Discharge on Physical Habitat

Changes in Physical Habitat Distribution

The distribution of habitat units varied in a non-linear, and unpredictable manner with changes in discharge (Fig. 7). Reach type I, with low gradient and generally a low degree of constraint, shows little increase in cascade/rapid habitat with an increase in discharge (Fig. 7a). It also has an unpredictable, and non-linear, change in the percentage of pools and riffles with a change in discharge. Reach type II, with medium gradient, but varying degrees of constraint shows a greater increase in cascade/rapid habitat with an increase in discharge than type I (Fig. 7b). The percentage of pool habitat decreases with an increase in discharge from almost 60% to less than 40%. This decrease occurs with a corresponding increase in riffles from around 35% to almost 50%, as well as the increase in cascade/rapid habitat (Fig. 7b). In the high-gradient reach (type III), which generally shows a greater degree of constraint than the other two reach types, we see a much larger increase in the percentage of cascade/rapid habitat with a corresponding increase in discharge (Fig. 7c). Coupled with this increase, we find a decrease in both riffle and pool habitats between 7.0 m³/sec to 28.3 m³/sec. Between

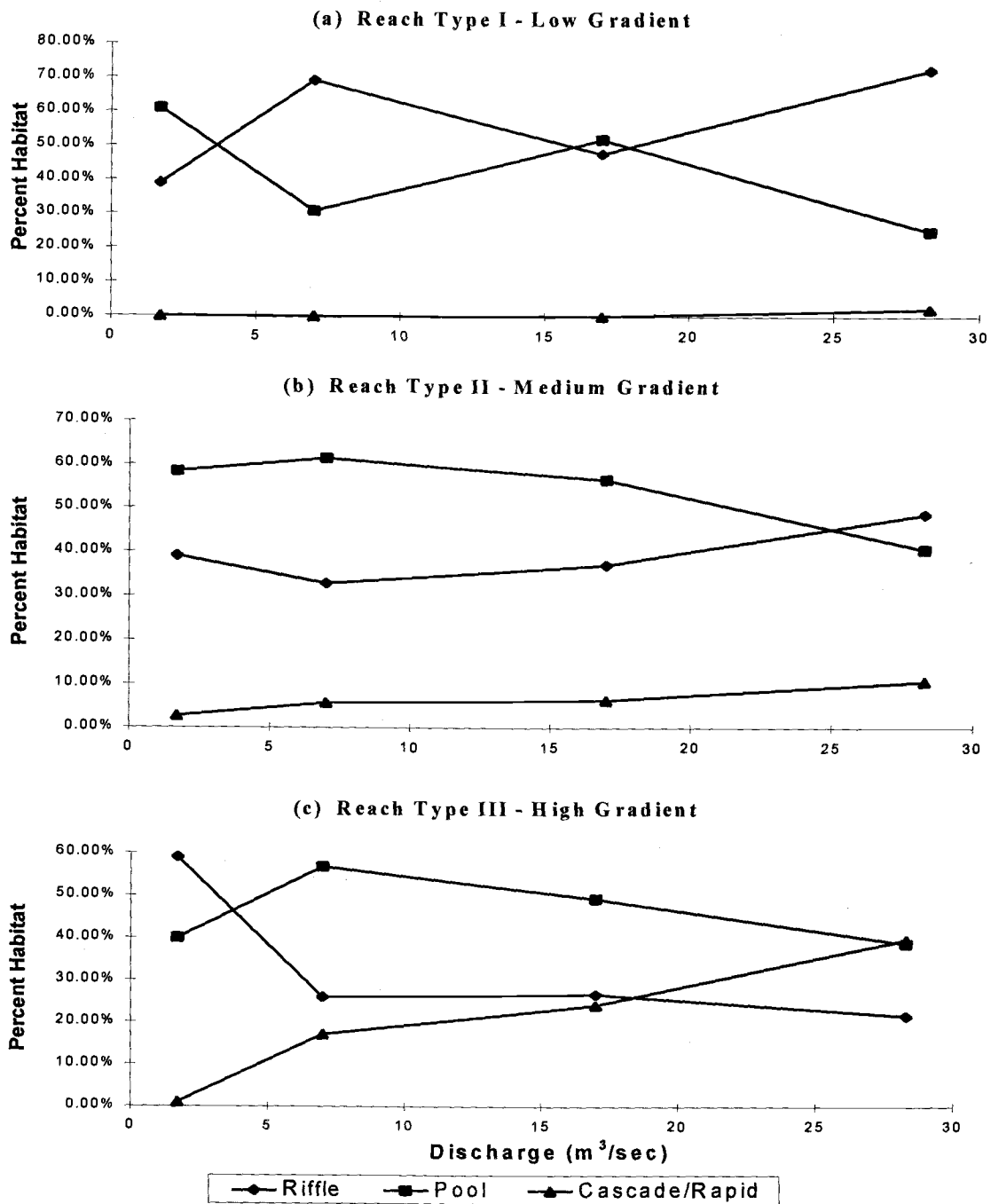


Figure 7: Distribution of habitat surface areas (by percentage) at each of the four different discharge levels for the three reach types present in the Deschutes River study area (a) low gradient, (b) medium gradient, and (c) high gradient. Percent habitat was determined through delineating and measuring habitat units present within a subsection of each reach type.

1.7 m³/sec and 7.0 m³/sec there is an increase in pool habitat with an increase in discharge, and a decrease in riffle habitat from almost 60% to under 25% (Fig. 7c).

Changes in Physical Habitat Abundance

Discharge also affected the amount of habitat available to fish by altering the overall channel width and habitat unit lengths (Fig. 8). A comparison of means using multiple sample t-tests showed that pools, riffles, and cascades generally change width, length, and surface area differently in response to changes in discharge; therefore, we calculated separate regression equations for each type of habitat unit within each reach type (Table 5). Individual reach types demonstrated differing tendencies towards increased width, length, and surface area with an increase in discharge, where width was always more correlated with discharge than surface area or length (Table 5). Habitat unit width, based on grouping all width measurements, was significantly correlated with discharge ($r= 0.593$, $p=0.0001$, $n=1309$):

$$\ln(\text{width}) = 1.368 + 0.229 \cdot \ln(\text{discharge}).$$

Habitat unit surface area was also correlated with discharge, although not as highly as was width ($r= 0.369$, $p=0.0001$)—with the equation:

$$\ln(\text{surface area}) = 4.358 \cdot (\text{discharge}^{0.0577}).$$

The relationship between discharge and habitat unit length was significantly correlated for each reach type, however, the actual correlations were lower than for the other features (I: $r=0.13$, II: $r=0.2$, III: $r=0.17$; $p<0.001$).

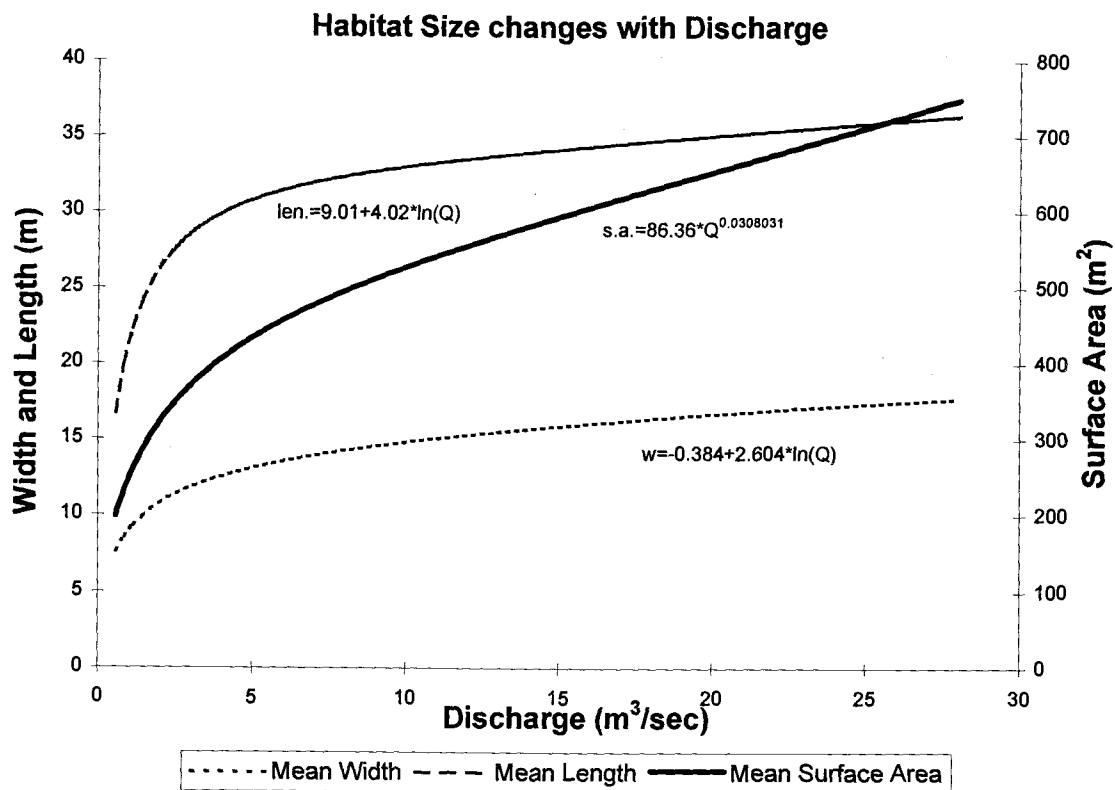


Figure 8: Weighted regression equations for changes in habitat unit width (w), length ($len.$), and surface area ($s.a.$) with an increase in discharge. These equations, which apply to the entire study area, are interpolated from regression equations calculated for all habitat types within each of the three reach types (described in text).

Table 5: Regression equations (best fit) for physical habitat unit morphological changes with discharge (Q). All measurement data (length, width, surface area) were transformed by a natural logarithm transformation. Equations are only given where $p < 0.05$.

Channel Unit and Reach Type	Regression Equation ($p < 0.05$)	Correlation with Q (discharge) (r)	% of variation explained (r^2)
Reach Type I - Width			
Pool (P) Width	$\ln(\text{width}) = 1.877 + 0.148 * \ln(Q)$	0.49	23.70
Riffle (R) Width	$\ln(\text{width}) = 1 / (0.337 + 5.72/Q)$	0.61	37.46
Cascade/Rapid (C) Width	no relationship ($p > 0.05$)	n.a	3.07
Pool + Riffle Width	$\ln(\text{width}) = 1 / (0.35 + 4.38/Q)$	0.55	30.26
P + R + C Width	$\ln(\text{width}) = 1 / (0.35 + 4.17/Q)$	0.51	25.70
Reach Type I - Surface Area			
Pool Surface Area	$\ln(\text{s.area}) = 1 / (0.151 + 1.115/Q)$	0.40	16.34
Riffle Surface Area	$\ln(\text{s.area}) = 1 / (0.149 + 1.61/Q)$	0.46*	21.33
C/Rapid Surface Area	no relationship ($p > 0.05$)	n.a	n.a
Pool + Riffle Surface Area	$\ln(\text{s.area}) = 1 / (0.150 + 1.355/Q)$	0.43	18.64
P + R + C Surface Area	$\ln(\text{s.area}) = 1 / (0.150 + 1.25/Q)$	0.38	14.39
Reach Type I - Length			
Pool Length	$\ln(\text{length}) = 1 / (0.27 + 1.51/Q)$	0.20	4.12
Riffle Length	no relationship ($p > 0.05$)	n.a	n.a
C/Rapid Length	no relationship ($p > 0.05$)	n.a	n.a
Pool + Riffle Length	$\ln(\text{length}) = 1 / (0.276 + 1.276/Q)$.13	1.77
P + R + C Length	no relationship ($p > 0.05$)	n.a	n.a

Table 5, Continued

Channel Unit and Reach Type	Regression Equation ($p < 0.05$)	Correlation with Q (discharge) (r)	% of variation explained (r^2)
Reach Type II - Width			
Pool Width	$\ln(\text{width}) = 1 / (0.36 + 3.22/Q)$	0.49	24.30
Riffle Width	$\ln(\text{width}) = 1.70 * Q^{0.0797573}$	0.62	38.43
C/Rapid Width	no relationship ($p > 0.05$)	n.a	n.a
Riffle + Pool Width	$\ln(\text{width}) = 1.79 * Q^{0.0699239}$	0.56	31.07
P + R + C Width	$\ln(\text{width}) = 1.82 * Q^{0.0668442}$	0.51	26.60
Reach Type II - Surface Area			
Pool Surface Area	$\ln(\text{s.area}) = 1 / (0.15 + 1.58/Q)$	0.43	18.33
Riffle Surface Area	$\ln(\text{s.area}) = 4.30 + 0.348 * \ln(Q)$	0.38	14.12
C/Rapid Surface Area	$\ln(\text{s.area}) = 4.12 * Q^{0.0638934}$	0.33	10.90
Pool + Riffle Surface Area	$\ln(\text{s.area}) = 4.49 * Q^{0.0582019}$	0.38	14.39
P + R + C Surface Area	$\ln(\text{s.area}) = 4.51 * Q^{0.0566757}$	0.37	13.50
Reach Type II - Length			
Pool Length	$\ln(\text{length}) = 1 / (0.25 + 3.05/Q)$	0.31	9.63
Riffle Length	$\ln(\text{length}) = 2.89 * Q^{0.0353982}$	0.14	2.06
C/Rapid Length	no relationship ($p > 0.05$)	n.a	n.a
Pool + Riffle Length	$\ln(\text{length}) = 1 / (0.27 + 2.16/Q)$.21	4.49
P + R + C Length	$\ln(\text{length}) = 1 / (0.28 + 2.19/Q)$	0.20	3.84
Reach Type III - Width			
Pool Width	$\ln(\text{width}) = 0.994 + 0.282 * \ln(Q)$	0.69*	48.23
Riffle Width	$\ln(\text{width}) = 1.33 * Q^{0.117917}$	0.69*	47.10
Rapid Width	$\ln(\text{width}) = 1.07 * Q^{0.143296}$	0.64*	41.32
Pool + Riffle Width	$\ln(\text{width}) = 1.33 * Q^{0.115749}$	0.70*	48.56
P + R + C Width	$\ln(\text{width}) = 1.34 * Q^{0.112836}$	0.68*	46.20

Table 5, Continued

Channel Unit and Reach Type	Regression Equation ($p < 0.05$)	Correlation with Q (discharge) (r)	% of variation explained (r^2)
Reach Type III - Surface Area			
Pool Surface Area	$\ln(\text{s.area}) = 3.81 * Q^{0.071312}$	0.44	19.73
Riffle Surface Area	$\ln(\text{s.area}) = 5.44 + 0.0012 * Q$	0.36	12.92
C/Rapid Surface Area	$\ln(\text{s.area}) = (2.15 + 0.00045 * Q)^2$	0.60	35.60
Pool + Riffle Surface Area	$\ln(\text{s.area}) = 4.99 + 0.046 * \sqrt{Q}$	0.39	15.11
P + R + C Surface Area	$\ln(\text{s.area}) = 5.23 + 0.0013 * Q$	0.42	17.80
Reach Type III - Length			
Pool Length	$\ln(\text{length}) = \exp^{(1.09 + 0.00013 * Q)}$.17	2.90
Riffle Length	no relationship ($p > 0.05$)	n.a	n.a
C/Rapid Length	$\ln(\text{length}) = 2.36 + 0.00148 * Q$	0.48	22.70
Pool + Riffle Length	$\ln(\text{length}) = (1.77 + 0.00009 * Q)^2$	0.12*	1.36
P + R + C Length	$\ln(\text{length}) = 3.08 + 0.00049 * Q$	0.17	2.75

* = lack of fit between simple regression model and data.

The above equations are based on actual measured changes to habitat unit width and length for each reach type (Table 5), but can be used to interpolate how the entire study area changes with an increase in discharge (Fig. 8). We added equations, weighted for the overall length of river they represent (detailed in the methods section), and determined how both width and habitat unit length were related to discharge (Table 6). These equations can then be applied to determine the expected change in habitat quantity with a change in discharge. Using these three equations we find that at a discharge of

1.7 m³/sec, the mean river width is 9.86 m. Actual measured river width from the 1.7 m³/sec flight video measurements worked out to 9.6 m. At a potential discharge of 7.0 m³/sec the interpolated mean river width is 13.95 m, representing a gain in total river surface area of:

$$\text{Mean width increase} = 13.95 - 9.86 = 4.09 \text{ m};$$

$$\text{Study area length} = 59,000 \text{ m};$$

$$\text{Surface area} = \text{length} \times \text{width} = 241,310 \text{ m}^2 (2.41 \text{ km}^2).$$

Table 6: Regression equations for width, habitat unit length, and habitat unit surface area by discharge for the Deschutes River study area. These equations are derived from interpolated changes in each habitat unit type by summing regression equations from Table 5, weighted by the percent of river they represent. P-values were less than 0.05 for each weighted regression equation.

Habitat Unit Morphology	Weighted Correlation Coefficient	Weighted Regression Equation for varying Discharges (Q) (p<0.05 for each weighted equation used)
Width	0.55	Mean Width = $-0.38 + 2.60 \cdot \ln(Q)$
Surface Area	0.38	Mean Unit Length = $86.36 \cdot Q^{0.308031}$
Length	0.17	Mean Unit Surface Area = $9.01 + 4.02 \cdot \ln(Q)$

Ground Truthing

Ground truthing of channel unit delineations at low-flow demonstrated that most riffle, pool, and cascade/rapid habitats were accurately delineated in the video.

However, we noticed that where basalt rock was present a channel unit could appear in the video to be very shallow, seeming as if many smaller rocks were present at the water surface. In reality these channel units were more accurately classified as pools, for they could be greater than 3 m in depth and the water often moved slowly around the basalt. This was taken into consideration when analyzing the videos, and made surface velocity a more important factor in determining the appropriate habitat category for the channel unit. Ground truthing of some channel-unit delineations at higher flows was also done, but did not bring to our attention any other potential delineation difficulties.

Changes in Water Temperature

Maximum and mean water temperatures were higher in the river after the irrigation diversions than water temperatures in the river before the irrigation diversions or in any of the irrigation canals (Fig. 9 and 10, respectively). The main river after the diversions had a mean discharge of 1.7 m³/sec, whereas mean discharge within the canals varied between 3.1 m³/sec (Swalley Valley Canal), 11.3 m³/sec (North Unit Main Canal), and 14.2 m³/sec (Pilot Butte Canal—also called 'North Canal', Central Oregon Canal). The highest water temperature recorded by the stowaway temperature loggers in the Deschutes River was 27.6°C, whereas the highest water temperature recorded in the canals was 22.4°C. The slope of the curve, representing water temperatures, remains relatively constant in the large canals, changes slightly in the smaller canal, and changes

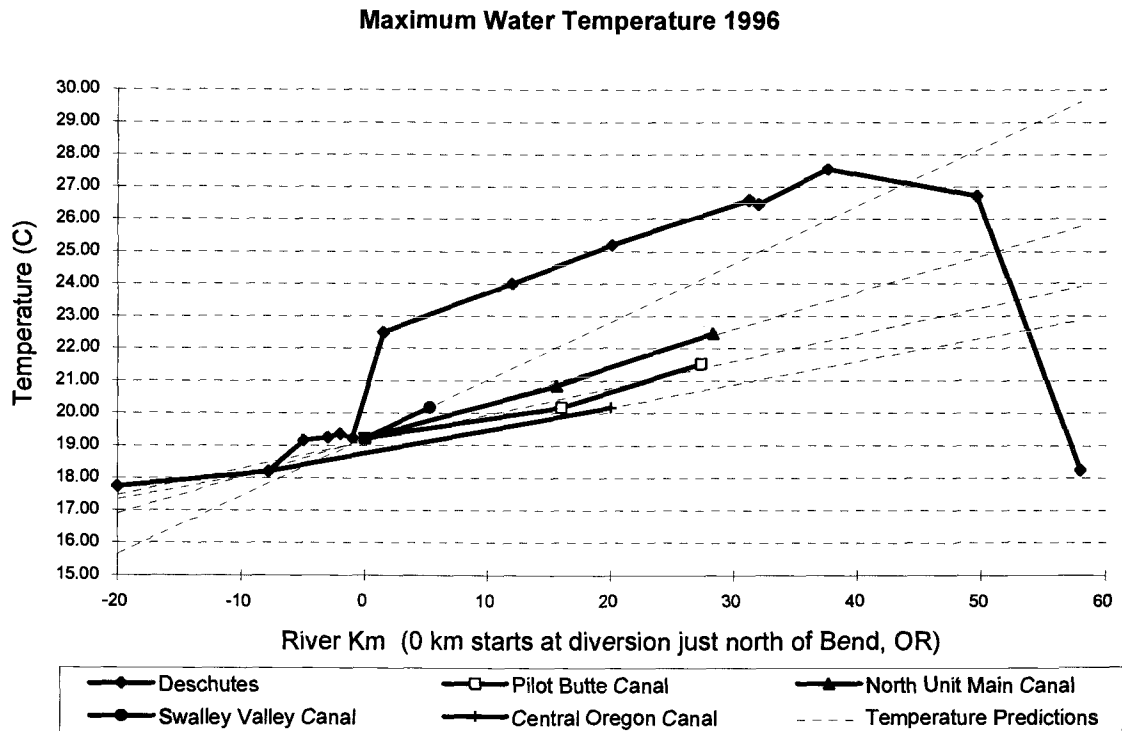


Figure 9: Maximum water temperatures for the Deschutes River, and four irrigation canals which divert water from the river, as recorded in summer 1996. Predicted water temperatures are given for each of the canals.

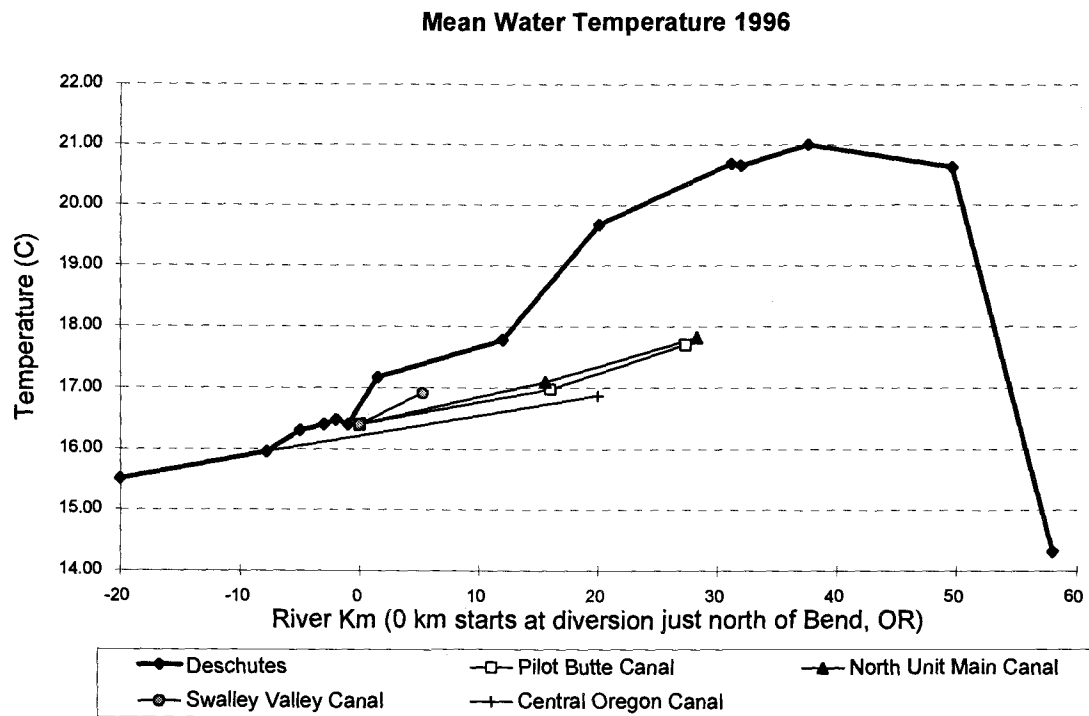


Figure 10: Mean water temperatures for the Deschutes River, and four irrigation canals which divert water from the river, as recorded in summer 1996.

drastically in the river at the point of the main diversion. Based on this data, the river without any diversion could potentially have had a maximum water temperature somewhere below 23°C (Fig. 9). The Swalley Valley canal, which in the summer of 1996 had a mean discharge of 3.1 m³/sec, showed a maximum water temperature of just over 20°C when the river was up to 23°C at the same distance from the diversion (Fig. 10).

Influence of Discharge on Trout Populations

Water Temperature and Discharge effects on Trout

Cluster analysis (based on Euclidean distance) placed a high percentage of our 126 sites into one cluster with few outliers. An analysis requesting seven clusters placed 90% of the sites into one cluster, leaving 12 sites as potential outliers: eight on the Deschutes River, one on Tumalo Creek, one on Squaw Creek, and two on the Metolius River. These site-outliers were distributed among our site-group categories and, coupled with the results from the ANOVA, are not likely to have heavily biased our results. However, had they all been found within one site-group category, or all within one river, we would have probably needed to remove these sites from our analysis in order to minimize the effects of confounding variables on our two-factor ANOVA. Additionally, outlier analysis (based on Sorensen distance), including water temperature and discharge

as well as all other physical habitat variables, only found 4 site outliers: two on the Deschutes River, and two on the Metolius River.

Principal components analysis of all site physical habitat data including water temperature and discharge placed water temperature and discharge on the first component, with loadings of -0.50 and 0.44, respectively. The first component accounted for 37 % of the variance in physical habitat of all sites. Turbidity, substrate embeddedness, and instream cover also weighted the first component, with loadings of -0.41, 0.38, and 0.34, respectively. Substrate, both dominant and subdominant, as well as embeddedness, weighted the second principal component, with loadings of 0.58, 0.37, and 0.48, respectively.

An increase in water temperature above 24°C, and a decrease below 14°C, were both associated with lower rainbow trout abundance ($p=0.0001$) and total trout abundance ($p=0.0016$) (Fig. 11). Brown trout abundance increased with water temperature above 24°C, but not significantly ($p=0.1175$). The abundance of all fish (total number, including non-salmonids) did not change significantly with changes in water temperature ($p=0.1361$), however the abundance of non-trout fishes increased with water temperatures above 24°C ($p=0.0024$) (Fig. 11). A similar pattern existed for rainbow trout density (abundance per unit volume), where density was the highest at medium water temperatures ($p=0.0001$) (Fig. 12). Total trout density closely followed rainbow trout density changes ($p=0.0001$). Brown trout density increased somewhat

with an increase in water temperature, but not significantly ($p=0.1205$), and density of non-trout species increased with an increase in maximum water temperatures above 24°C ($p=0.0031$) (Fig. 12). Rainbow trout IRB/volume (weight/m^3) again followed the same pattern, with decreased IRB with maximum water temperatures above 24°C , and also with water temperatures below 14°C ($p=0.0005$) (Fig. 13). Brown trout IRB/volume generally did not show differences between water temperatures ($p=0.1177$) but were somewhat higher with maximum water temperatures above 24°C (Fig. 13).

Rainbow trout abundance decreased with an increase in discharge, as did total trout abundance; however, neither decreases were significant ($p=0.1752$, and $p=0.2028$; respectively) (Fig. 14). Brown trout abundance increased with an increase in discharge ($p=0.0220$) (Fig. 14). Non-trout abundance was highest in the lowest discharge category ($p=0.0002$); whereas, the total number of all fish (including non-salmonids) was lowest in the medium discharge category and higher in the low and medium categories ($p=0.0004$) (Fig. 14). Trout densities followed a similar pattern to abundances with rainbow trout and total trout densities decreasing with an increase in discharge between the medium and high discharge categories ($p=0.0001$ and $p=0.0002$; respectively) (Fig. 15). Brown trout density increased with an increase in discharge ($p=0.0613$), and non-trout species were highest in the low discharge category ($p=0.0002$) (Fig. 15). Rainbow trout IRB/volume decreased with an increase in discharge ($p=0.0569$), and brown trout IRB/volume increased with an increase in discharge ($p=0.0259$) (Fig. 16).

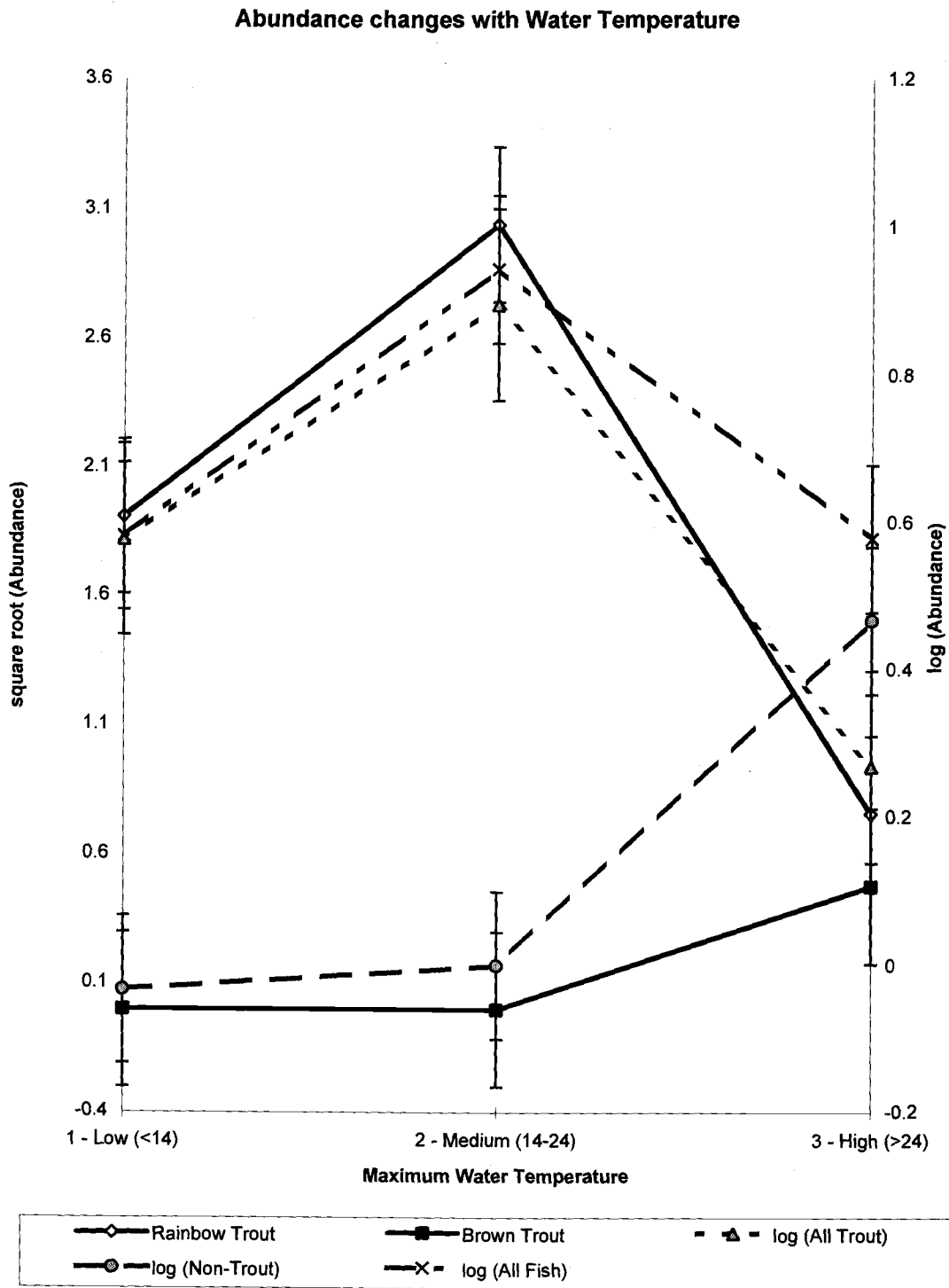


Figure 11: Abundance of fishes in study sites relative to changes in water temperature (low: maximum <math><14^{\circ}\text{C}</math>, medium:

Density changes with Water Temperature

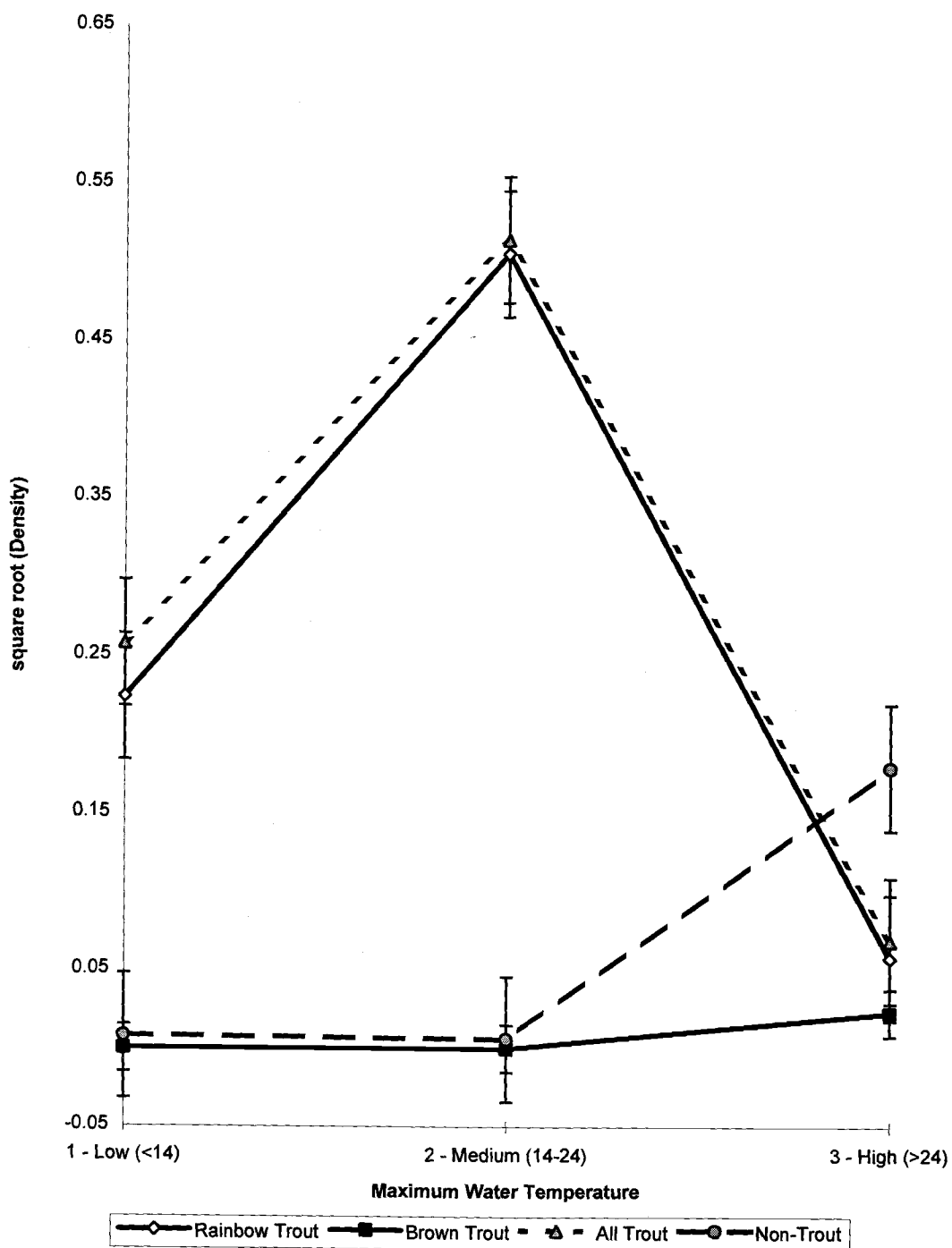


Figure 12: Density (abundance/m³) of fishes in study sites relative to changes in water temperature (low: maximum <14°C, medium: 14-24°C, high: >24°C).

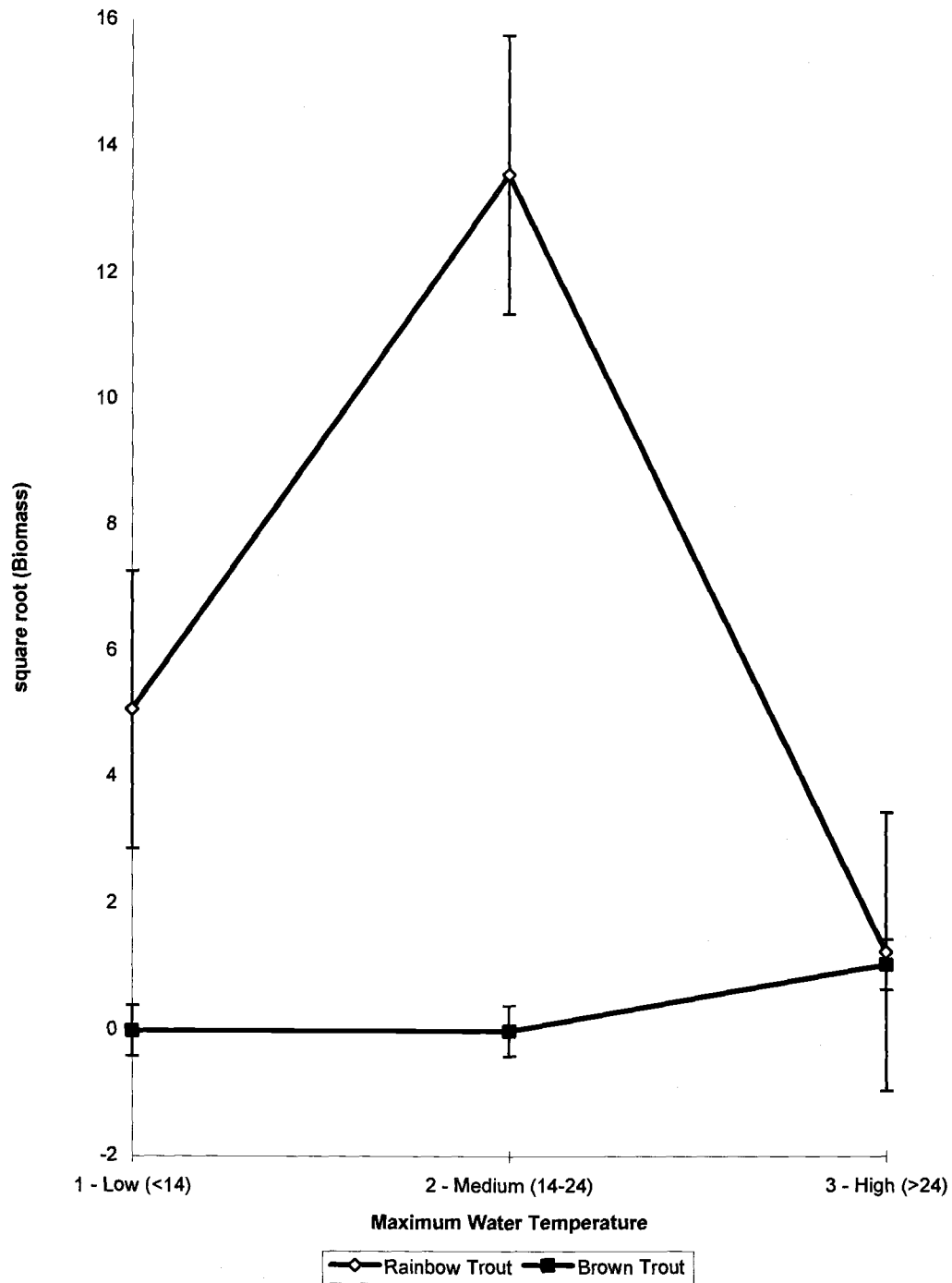
Biomass changes with Water Temperature

Figure 13: Biomass/m³ (Index of Relative Biomass based on trout length) of rainbow trout and brown trout in study sites relative to changes in water temperature (low: maximum <14°C, medium: 14-24°C, high: >24°C).

Abundance changes with Discharge

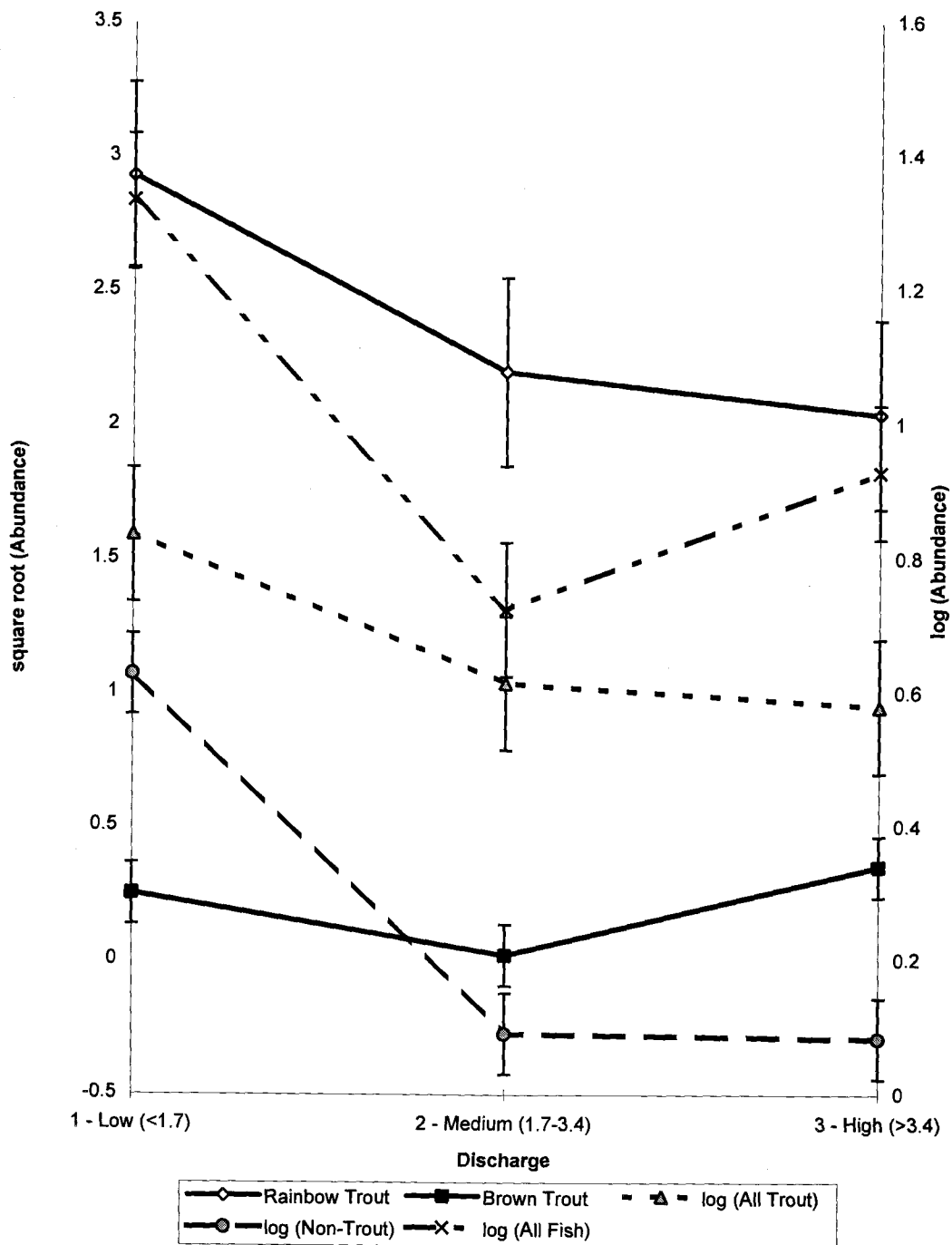


Figure 14: Abundance of fishes in study sites relative to changes in discharge (low:<1.7 m³/sec, medium: 1.7-3.4 m³/sec, high: >3.4 m³/sec).

Density changes with Discharge

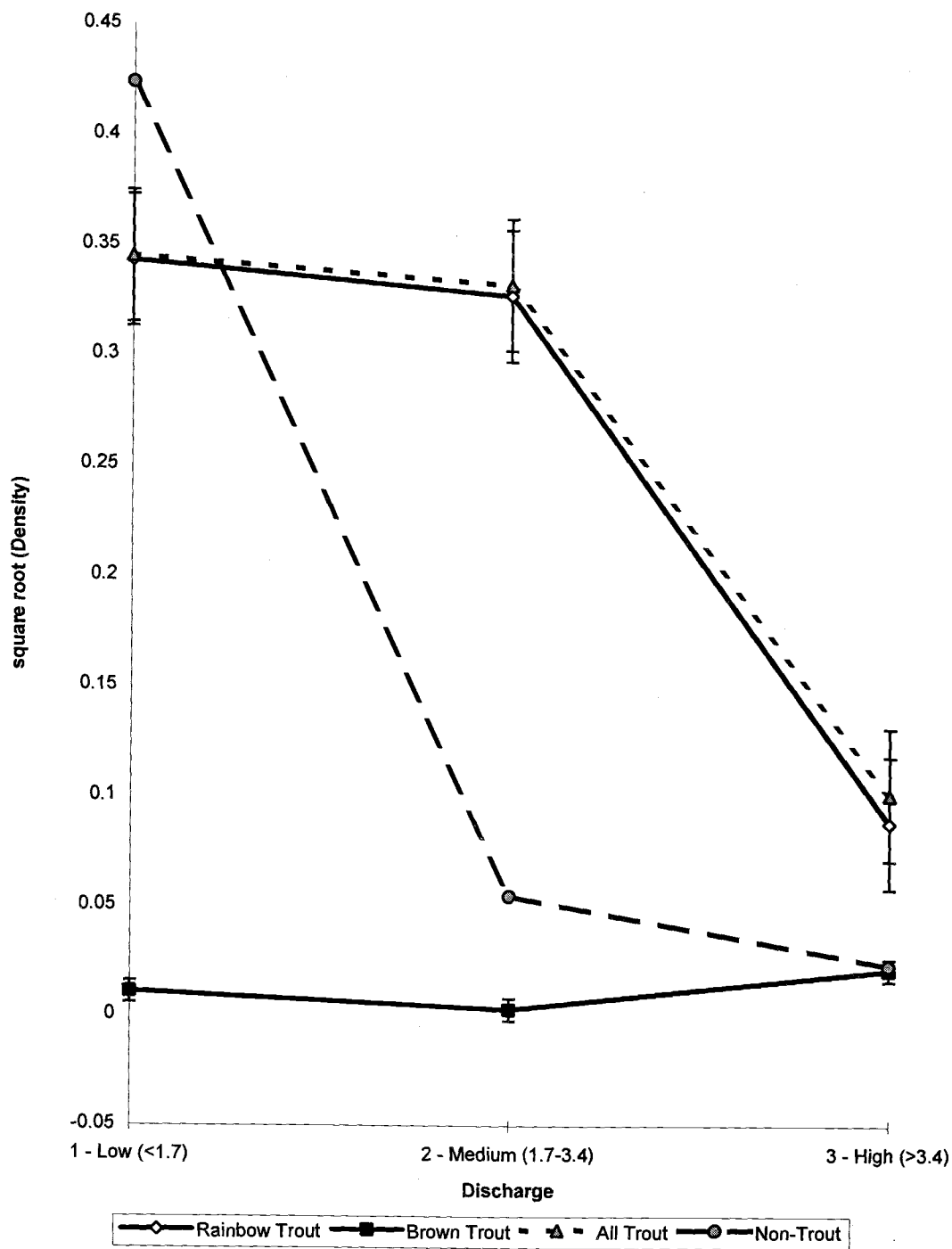


Figure 15: Density (abundance/m³) of fishes in study sites relative to changes in discharge (low: <1.7 m³/sec, medium: 1.7-3.4 m³/sec, high: >3.4 m³/sec).

Biomass changes with Discharge

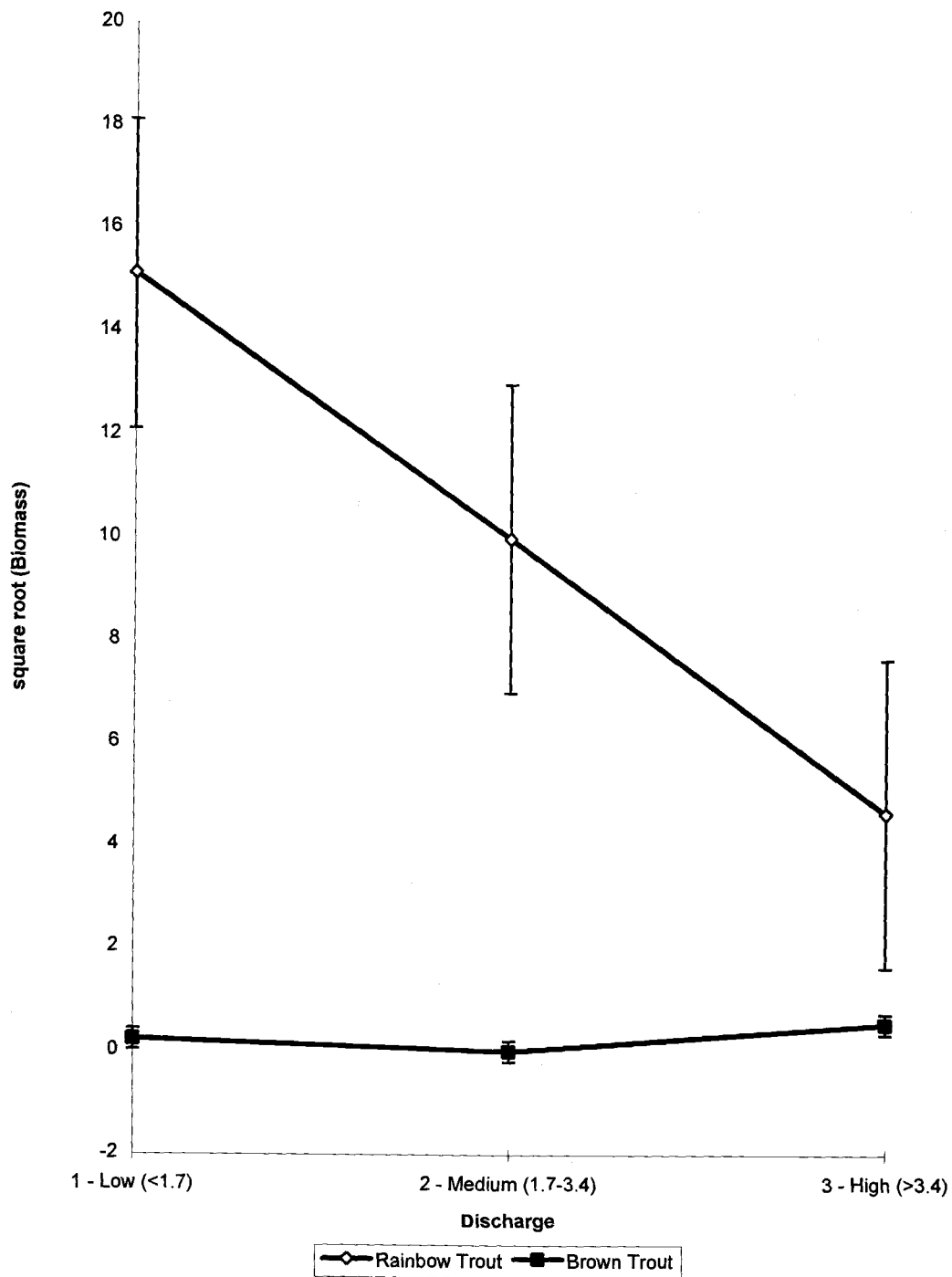


Figure 16: Biomass/ m^3 (Index of Relative Biomass based on trout length) of rainbow trout and brown trout in study sites relative to changes in discharge (low:$1.7 m^3/sec$, medium:

Habitat-Unit Analysis

For this analysis, all 126 habitat units were treated individually. Water temperature was negatively correlated with discharge (Table 7). Depth, width, length, and in-stream cover were positively correlated with discharge. But, depth was the variable most highly correlated (Table 7). These correlations indicate that habitat unit size is a function of stream size. Water temperature was strongly negatively correlated with discharge (Table 7). It was positively correlated with residence time (discharge/habitat unit volume), and with habitat unit width (Table 7). It was negatively related to gradient, and in-stream cover.

Table 7: Correlation between habitat features measured within the Deschutes River and selected tributaries. Length, Width and Depth are measurements of individual habitat units.

	Discharge (m ³ /sec)	Water Temperature (°C)	Width (m)	Depth (m)	Length (m)	In-stream cover	Residence Time	Gradient
Discharge	—	-0.56	0.27	0.64	0.24	0.20	X	-0.22
Water Temperature	—	—	0.40	X	X	-0.39	0.39	-0.45
Width	—	—	—	0.37	0.51	X	0.56	-0.51
Depth	—	—	—	—	0.50	0.19	0.28	-0.32
Length	—	—	—	—	—	X	X	-0.37
In-stream cover	—	—	—	—	—	—	X	0.27
Residence Time	—	—	—	—	—	—	—	-0.31

X - indicates no significant ($p > 0.05$) correlation between variables

Multiple linear regression, at the habitat unit level, using five variables: mean seasonal water temperature, discharge, and habitat unit length, width, and depth; was used to determine prediction equations for trout populations (Table 8). A 'model selection' module of a statistical analysis program was first used to determine the best models. From these models, the multicollinearity between variables within each equation were checked, and variables were removed which were highly ($r^2 > 0.5$) correlated with the other variables. The variable with the highest p-value in each case was removed. In addition, variables were removed which were not significant to the model ($p > 0.1$).

Table 8: Prediction equations for trout populations from habitat variables in the Deschutes River study area. Length, width, and depth are morphological measurements of habitat units. Water temperature is seasonal mean. 'S' represents a square-root transformed variable, and 'L' represents a logarithm transformed variable. 'IRB' is an index of relative biomass based on trout length-weight relationships as given by Carlander (1969).

Dependent Variable	Coefficients	P level	Predictor Variables	R ² (adj.)
S (Abundance Rainbow Trout)	1.34		Y-intercept	24.9%
	.88	0.0027	Depth	
S (Abundance Brown Trout)	-0.83		Y-intercept	23.2%
	0.04	0.0002	Water Temperature	
	0.27	0.0406	Depth	
	0.01	0.0019	Habitat Unit Length	
L (Abundance of Trout)	0.42		Y-intercept	6.2%
	0.27	0.0030	Depth	

Table 8, Continued

Dependent Variable	Coefficients	P level	Predictor Variables	R ² (adj.)
S (Abundance of Non-Trout)	-2.42		Y-intercept	23.4%
	0.19	0.0002	Water Temperature	
	0.05	0.0001	Habitat Unit Length	
S (Rainbow Trout Density) (Abundance/m ³)	0.40		Y-intercept	20.6%
	0.01	0.0001	Width	
	0.01	0.0150	Discharge	
S (Brown Trout Density) (Abundance/m ³)	-0.02		Y-intercept	7.0%
	0.002	0.0129	Water Temperature	
	0.0003	0.0275	Habitat Unit Length	
L (Trout Density) (Abundance/m ³)	0.43		Y-intercept	21.7%
	-0.013	0.0001	Width	
	-0.01	0.0335	Discharge	
S (Non-Trout Density) (Abundance/m ³)	-0.138		Y-intercept	5.0%
	0.017	0.0069	Water Temperature	
S (Rainbow Trout IRB/m ³)			Not Significant	0.0%
S (Brown Trout IRB/m ³)	-0.796		Y-intercept	4.2%
	0.084	0.0124	Water Temperature	
L (Trout IRB/m ³)	0.157		Y-intercept	6.2%
	-0.041	0.0030	Width	

Water temperature was positively related to higher brown trout abundance, density, and IRB, as well as higher non-trout abundance and density (Table 8). It was not a predictor of rainbow trout populations, or total trout populations. Depth of a habitat unit was positively related to trout abundance (both rainbow and brown). Discharge was a better predictor of rainbow trout, and total trout density measures than

depth, and as they were both highly correlated, depth was removed from these regression equations (Table 8). Habitat unit length was somewhat predictive of brown trout populations, where a greater abundance and densities were found within longer habitat units. Habitat unit width was negatively related to total trout density and total trout IRB per unit volume; however, was positively related to rainbow trout density (Table 8).

DISCUSSION

The Deschutes River study area, under its current summer flow regime, has high maximum and mean water temperatures. Maximum water temperature exceeds the incipient lethal level generally given for trout, of approximately 25°C to 26°C (Weatherley et al. 1991, Jensen 1990, Elliot 1994, 1990, 1988, 1985, 1981, 1975a, 1975b, Preall and Rigler 1989, Edwards et al. 1979); and the mean water temperatures are far above those preferred by trout and those which benefit trout growth (Filbert and Hawkins 1995, Papoutsoglou and Papapaskeva-Papoutsoglou 1978, Sperber et al. 1977). Because of these direct physiological effects of high water temperature, the extreme temperature conditions of the Deschutes River denote critical habitat limitations for rainbow and brown trouts (Vigg and Burley 1991, Bailey et al. 1991, Regier 1990, Imhof et al. 1990, Christie and Regier 1987, Bergman 1987, Jones and Sidell 1982, Magnuson 1979, Crawshaw 1977, Brett 1971, Beamish 1964).

High water temperature has frequently been related to smaller trout populations (e.g. Tait et al. 1994, Christie and Regier 1988, Conder and Annear 1987, Magnuson et al. 1979, Binns and Eisermann 1979). This might be connected to lethal exposure levels (e.g. Elliot 1994, 1985, 1981), sub-optimal conditions decreasing growth rates (Filbert and Hawkins 1995, Donald et al. 1980), or non-selection or avoidance of habitat with higher water temperatures (Rahel and Hubert 1991, Baltz et al. 1987, Bowlby and Roff 1986).

Rainbow trout populations on the Deschutes increased and decreased with water temperatures as would be expected from known temperature preferences (Filbert and Hawkins 1995, Papoutsoglou and Papapaskeva-Papoutsoglou 1978, Sperber et al. 1977). Rainbow trout populations were highest in sites with maximum water temperatures between 14°C and 24°C (mean 10°C to 19°C), and decreased significantly at lower and higher water temperatures. These low and high temperature habitats represent a range of temperatures which are limiting to trout abundance, density and IRB per unit volume. Therefore, high summer water temperature probably limits rainbow trout abundances in this system more than does availability of physical habitat.

Brown trout did not respond to changing water temperature in the same manner as did rainbow trout, with abundance, density, and IRB per unit volume showing a non-significant increase with water temperature. This difference could represent a difference in species preferences for water temperature (Regier et al. 1996, Lin 1995, Reeves et al. 1993, Reeves et al. 1987), with the introduced brown trout adapted, or less sensitive, to a broader range of water temperatures. Further research may help to decipher this differential response to water temperature between rainbow and brown trouts within the Deschutes River.

Water temperature can be heavily influenced by discharge condition (see e.g. Li et al. 1994, Adams et al. 1993, Voelz and Ward 1990), and an increase in discharge might help to alleviate the water temperature problem in the Deschutes River study area. The canals at 20 km from the irrigation withdrawals are 20°C to 21°C, whereas the main

river has reached 25.2°C. The main difference here is the amount of water. If anything, one would expect the water temperature in the canals to be influenced by their lack of shade (either bankside vegetation or topographic); whereas the river runs through a valley canyon and also has some riparian shading. The relatively lower summer water temperatures in the canals demonstrate that an increase in discharge will likely lower water temperatures in the main river, and that even a doubling of the mean summer flow, from 1.7 m³/sec to 2.8 m³/sec, could result in a biologically significant reduction in water temperature in the main river.

While an increase in discharge might help to lower water temperature, it would also play an important role for trout by increasing habitat availability. Discharge was positively correlated with depth throughout our 126 ground sites, and also showed a positive correlation with channel width. Our videographic analysis found changes in habitat with changes in discharge. Habitat size for the entire study area, as measured by changes in channel width and habitat unit length, increased logarithmically with an increase in discharge.

Changes in channel morphology with discharge has been found in other research. Leopold and Maddock (1953) found a relationship between width and discharge that is fairly similar to ours. In comparing our results to theirs we calculated that our equation yields a relatively narrower width estimate for discharge changes (equaling ½ the width of their 'average' river); however, this difference would be expected as the Deschutes River is relatively constrained due to basalt formations. We would therefore expect that

the Deschutes would compensate for this constraint by either depth or velocity increases, or both, above the general average river system as given in Leopold and Maddock (1953).

We examined the potential changes to habitat unit distribution in order to determine how pool habitat, which is generally preferred by trouts (Gowan et al. 1994, Decker and Erman 1992, Scott and Crossman 1973), would be affected by an increase in discharge. We found that habitat unit distribution was strongly influenced by discharge in the Deschutes River; however, the relationship was non-linear, and unpredictable. Many physical factors interplay within this system, and each one is constrained by a complex set of interacting variables such as gradient and valley slope, which may be influencing the non-linear response between discharge and habitat distribution (e.g. Ferguson and Ashworth 1991). Compared to other river systems in Oregon, the changes in gradient and valley slope found within the Deschutes River study area are unique: lacking the traditional concave change in gradient, and with a non-linear change in valley slope along its longitudinal profile (see Fig. 3).

In addition, it is likely that the river flow within the Deschutes does not reach equilibrium with the channel bed throughout the winter. Winter flows fluctuate frequently, and over a broad range of discharges. For example, the winter canal flow schedules can add or subtract up to $17 \text{ m}^3/\text{sec}$ to the main flow of the river. This means that the flow energy of the river changes frequently, and these changes would be accompanied by changes in sediment load which could affect the riffle-pool patterns

(Gregory et al. 1994, Wohl et al. 1993, Clifford 1993, Beven and Carling 1992, Carling 1991, Yang and Stall 1981, Dury 1977,). Unfortunately, winter flow conditions were too dangerous to examine this system at close range.

Besides the complexity of the system, habitat unit nomenclature might be playing a role within this non-linear response. We based our habitat unit delineations on traditional naming systems, which have been based on river systems at low flows (e.g. Rosgen 1994, Hawkins et al. 1993). The observed higher flows are more similar to flood stages than they are to natural larger river systems. In delineating pool habitat we attempted to look for lower water surface velocities, and deeper-seeming sections with an absence of supercritical flows, however, whether these habitat units would act ecologically as pool units is problematic.

Given that discharge affects physical habitat distribution and abundance, we investigated the effect of different discharge regimes on resident trouts. Brown trout populations (abundance, density, and IRB per unit volume) were found generally to increase with an increase in discharge; however, rainbow trout abundance and IRB per unit volume showed no change with an increase in discharge, and rainbow trout density declined with an increase in discharge. Again, a differential response between the individual trout species was observed, as was found for the effects of water temperature.

Research has often shown that trout populations are correlated, directly or indirectly, with habitat availability (see Table 1). Our findings, of increased river width

and therefore habitat size with an increase in discharge, suggest that increasing discharge would increase the overall amount of available habitat. Therefore, the observed increase in brown trout is perhaps explained by the increase in available habitat. The abundance of brown trout was related, using multiple linear regression, to increases in habitat depth and habitat unit length.

The observed decrease in rainbow trout density with an increase in discharge is less easily understood; however, there might be several plausible explanations for this phenomena. The response of rainbow trout density to discharge could be influenced by the negative correlation between water temperature and discharge within our study sites. High discharge sites corresponded to the lowest water temperature sites, which showed reduced rainbow trout populations. However, this explanation doesn't account for the decrease in rainbow trout at the medium discharge category. The medium discharge category was correlated with the medium water temperature category, which showed the highest levels of rainbow trout.

Increases in discharge might be coupled with increases in water velocity, especially considering the high degree of constraint present at many of our sites. This could have the effect of reducing rainbow trout populations. Rimmer (1985) showed that higher water velocities require increased energy expenditure by trout, and Fausch (1984) found trout competed for optimal velocity habitat where food resources were maximized and energy expenditure was minimized. Because of the constrained nature of many of our research sites, water velocities are likely to increase in greater proportion

than habitat volume with higher discharges: the river cannot spread out into the banks, and therefore velocities escalate. This could account for the observed decrease in rainbow trout densities with increases in discharge. Further research would need to be done in order to examine how velocities are changing within these river systems.

Emigration of rainbow trout from warmer to cooler waters may have augmented or concentrated the populations within lower-discharge sites which were adjacent to higher-temperature sites. Gowan et al. (1994) and Riley and Fausch (1995) remind us that trout are not necessarily affixed to one location within a river but have been known to move, especially if habitat conditions are unsuitable. Within the Deschutes River, for example, there sometimes exist cooler thermal refugia habitat around areas with higher water temperatures. Both locations might fall within the same discharge category, but the one with cooler water may have an over-abundance of trout that are escaping from unsuitable water temperatures. Our research methods, which looked for study sites conforming to a high temperature regime, would find places which had high water temperatures, but may have been depopulated by trout in their search for cooler habitats. Locations upstream or downstream which had a similar discharge regime but lower water temperatures would have a higher abundance of trout without this abundance being directly related to discharge.

Comparing the effects of discharge on trout across four different rivers might have confounded the result to some degree. Rainbow trout were present in all of the four study streams, whereas brown trout were present primarily in the Deschutes River and

Squaw Creek: both with generally high water temperature regimes. Decreased presence of brown trout within the colder water tributaries may be due to reduced tolerance of low water temperatures or an upwards shift in thermal tolerance. Therefore, the effect of discharge on brown trout is not as confounded by a comparison across river systems with different temperature regimes as it is with rainbow trout.

Multiple regression indicated that discharge was not a very strong predictor of either brown or rainbow trout compared to water temperature and habitat morphological variables. Coupled with the knowledge that depth and width variables will increase predictably with an increase in discharge (Leopold et al. 1964, Leopold and Wolman 1957, Leopold and Maddock 1953), we feel that these, rather than discharge, are probably better habitat variables to use in order to predict changes to trout populations within this river system.

However, it should be understood that the regression equations given herein can only demonstrate the relationships between trout and those habitat features that were included within this study. We did not measure changes in food production or benthic invertebrate biomass, which have been shown to be highly correlated with trout abundance (Jowett 1992, Jowett, 1995).

These results demonstrate that current instream flow methodologies would not be adequate to determine instream flow requirements for trout on the Deschutes River. These methodologies frequently base minimum flow estimations on non-universal

relationships between fish and their habitat, using microhabitat preference curves or weighted usable area models (see Fausch et al. 1988, Scott and Shirvell 1987, Mathur et al. 1985, Annear and Conder 1984 for reviews). Jowett (1995) found, for example, that food production and invertebrate biomass were not correlated with weighted useable area. However, the exclusion of the effect of discharge on water temperature, from instream flow methodologies, is probably the most serious defect which inhibits their use on the Deschutes River and perhaps many other river systems; especially considering the observed correlation that can occur between these factors. Water temperature was highly correlated with discharge in the Deschutes River, physiologically important to trout, and played an important role in predicting changes in trout abundance, density, and IRB per unit volume.

The use of aerial videography for stream habitat delineation is a relatively new technique which has proven effective and cost efficient for examining the potential changes with discharge on the Deschutes River. Meisner (1986) presents an overview of videographic methods, and the use of photographic remote sensing (a precursor to videography) for hydrology and watershed management is given in Zink et al. (1960). Greentree and Alderich (1976) were one of the first groups to apply aerial photography technology specifically to habitat surveys. They showed, using cost analysis, that although this technique could be expensive, it was consistently cheaper and faster than a ground-based study of the same magnitude. Hilton (1984) also found a high level of efficiency in using aerial photographs rather than ground-based research for surveying

and quantifying habitat features such as the location and size of pools, rapids, and riffles, vegetation coverage and type, temperature, turbidity, erosion and sandbank movement, and channel stability.

Aerial videography allowed us to examine habitat in the Deschutes River when conditions would otherwise have made the same research on the ground dangerous and expensive. Using this technique, different river stages, including flood conditions, could be examined. As well, we could survey parts of the river that are privately owned, which we wouldn't have otherwise had access to.

Aerial photography and videography are useful tools to the stream ecologist, however, their limitations must be understood. The overall accuracy of using videography to delineate stream habitats varied with recording conditions, and with river stage. We found it easier to delineate stream habitat when there was no direct sunlight on the river. However, we also found that rain and excessive cloud cover tended to diminish the video resolution. Measurements were limited by the video resolution to a maximum of 0.5 m on each edge being measured because of pixel limitations (so 1 m on a width or length measurement). Shading and overhanging bankside vegetation also limited measurement accuracy. We researched and attempted to correct for known problems such as shadowing, focusing difficulties due to auto focus settings, and altitude variations and their effects on scaling (Avery and Berlin 1992, Lillesand and Kiefer 1994). Jennings et al. (1992) noted a problem with glare on the water surface when filming in bright sunlight. We also experienced this, but could not specifically schedule

the helicopter flights to avoid it, and found it sometimes useful for detecting very calm, slow moving water. Hefner and Moorhead (1991) review the importance of determining the required scale and resolution of the videography before the flight in order to obtain accurate results. Even with this planning we note that our altitude did not always remain constant above the river water surface, which made scale determination calculations especially cumbersome. Thermal updrafts of hotter air, especially during our summer flight, and also windy conditions made the helicopter move vertically and horizontally. A smaller scale occurs when the altitude increases. A more accurate GPS unit to record horizontal and vertical position data points for the entire flight would help make scale corrections easier and more accurate. As well, a laser altimeter to record position relative to the ground would help to determine image scale more accurately.

Field research is often done under the incorrect assumption that the systems examined are operating at a theoretical 'maximum carrying capacity', whereas in actuality they must operate under natural constraints, with random variation playing a role. For example, some of our sites were potentially heavily influenced by societal factors such as recreational fishing, and therefore may have the ability to produce more trout, but the numbers are not there. This is not necessarily reflected by measuring the physical habitat conditions. If we base conclusions on the assumption that sites with lower trout abundance contain poorer quality habitat we could be in considerable error. Without unlimited time and funding, we are necessarily limited in this respect to making

the most out of such data by recognizing potential confounding factors and natural variability.

We were concerned that selection of sites and assignment to treatment groups (discharge and water temperature) would meet independence and replication assumptions in order to use a one-way ANOVA to compare treatment effects. Typically, treatment groups are randomly assigned, whereas we had to find sites which met the treatment criteria but were similar in other respects. To test the validity of our ANOVA results we were careful to examine and compare physical habitat differences of each site that were not due to discharge and water temperature categories. Results from our site habitat cluster analysis, as well as an examination of habitat variables, convinces us that, in part, we managed to compare the effects on trout populations based on differences related to water temperature and discharge levels more than on other qualities of the sites.

In summary, water temperature is the most important factor in predicting changes to trout populations. In this respect, an increase in discharge is important to the extent that it will decrease water temperature, and also to the extent that it will increase habitat depth and surface area. Trout populations found in areas with mean water temperatures above 19°C had lower abundances, decreased density, and lower IRB per unit volume than sites with lower water temperatures. When water temperature is not limiting, discharge was important for its direct relationship with channel depth and width.

Future management of this section of the Deschutes River should include the consideration that increasing discharge will likely significantly lower water temperatures; therefore, providing more optimal habitat conditions for the trout. This decrease in water temperature could act to reduce introduced brown trout populations, as they were shown to be more related to higher water temperatures; however, this decrease would likely be coupled with an increase in rainbow trout populations as water temperatures decreased to provide more favorable conditions. Within this section of the Deschutes the increase in discharge would likely cause increases in habitat volume greater than increases to water velocities, because the river channel's mean annual flow of 17 m³/sec already structures the channel for higher flow conditions (see Leopold et al. 1964). Therefore, if rainbow trout populations are negatively affected by higher water velocities at higher discharges, they would be less affected within this section of the Deschutes than the other locations examined in this research. Recommendations for improving trout habitat include an increase in discharge from current 0.9-1.7 m³/sec to between 3.5-17 m³/sec; where, 3.5 m³/sec represents the flow of the Swalley Valley Canal—which is approximately 3°C colder than the Deschutes, up to 17 m³/sec—which represents the current mean annual flow of this section of the Deschutes River.

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