
Prediction of Stream Carrying Capacity for Steelhead (*Oncorhynchus mykiss*): the Unit Characteristic Method

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ABSTRACT

We describe and demonstrate the Unit Characteristic Method (UCM) as a means by which measurements of habitat from typical stream surveys can be used to estimate the capacity of a stream to rear juvenile steelhead (*Oncorhynchus mykiss*). Channel unit features of importance include surface area by unit type, depth, substrate, and cover. The influence of a stream's primary productivity is represented in the method through measures of alkalinity and turbidity. We tested the fit of model predictions to juvenile steelhead production observed in seven watersheds ranging in size from 26 to 1,420 km². Model predictions of capacity were significantly correlated to observed maximum production of juvenile steelhead ($P < 0.005$, $R^2 = 0.88$), as was watershed area ($P < 0.005$, $R^2 = 0.88$). The UCM predictions revealed that parr capacity was unevenly distributed in the watersheds, and that habitat quality (smolt capacity/m²) differed between reaches among all watersheds by up to 15-fold across seven basins surveyed, and ranged more than 10-fold between reaches within four of seven test watersheds. Thus, the UCM can be used to discriminate stream reaches and features that either warrant habitat restoration or conservation. Key factors driving high or low habitat quality differed between reaches, and included pool area, riffle depth, boulder substrate, alkalinity, fine sediment, and turbidity. The UCM provides a framework for understanding the habitat features that determine the production potential of a basin, for identifying factors that limit production, and for predicting potential fish benefits from differing habitat management strategies.

INTRODUCTION

Problem and Need

The need to accurately estimate carrying capacity of streams for salmonids has been accentuated by the recent focus on assessing population viability and planning for recovery of salmon and steelhead populations listed under the Endangered Species Act (ESA). This focus on restoring healthy fish populations has placed a burden on resource managers to choose among competing proposals designed to restore stream habitats, restore fish passage, reduce harvest, or alter the use of hatchery fish. More than ever, resource managers need a reliable basis for determining which combination of projects will provide the greatest benefits to targeted fish populations. Estimation of fish benefits from each strategy relies on accurate knowledge of the suite of factors, and the magnitude of influence from each, that determine a stream's capacity to produce the species of interest. Further, this same knowledge is needed to determine how a population is performing relative to its potential in a given basin.

Fisheries managers are often frustrated by the poor precision of carrying capacity estimates derived from stock-recruitment relationships, and the high cost of estimating all components of adult recruitment restricts data collection to a few streams. The estimation of stream carrying capacity has long been a foundation of assessments and strategies for managing salmon and trout populations, primarily as a parameter of stock-recruitment functions that predict harvestable surpluses (Beverton and Holt 1957; Ricker 1975). The traditional approach for estimating carrying capacity has been to fit a relationship between adult recruits and the number of parents that spawned them. This approach requires a long time series of data, but such data are lacking for the great majority of salmonid-producing basins. Even when the data are available, the statistical fit, and thus the confidence in capacity estimates, is often poor (Cramer 2000). Further, the statistical approach is not helpful for identifying the specific habitat factors that are limiting the population, nor in estimating the benefits from selected stream alterations in a small portion of the watershed.

The joint need to estimate (1) carrying capacity and (2) fish benefits from specific habitat changes highlights the value of developing methods to estimate salmonid carrying capacity directly from measurements of stream habitat features. Cramer and Ackerman (2008) describe the Unit Characteristic Method (UCM) as an analytical framework intended to fill these needs. In this chapter, the UCM to predict carrying capacity of steelhead (*Oncorhynchus mykiss*) is described and tested in seven basins ranging in size from 26 to 1,420 km². Data from state and federal agencies on stream features and juvenile steelhead abundance are used to determine the fit of predicted to observed smolt production at carrying capacity. Results from these test basins are

used to evaluate the sensitivity of UCM to the different habitat factors it includes, and to evaluate variation in habitat quality for producing steelhead within and between basins.

Approach

The UCM quantifies stream carrying capacity for salmonids in terms of stream features that can be targeted by actions to conserve or restore habitat, and are measured during stream habitat surveys that follow protocols typical of most natural resource agencies. Hawkins et al. (1983) noted from their review of studies on channel unit classifications that, “variation in the structure and dynamics of the physical environment are primary factors affecting production and diversity of stream biota.” Further, “Differences in habitat quality among channel units are often associated with differences in morphology (e.g., depth, width, shape), water velocity (hydraulics) and bed roughness (substrate size).” The UCM is based on empirical evidence of relationships between fish production and driving factors such as those noted by Hawkins et al. (1983), and utilizes stream inventory data as model inputs. The UCM is similar to the method used by Nickelson (1998), who described methods for estimating stream capacity for rearing juvenile coho based on the area of channel unit types.

We define stream carrying capacity as the maximum number of juveniles that a stream can produce under average environmental conditions for the juvenile life stage most limited by availability of suitable space. This definition recognizes that realized maximum production will vary temporally with environmental conditions, and that the life stage most constrained by space may vary between streams. Capacity is generally most constrained for steelhead during summer for age > 1 parr (Bjornn 1978; Everest et al. 1987; Reeves et al. 1997; Cramer and Ackerman 2008), thus this is the season and life-stage targeted by the UCM for predicting capacity.

In some instances, availability of over-winter habitat may limit production (Solazzi et al. 2000; Solazzi et al. 2002). Accordingly, a winter capacity function is included in the UCM in case the number of parr entering the winter exceeds the capacity of winter habitat.

METHODS

Model Development and Structure

A combination of literature search, researcher interviews, and findings from our own field studies was used to assemble data from which parameters could be estimated to relate maximum rearing densities to habitat features. Habitat features incorporated into the model included those features that can be, and typically are, measured during stream survey inventories conducted by government agencies (e.g. USFS 1999; Pleus et al. 1999; Moore et al. 2002). In addition, the

water quality variables of turbidity and alkalinity are included within the model, and regional samples of these parameters are generally available through state and federal agencies.

The UCM assigns a standard density of age>1 parr to each unit type, and then increments or decrements that density according to the amount that habitat features of channel size, substrate, depth, and cover deviate from the model's expected value. The combined capacity of units within a reach is then scaled by factors affecting productivity. That is:

$$(1) \quad Capacity_i = (\sum area_k \cdot den_j \cdot chnl_{jk} \cdot dep_{jk} \cdot cvr_{jk}) \cdot prod_i;$$

Where

Capacity = maximum number of age>1 parr supported under average environmental conditions,

i = stream reach. "Reach" is a sequence of channel units that compose a geomorphically homogenous segment of the stream network,

j = channel unit type,

k = individual channel unit,

area = area (m²) of channel unit *k*,

den = standard fish density (fish/ m²) for species *i* in unit type *j*,

chnl = discount scalar for unproductive portions of large channels with expected value of 1.0,

dep = depth scalar with expected value of 1.0,

cvr = cover scalar with expected value of 1.0, and

prod = productivity scalar for the reach, with expected value of 1.0. This scalar combines the separate effects from four additional factors defined in Equation (2).

Variables that are represented as scalars having an expected value of 1.0 in this function are defined by a separate function that relates that variable to fish density. These scalars represent proportional changes to parr density compared to the standard fish densities (*den*). The value of the variable when the scalar is 1.0 represents the average value of that variable for the data set from which the standard fish density was determined. For example, the standard densities for steelhead parr (Table 1) are taken from a set of Oregon coastal streams, so the scalar value for *dep* would be set to 1.0 for the average depth in the Oregon coastal streams that were sampled. Depths greater than average would receive a scalar > 1, and depths shallower than average would receive a scalar <1. The sequence of calculations is illustrated in Figure 1, and the formulas and range of values for each of these scalars are given in Table 1 and Figure 2. To estimate smolt output at capacity, the parr capacity is multiplied by an over-winter survival rate, which is assumed to be density independent.

Substantiating evidence for the functions used in the UCM has been described by Cramer and Ackerman (2008). Here we describe the logic for translating that evidence into quantitative functions describing steelhead habitat.

Table 1. Formulas, definitions and values of variables and parameters used in the UCM.

Parameter/Function	Value/Equation	Source(s)
<i>den (fish/m²)</i>		
Backwaters	0.05	Johnson et al. 1993
Beaver Ponds	0.07	
Cascades	0.03	
Glides	0.08	
Pools	0.17	
Rapids	0.07	
Riffles	0.03	
<i>chnl</i>		
Glides	If $W > 24$: $(W-24)*0.35/W + 24/W$	Cramer et al. 1998; O'Neal and Cramer 1999; Romey et al. 2001
Pools	If $W > 24$: $(W-24)*0.75/W + 24/W$; and If $L > 4*W$: $L = 4*W$	
Riffles	If $W > 24$: $(W - 24)*0.15/W + 24/W$	
<i>dep</i>		
Pools	If D is <0.10 : $0.0*D$	Beecher et al. 1993; Dambacher 1991; Bisson et al. 1988;
	If D is $0.10-0.80$: $(0.30* D - 0.027)/0.17$	
	If D is >0.80 : $0.22/0.17$	
Riffles	If D is <0.1 : $0.0*D$	et al. 1995; Bovee 1978; D.B. Lister and Associates, unpublished data;
	If D is $0.10-0.16$: $(0.5*D - 0.050)/0.03$	
	If D is $0.16-0.30$: $(0.29*D - 0.017)/0.03$	
	If D is $0.30-0.80$: $(0.25*D - 0.003)/0.03$	
	If D is $0.80-0.90$: $0.20/0.03$	
	If D is $0.90-1.50$: $(-0.32*D + 0.485)/0.03$	
	If D is >1.50 : 0	
<i>cvr</i>		
Pools and Glides	If wood complexity = 1: 0.58	Johnson et al. 1993; Johnson 1985
	If wood complexity = 2: 1.00	
	If wood complexity = 3: 1.42	
	If wood complexity = 4 or 5: 1.84	
Boulders	If $B_{Pr} < 0.25$: 1.0	
	If B_{Pr} is $0.25-0.75$: $1+12*(B_{Pr} -0.25)$	
	If B_{Pr} is >0.75 : 7.0	
<i>turb</i>		

Parameter/Function	Value/Equation	Source(s)
<i>drift</i>	If D_R is <0.3m: $10^{(2-(1+0.024*T)^{0.1})}/10^{2-0.1}$	Lloyd et al. 1987
	If D_R is 0.3-0.5m: $10^{(2-(1+0.024*T)^{0.3})}/10^{2-0.3}$	
	If D_R is > 0.5m: $10^{(2-(1+0.024*T)^{0.5})}/10^{2-0.5}$	
<i>drift</i>	If $R_P > 0.5$: 1.0	Waters 1962; Waite and Carpenter 2000
	If R_P is ≥ 0.5 : $0.1+1.8*R_P$	
<i>fines</i>	If F_P is <0.1: 1.0	Bjornn et al. 1977
	If F_P is ≥ 0.1 : $1.11 - 1.1*F_P$	
<i>alk</i>	Alkalinity (mgCaCO ₃ /l) ^{0.45} /4.48	Ptolemy 1993
<i>winter</i>	If $C_P < 0.15$: $0.20+(C_P)/0.15*0.8$	USFWS 1988; Bjornn 1971; Bustard and Narver 1975; Hartman 1965; Swales et al. 1985
	If $C_P \geq 0.15$: 1.0	

W = wetted width of unit in meters.

L = length of unit in meters

D = depth in meters (maximum in pools; mean in riffles)

B_{Pr} = Proportion of substrate in riffles that is comprised of boulders

D_R = Mean depth of riffles within the reach

R_P = Proportion of surface area of reach comprised of riffle and rapid habitat types

F_P = Proportion of substrate in riffles that is comprised of fines

C_P = Proportion of substrate in the stream comprised of cobbles

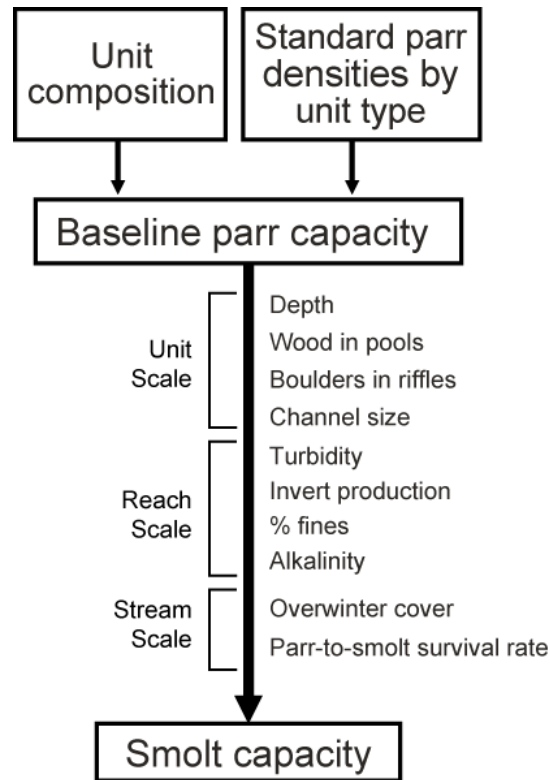


Figure 1. Diagram of the sequence of functions within the UCM.

Model Functions

Standard Fish Densities (den).—Rearing densities for different channel unit types from Johnson et al. (1993) were chosen to represent the *den* term in Equation 1 (Table 1). Johnson et al. (1993) presented findings from 19 coastal Oregon streams that were sampled over multiple years and were fully seeded. These densities are referred to in the UCM as the “standard densities” and the streams from which they were derived are termed the “standard streams”. These “standard densities” were applied to all seven watersheds, and the various scalars in equation (1) then adjusted these densities to be appropriate for the habitat features in each channel unit, reach, and watershed, as described below.

Channel Size (chnl).—Large river channels tend to support much lower densities of rearing parr per area than smaller channels (Johnson 1985; Jepsen and Rodgers 2004) due primarily to the preference of steelhead parr for shoreline areas, and to the head and tail sections of pools within larger channels. Bjornn and Reiser (1991) showed that counts of age-0 Chinook increased with pool surface area up to pool sizes of 200 m². Beyond this pool size, there was no further increase in the number of fish counted. Data from the Sandy River, Oregon, suggest that calm areas (velocity <0.15 m/s) tended to form in mid-sections of pools longer than four channel widths, and

80% of pools were under that length (Cramer et al. 1998). We have observed that such calm areas are seldom used by juvenile steelhead, so we set the UCM to only assign pool area for the pool length up to four channel widths.

Fish use of the mid-river portion of wide river channels is limited (Beechie et al. 2005). Direct underwater observation data from the Salmon River (tributary to the Sandy River, Oregon) and the Clackamas River, Oregon, indicate there is a stream size at which channel geometry and hydraulics result in less favorable habitat for juvenile salmonids in midstream, and that this difference depends on the type of channel unit (pool, riffle, or glide) (O'Neal and Cramer 1999; Romey et al. 2001). In the smaller of the two rivers, the Salmon River, the mean channel width was 21 m and steelhead parr counts in the midstream lane, averaged for 16 channel units, was significantly ($P < 0.05$) greater than from either of the side lanes. However, in the Clackamas River where mean channel width was 40 m, the midstream lane consistently produced much lower counts of steelhead than the side lanes ($P < 0.01$) in riffles (15% of side lanes) and glides (35% of side lanes). Accordingly, the UCM incorporates these findings into the *chnl* scalar of Equation (1), by assigning densities in the midstream portion of large channels (>12 m from shore) that are 15% of the standard in riffles, 35% of the standard in glides, and 75% of the standard in pools (Table 1; Figure 2).

Depth (dep).—The depth scalar accounts for the effect of depth on juvenile steelhead use independent of cover. In a study of a Washington stream in which cover from wood, vegetation, or boulders was absent, Beecher et al. (1993) found that steelhead parr strongly avoided areas with depth <0.15 m, and their use increased with depth from 0.15 to 0.76 m, with no change in depth preference beyond 0.76 m. Preference of steelhead parr for a similar range of depths was confirmed in separate studies by Everest and Chapman (1972), Fausch (1993) and Dambacher (1991). Bisson et al. (1988) and Roper et al. (1994) also reported that steelhead parr use increased with depth in wadable streams.

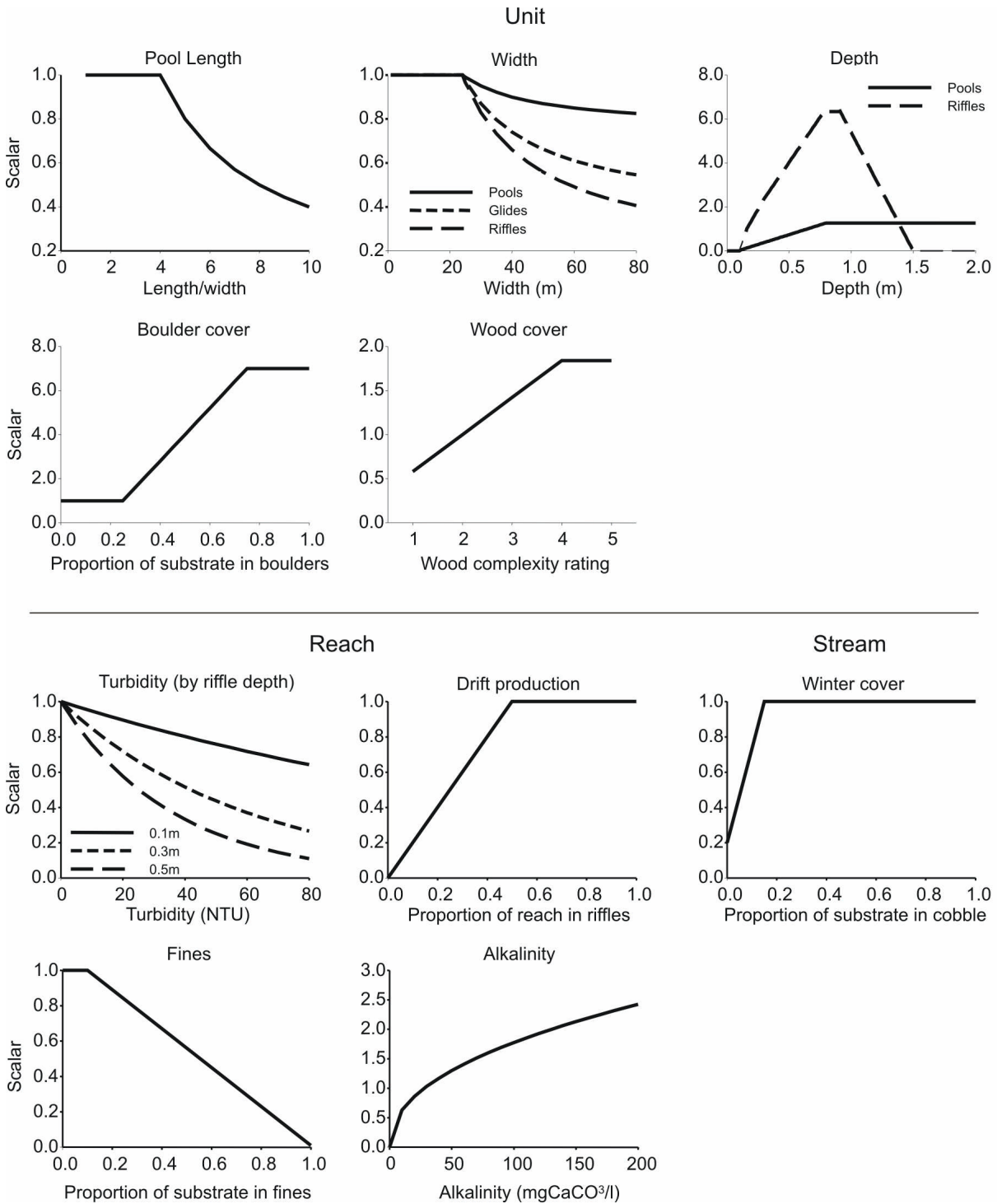


Figure 2. Habitat preference relationships applied within the UCM for scaling standard parr densities to those expected under the specific habitat features in a given stream.

Although steelhead parr prefer increasing depth in riffles up to 0.8 m, there is also evidence that this preference declines as riffle depth exceeds 0.9 m (Bovee 1978; Conner et al. 1995). Conner et

al. (1995) found that the range of depths preferred by juvenile steelhead grew smaller as velocity increased, and that juvenile steelhead only preferred deep areas where velocity was moderate. Hydraulic forces dictate that mid depth velocities in riffles will increase as depth increases, due to the reduced influence of friction with the streambed. Thus, increasing velocity is likely the cause of reduced preference by steelhead parr for depths >0.9 m. Accordingly, we assumed parr densities would decrease at depths > 0.9 m in riffles. The “*dep*” scalar increases linearly with increasing depths of 0.1 to 0.8 m in pools and riffles, and decreases linearly at increasing depths from 0.9 m, to a value of 0 at depths >1.5 m in riffles (Table 1; Figure 2). We found no clear correlation of steelhead parr densities to depth in other unit types, so we made no depth adjustment for other unit types.

The weighting factor for depth preference in the UCM was set at 1.0 for the average depth in the streams from which standard densities were derived by Johnson et al. (1993). However, Johnson et al. (1993) did not report depth, so the standard depth was defined as the mean of those reported by Oregon Department of Fish and Wildlife (ODFW) (online data 2005b) for channel units in 10 of the streams sampled by Johnson et al. (1993).

Cover (cvr).—The UCM accounts for the effects of cover (*cvr* term in Equation (1)) on steelhead capacity by relating availability of wood in pools and glides, and boulders in riffles, to steelhead densities (Table 1; Figure 2).

Boulders provide important cover for steelhead parr in riffles (Don Chapman Consultants 1989; Dambacher 1991; Ward and Slaney 1993). Two approaches were developed to use existing stream survey data to account for the effect of boulder cover in riffles on steelhead capacity. In cases where only the dominant type of substrate was recorded, boulder dominance received a multiplier of 6.0, and other substrates had a multiplier of 1.0 (based on data of Johnson 1985). If substrate was recorded as percentage composition, then the multiplier was 1.0 for <25% boulders, and increased linearly up to 7.0 when boulders composed 75% of substrate. Boulders composed 25% of substrate in the streams from which standard densities were derived.

While boulders are the key form of cover in riffles, woody debris provides the most important form of cover in pools and glides (Bustard and Narver 1975; Johnson et al. 1993). The scalar for effects of woody debris cover was based on findings from Johnson et al. (1993), as described in Cramer and Ackerman (2008). The UCM uses inputs of wood complexity rated for each channel unit on a scale of one to five, with fish densities increasing as the wood score increased (Table 1, Figure 2). The wood cover scalar was calibrated to a value of 1.0 for the median wood complexity score of 2.0 observed in pools and glides of the standard streams.

Productivity (prod).—At the reach scale, there are stream productivity factors (*prod*) that influence all units of a reach in common. The UCM scales the effects of productivity on parr

capacity based on four factors: turbidity (*turb*), invertebrate habitat (*drift*), fine sediments (*fines*), and stream alkalinity (*alk*). That is:

$$(2) \quad prod_i = turb_i \cdot drift_i \cdot fines_i \cdot alk_i$$

where:

turb = turbidity during summer low flow (measured in NTUs),

drift = percentage of reach area in fastwater habitat types that produce invertebrates,

fines = percentage of substrate in riffles composed by fines, and

alk = alkalinity during summer low flow (measured as mg/l CaCO₃).

Before being used to calculate *prod_i*, each of these variables were converted to a scalar with a value of 1.0 corresponding to the mean or median value of the variable in the standard streams.

Turbidity (*turb*) influences productivity by reducing light penetration, which reduces primary production. Cramer and Ackerman (2008 review published evidence for biological production in streams that links sunlight to primary production, then to invertebrate production, and finally to salmonid production. In the UCM, any reduction in primary production during the low flow season would reduce steelhead capacity by the same percentage. A relationship described by Lloyd et al. (1987) was used to predict the effect of turbidity on primary production (Table 1; Figure 2), accounting for increasing attenuation of light with water depth. Mean riffle depth is used for the value of depth in the equation, because riffles are the primary location in the stream that produces most invertebrates that salmonids feed on (Hawkins et al. 1983; Rader 1997). The maximum depth we applied was 0.5 m, because velocity increases with depth in riffles, and may limit invertebrate production. If turbidity data were not available, and the stream was regarded to be a typical clear stream, the turbidity scalar was assumed to be 1.0.

The UCM uses the percentage of area in fastwater habitats (riffles, rapids, and cascades) as an index of invertebrate production (*drift*) (Cramer and Ackerman 2008). Waters (1962) found that trout consumption of mayflies per surface area in pools (0.45 g/m²) exceeded the production of mayflies per area of riffles (0.28 g/m²) where the drifting mayflies were produced, which indicated that at least 60% of the stream area had to be riffles in order to produce the abundance of mayflies that were consumed in the pools. This finding was the basis for the assumption in the UCM that invertebrate food supply limits production in a stream reach if fastwater habitat types compose less than 50% of the surface area of the reach. We assumed that food capacity to support salmonids dropped linearly as the percentage of fastwater habitat types dropped below 50%, and we assumed that a minimum of 10% food capacity was retained even where fastwater habitat types were absent (Table 1; Figure 2). These assumptions were corroborated by observations in

low-gradient streams of the Willamette Valley where abundance of salmonids was positively correlated to the percentage of area in riffles over the range of 4 to 50%, with salmonids composing less than 1% of fish in streams that had less than 11% riffle (Waite and Carpenter 2000).

The findings of Bjornn et al. (1977) were used to establish a UCM scalar that reduces stream capacity for parr rearing as fine sediments (*finer*) reach 10% or higher of substrate in riffles (Table 1; Figure 2). Density of juvenile steelhead in summer and winter was reduced by more than half when enough sand was added to fully embed the large cobble substrate in an experimental stream (Bjornn et al. 1977).

Alkalinity (*alk*) is a commonly measured analyte in streams that is useful as a surrogate of nutrient concentrations. Ptolemy (1993) found a positive relationship between total alkalinity and salmonid abundance across 226 streams in British Columbia and confirmed the relationship with data from 37 streams in six countries ($R^2 = 0.86$). We used the relation developed by Ptolemy (1993) to scale the effects of stream productivity to the median alkalinity of 28 mg/l CaCO_3 in mid-summer for Oregon coastal streams from which standard parr densities were derived (Table 1; Figure 2).

Over-winter Survival

The UCM predicts the capacity of age>1 parr, but these parr must still survive through the winter before they undergo parr-to-smolt transformation and migrate to sea the next spring. Many studies have demonstrated that steelhead typically seek refuge in the winter within the interstices of cobble and boulder substrate (Hartman 1965; Bjornn 1971; Bustard and Narver 1975; Swales et al. 1985; and USFWS 1988). Several studies have demonstrated that steelhead pre-smolts will migrate from an area in the fall where cobble-boulder substrate is in short supply, but these fish typically find appropriate winter habitat further downstream (Bjornn 1978; Tredger 1980; Leider et al. 1986). Thus, the model uses availability of cobble substrate throughout the stream network as an index of winter capacity for steelhead parr (*winter* in Equation 1). The UCM assumes that 15% of substrate comprised by cobbles is sufficient to support the numbers of parr surviving the summer, and winter capacity would drop linearly to a minimum scalar value of 0.20 if cobbles were absent (Table 1; Figure 2).

The over-winter capacity scalar is subsequently multiplied by the expected winter survival for age>1 parr to complete the translation of parr capacity into smolt capacity. Over-winter survival of steelhead parr is typically between 35 and 65% (Chilcote et al. 1984; Reeves et al. 1990; Tautz et al. 1992; Ward and Slaney 1993; Kiefer and Lockhart 1999). We assumed 50% survival to convert parr capacity to smolt capacity, unless data for a specific basin led us to assume otherwise.

Test Basins

Capacity estimates from the UCM were corroborated through comparison to observed parr and smolt production from seven steelhead-producing basins (referred to as test basins) of varied habitat characteristics and locations throughout Oregon (Figure 3). Though the UCM predicts parr capacity during summer low flow, abundance of juvenile steelhead is most often sampled when they emigrate from a stream as smolts in the spring. The abundance of smolts reflects the cumulative effects of all freshwater limitations to production, and thus is a useful index of carrying capacity. Our application of the parr-to-smolt survival rate described earlier facilitated comparisons of UCM estimates to juvenile steelhead production.

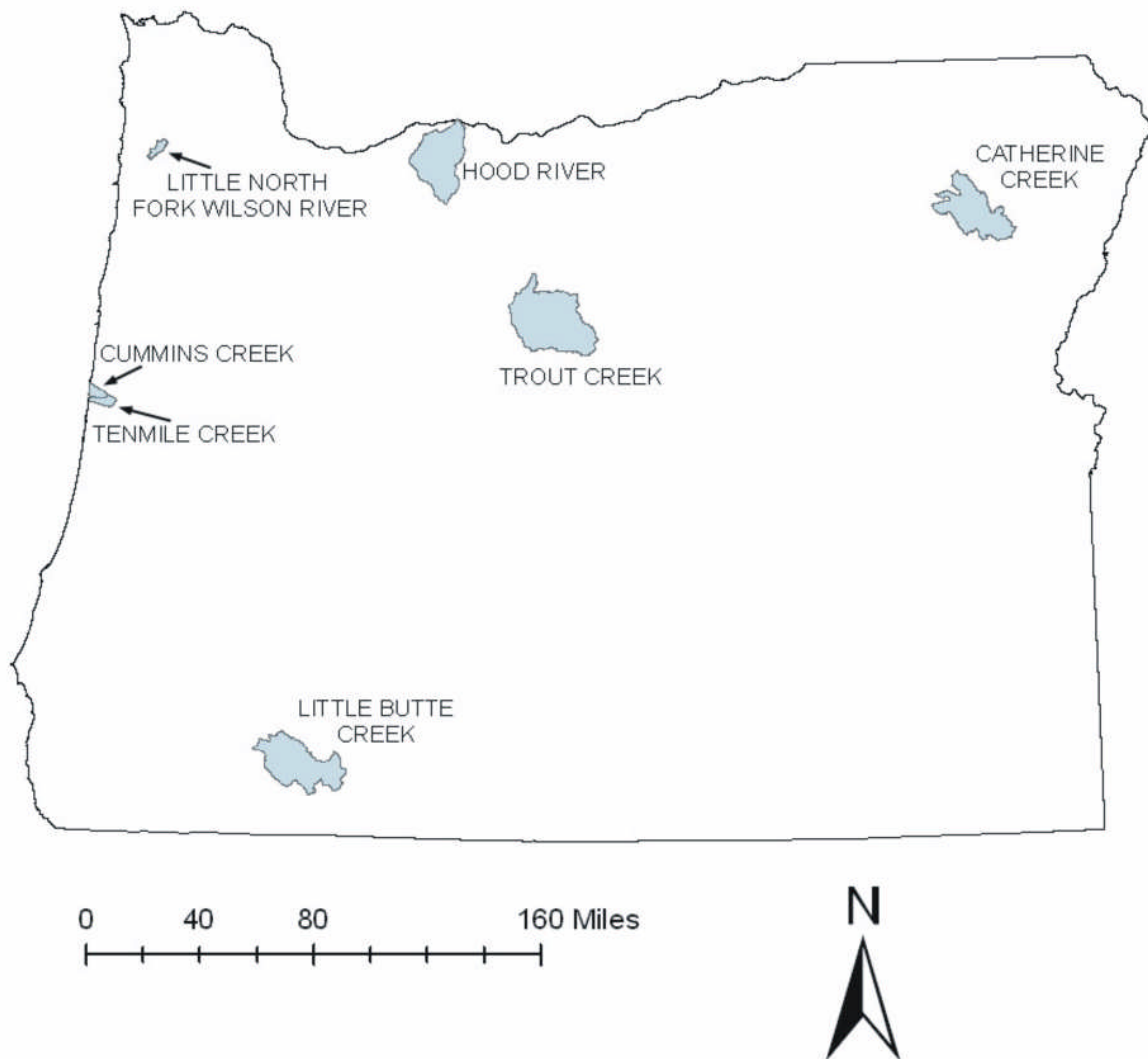


Figure 3. Map displaying relative location of test watersheds within Oregon.

Watershed areas ranged from 26 to 1,420 km² (Table 2). One of the basins (Hood River) was strongly influenced by glacial melt-waters during summer, three basins drained arid watersheds to

the east of mountain ranges (Trout Creek, Catherine Creek, and Little Butte Creek), and three basins were in a wet coastal region (Cummins Creek, Tenmile Creek, and Little North Fork Wilson River). Either parr or smolt production of steelhead had been estimated by the ODFW in these watersheds using direct sampling methods for five to 11 years (Table 2).

Table 2. Drainage area and estimated abundance of juvenile steelhead in watersheds used to test the UCM. Tenmile and Cummins Creek population estimates are in terms of parr. Remaining watersheds are in terms of smolts.

Watershed	Watershed Area (km ²) ¹	Years of Population Estimates	Minimum Population	Average Population	Maximum Population
Tenmile Creek ²	60	1991-1995	12,180	15,270	19,784
Cummins Creek ³	26	1996-2000	4,798	5,743	7,171
Little North Fork Wilson River	52	1998-2004	3,524	10,108	20,686
Little Butte Creek	966	1998-2004	15,634	21,801	27,425
Hood River	912	1994-2004	4,936	14,242	27,193
Trout Creek ⁴	1,420	1998-2004	11,643	25,888	51,199
Catherine Creek ⁴	267	1997-2001	10,377	13,029	19,865

1. Approximation of watershed area above downstream migrant trap.
2. Population was monitored in 1996-2000, but ODFW (who conducted sampling and population estimates) determined that production estimates in those years were unreliable.
3. Population was monitored in 1991-1995, but data indicated the basin was underseeded in those years.
4. Population estimates reflect smolts normalized to age 2. See subsequent methods section.

Habitat data that were inputs to the UCM were obtained from surveys by ODFW and United States Forest Service (USFS) using their standard protocols (Table 3). Steelhead distribution in these basins was defined using 1:100K data from the ODFW Fish Distribution Data Development Project (ODFW online data 2005a). Water quality data were obtained from the Oregon Department of Environmental Quality (ODEQ online data 2006). In some basins, habitat data did not provide complete coverage for the range of steelhead rearing distribution. Typically, unsurveyed habitat was at the upper extent of steelhead presence and in small tributaries. In these situations, we assigned parr per meter values predicted by the UCM from the surveyed reach that we judged to be most similar. Similarity was judged by such factors as gradient, watershed area, valley form, channel form, flow, elevation and precipitation. Most often, this judgment led to use of the nearest reach with similar width and gradient.

Table 3. Sources of outmigrant and habitat data used within the UCM test basins.

Basin	Outmigrant Data	Habitat Survey Data
Tenmile Creek	Solazzi et al. 2002	Pers. comm., Steve Johnson, ODFW
Cummins Creek	Solazzi et al. 2002	Pers. comm., Steve Johnson, ODFW
Little North Fork Wilson	Dalton 2001; Pers. comm.,	ODFW online data 2005b, Tim Dalton, ODFW
Little Butte Creek	Vogt 2004; Pers. comm., Jay Doino, ODFW	ODFW online data 2005b
Hood River	Olsen 2005	ODFW online data 2005b; Unpublished data, US Forest Service, Mt. Hood NF.
Trout Creek	Pers. comm., Tom Nelson, ODFW	ODFW online data 2005b; Unpublished data, US Forest Service, Ochoco NF.
Catherine Creek	Reischauer et al. 2002	ODFW online data 2005b; Unpublished data, US Forest Service, Wallowa-Whitman NF

In some instances, measurements of some habitat attributes were not directly applicable to the UCM. For instance, substrate composition was only classified into dominant and sub-dominant types in some reaches. In this particular situation, habitat data from streams around Oregon were used to draw correlations between dominant/sub-dominant substrate types, and the percentage of substrate most likely represented by those classifications. If a clear basis could not be derived to translate existing survey data into the inputs called for by the UCM, then no adjustment was made for the function (e.g. wood complexity data were not collected in Trout Creek). This practice assumes that the unmeasured factor value was equal to the average from the standard streams. Basin coverage of habitat data to supply inputs for the UCM was generally good. The reaches that accounted for over 90% of the capacity predictions were fully surveyed in all test streams except Little Butte Creek and Trout Creek, where 81% and 69% of the predicted capacities were generated from the reaches that had been surveyed.

Directly sampled production data from each test basin was examined for evidence that juvenile production reached capacity (full seeding) in some of the years sampled. Evidence of full seeding with juveniles was deduced from high smolt production in some years relative to that expected based on watershed area (Cramer and Ackerman 2008), or consistency in smolt production across several years. Only Catherine Creek in the Grande Ronde Basin appeared not to have reached full seeding.

In Tenmile Creek and Cummins Creeks, both direct ocean tributaries in Oregon, the size of the summer rearing population of parr was estimated via snorkeling and electrofishing surveys by the ODFW between 1991 and 2000. In Tenmile Creek, only population estimates from 1991 to 1995 were included in the analysis, because those were the only years ODFW deemed the estimates sufficiently reliable (pers. comm., Steve Johnson, ODFW). In Cummins Creek, we used parr

population estimates for 1996 to 2000 in our analysis, because smolt abundance was high and stable compared to lower, but increasing abundance during 1991 to 1995. Parr estimates for these two basins were converted to estimates of smolt production by assuming 50% survival from parr to smolt.

Hood River was the only basin tested where we assigned other than 50% for over-winter survival. Glacial influences in Hood River resulted in a high volume of fines, which embedded the available cobble and restricted over-winter cover. High percentages of fines in the substrate have been implicated in stimulating emigration and reducing overwinter rearing densities for salmonids (Bjornn et al. 1977; Bjornn 1978; Hillman et al. 1987). Accordingly, we applied a 35% parr-smolt survival rate to the Hood basin as was done by Underwood et al. (2003).

We defined observed capacity as the 80th percentile of population estimates for each watershed. The 80th percentile was chosen to ensure that the estimate represented years in which production was maximized, yet avoided positive bias that could result if we used only the year of greatest production, which may have resulted from unusual circumstances.

RESULTS

Range of Habitat Features Tested

A wide range of habitat features used in the UCM were represented across the test basins. The UCM was populated with data from 190 reaches across seven basins. For most habitat attributes, there was a several-fold range in the median values between reaches within each basin (Figure 4). Only a few notable differences existed between basins including: the proportion of pools, the proportion of fines in riffles, and alkalinity (Figure 4). The percentage of pools was generally higher, and the percentage of fines was lower in coastal basins than elsewhere. The percentage of stream surface area composed by pools, riffles, rapids, and glides was consistent between the three coastal basins, and more variable among the interior and glacial basins (Table 4). Alkalinity was higher in the interior basins than in coastal or glacial basins. Hood River basin, although having a full range of channel sizes from small tributaries to the main river, included the widest channels, lowest proportion of pools, deepest riffles, and the highest percentage of fines. Wood complexity rarely exceeded a score of 2.0 in any of the basins, and only reached a median of 2.0 in the Cummins Creek basin, where landslides and habitat restoration had recently introduced substantial quantities of large wood.

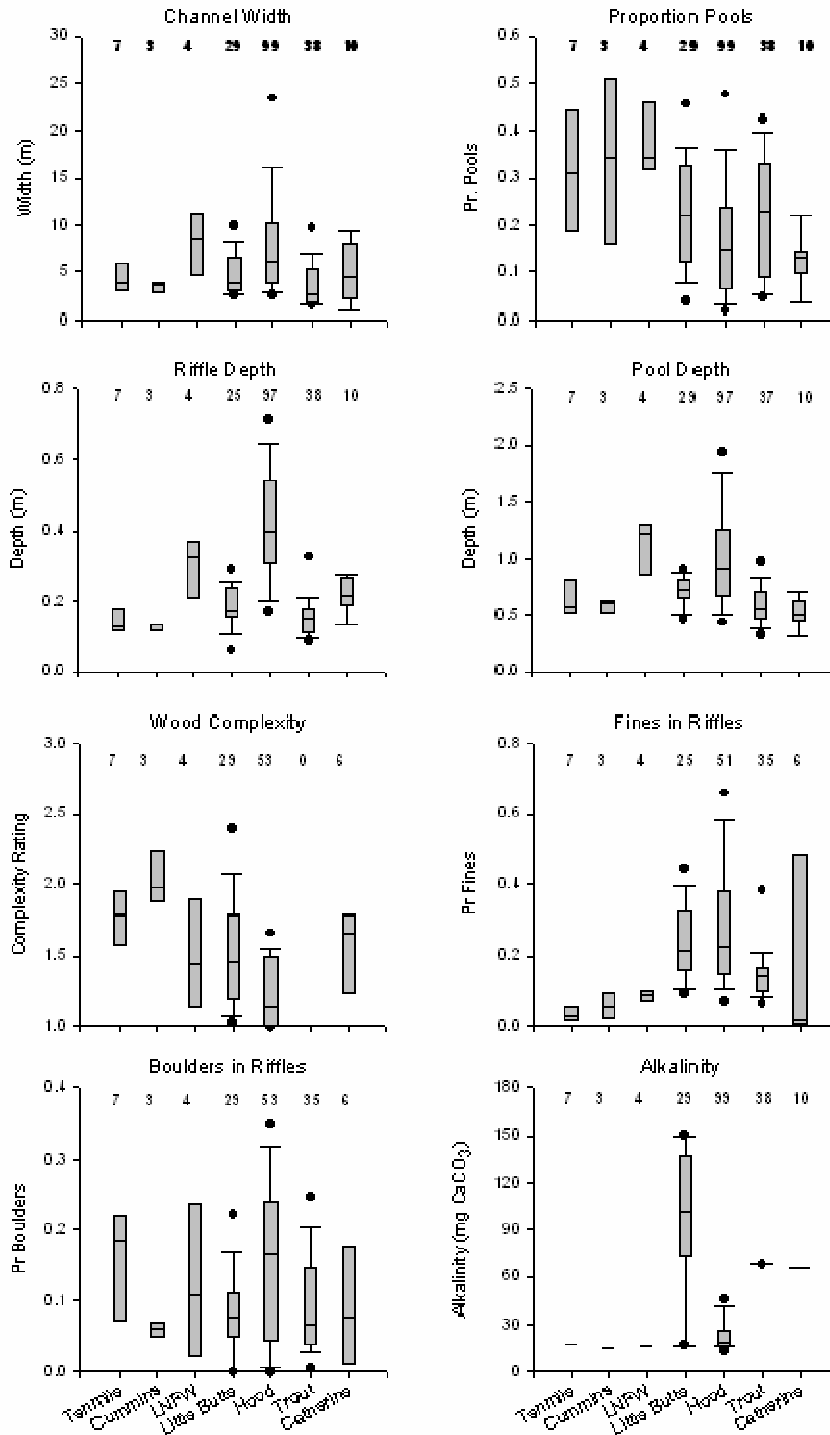


Figure 4. Habitat attributes associated with each basin where UCM capacity estimates were made. Plots constructed using mean values from reaches within each basin where data for a particular attribute were available. Box is defined by 25th 50th, and 75th percentiles, whiskers represent the 10th and 90th percentiles, and points represent 5th and 95th percentiles. Sample size (n) is located above each box and varies between plots because data on all attributes was not collected in every reach.

Table 4. Habitat unit composition of test basins. Values represent the mean value from all reaches incorporated into the UCM.

	% Glide	% Pool	% Rapid	% Riffle
<i>Coastal Basins</i>				
Tenmile Creek	7%	41%	22%	28%
Cummins Creek	3%	41%	31%	24%
Little N. Fk. Wilson	14%	40%	12%	26%
<i>Interior Basins</i>				
Little Butte Creek	9%	38%	23%	24%
Hood River	2%	16%	54%	19%
Trout Creek	6%	30%	8%	50%
Catherine Creek	3%	13%	38%	45%

Observed and Predicted Smolt Capacity

Direct sampling of parr or smolt production in test basins showed variability between years (Figure 5). Repeatability of high juvenile production was a criterion for determining full seeding of capacity. Production for the highest three years ranged less than 25% within each basin, except in Trout Creek and Catherine Creek. In Trout Creek, unusually high smolt abundance in 1998 resulted from exceptionally rapid growth in 1997, followed by an unusually high percentage (64%) of age-1 smolts in 1998. Most smolts have been age 2 in other years (pers. comm., T. Nelson, ODFW, Madras, OR). Thus, the unusually high abundance of smolts in 1998 was not regarded as evidence of unmet capacity in other years. No such event occurred in the highest year of smolt production in Catherine Creek and spawner abundance was believed to be low compared to historic levels (pers. comm., R. Carmichael, ODFW, La Grande, OR). Therefore, direct estimates of smolt production in Catherine Creek did not qualify for estimating observed carrying capacity. Estimates of observed capacity for the six qualifying test basins are given in Table 5.

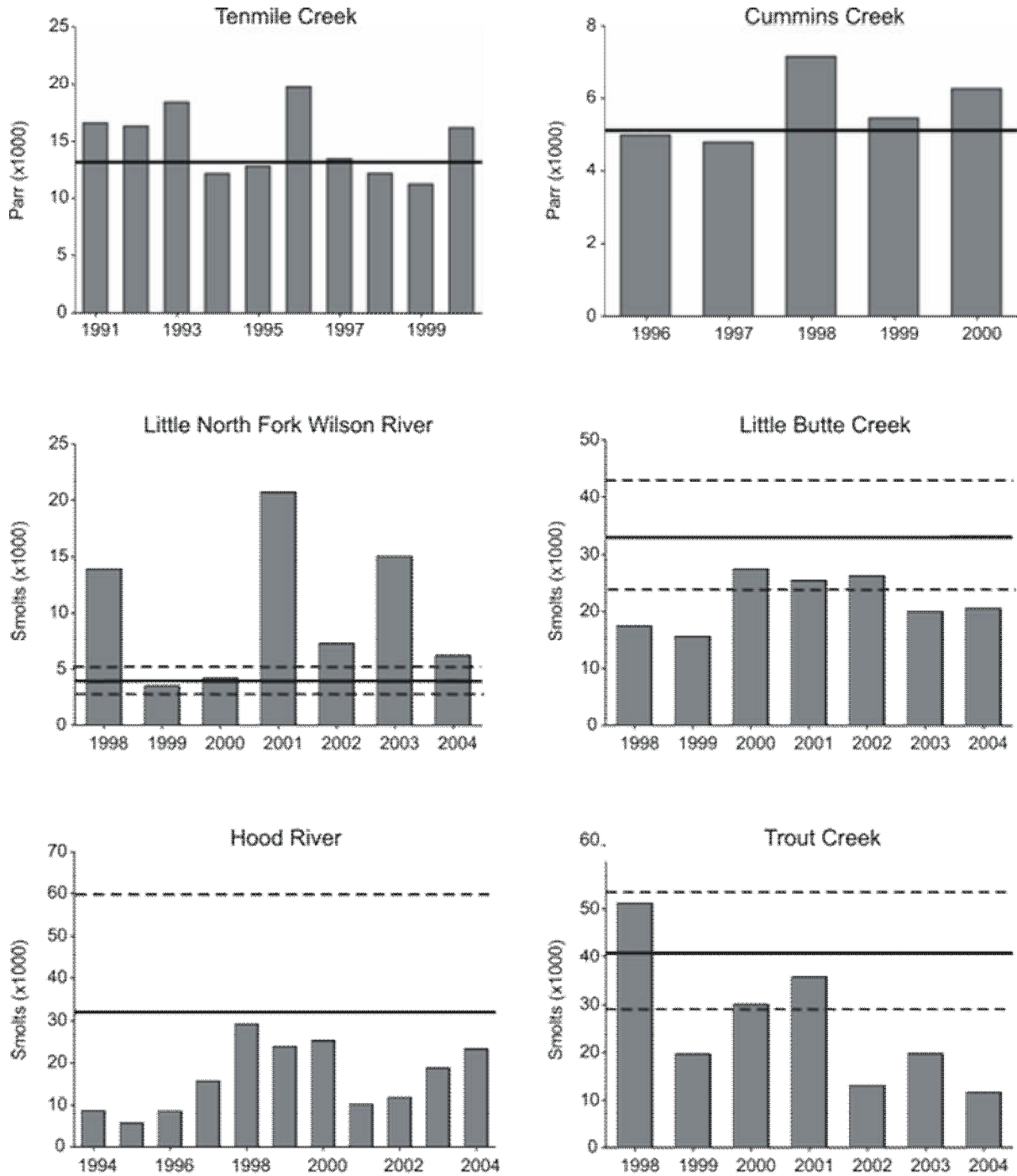


Figure 5. Annual estimates of steelhead parr or smolts produced in each test basin. Data from sources in Table 3. Solid horizontal line represents the UCM capacity estimate based on a 50% Sow (35% in Hood River). Dotted lines represent the range of the UCM capacity estimates assuming a 35%-65% Sow.

Parr capacity predictions from the UCM ranged from 5,127 in Cummins Creek (the smallest of tested watersheds) to 91,505 in the Hood River basin (Table 5). These capacities expressed in terms of smolts were 2,563 and 23,843 respectively. Because parr in the Hood River basin were assigned lower winter survival (35%) than other test basins (50%), predicted smolt capacities in Little Butte Creek and Trout Creek were greater than for Hood River basin (Table 5). Basin-wide averages for predicted densities at parr capacity ranged from 5.4 parr/100 m² in the Hood River to 11.0 parr/100 m² in Catherine Creek (Table 5).

Table 5. UCM predictions of parr and smolt capacity at the assumed over-winter survival (S_{ow}) in test basins, compared with observed capacity based on direct estimates of juvenile production. The observed capacity represents the 80th percentile of observed production estimates (Table 2). The observed capacity and prediction deviations are based on parr for Tenmile and Cummins creeks, and based on smolts for the remainder of the basins.

Basin	Predicted Parr Capacity	Predicted Parr/100m ²	Assumed S_{ow}	Predicted Smolt Capacity	Observed Capacity	Prediction Deviation
Tenmile Cr.	13,253	6.7	50%	6,676	16,974	-22%
Cummins Cr.	5,127	7.0	50%	2,562	6,452	-21%
Little N. Fk. Wilson	7,913	6.4	50%	3,957	14,797	-73%
Little Butte Creek	65,982	8.1	50%	32,991	26,024	+27%
Hood River	91,505	5.4	35%	32,026	23,843	+34%
Trout Cr.	81,575	9.9	50%	40,787	34,620	+18%
Catherine Cr.	47,787	11.0	50%	23,894	—	—

Smolt capacities predicted by the UCM were highly correlated to observed capacities across the six test basins that had evidence of full seeding ($R^2 = 0.88$; $P < 0.005$) (Figure 6). However, watershed area by itself was equally well correlated to observed capacities across the six test basins ($R^2 = 0.88$; $P < 0.005$; Figure 7), and the UCM predicted capacity was also correlated to basin area ($R^2 = 0.92$). Predicted capacities in the three largest basins all exceeded the 80th percentile of observed juvenile production, indicating there may be a tendency for the UCM to over-predict capacity in larger basins. Deviations of predicted from observed capacities were modest for five of the six basins, ranging from -22 to +34% (Table 5). Only in the Little North Fork Wilson basin did predicted capacity (3,957) deviate substantially from observed capacity (14,797; -73%).

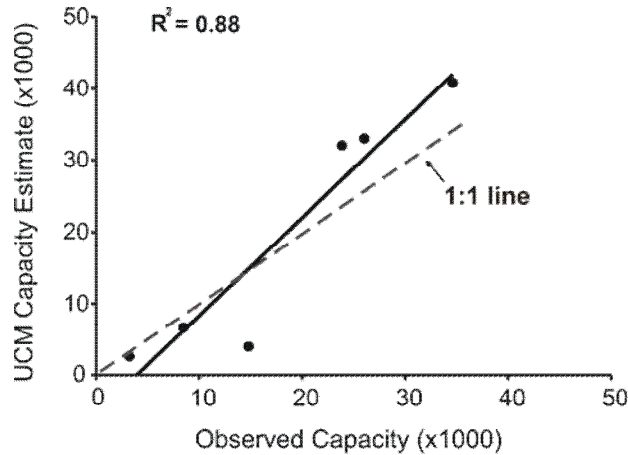


Figure 6. Relationship of predicted to observed smolt capacities for the six test basins. Catherine Creek excluded from the comparison because it was not believed to be fully seeded. Solid black line is least-squares regression line. The dashed gray line indicates 1:1 relationship.

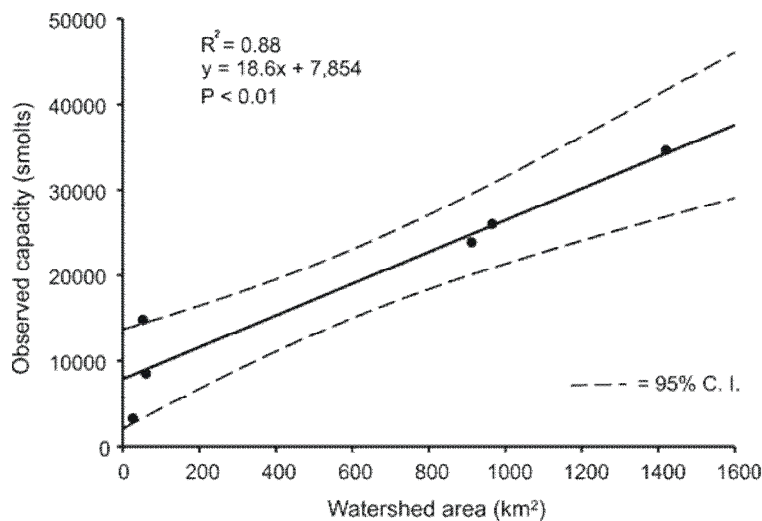


Figure 7. Regression of observed smolt capacity on watershed area in the six test basins.

Observed parr abundances were most consistently near the predicted capacity in Cummins and Tenmile creeks, where parr abundance was slightly above or below the predicted value in a balanced number of years (Figure 5). These were the only two basins in the test set for which juvenile production was estimated directly for age-1+ parr, rather than for smolts. Thus, no assumption about over-winter survival was necessary for these basins, but in all other basins, an assumed winter survival rate had to be assigned to the parr capacity estimate to calculate smolt production the following spring.

In two of the six basins analyzed, Little Butte Creek and Hood River, the observed annual parr abundance, derived from smolt sampling, fell below the UCM predicted capacity in all years sampled. If we assumed winter survival was 35% in Little Butte Creek, then estimated parr abundance reached the UCM predicted capacity in three of seven years (Figure 5). The Hood River was the only test basin for which smolt sampling indicated parr abundance was less in all years sampled than that predicted by UCM, assuming the low range of winter survival (35%). In contrast, smolt abundance exceeded the predicted capacity in six of eight years sampled in the Little North Fork Wilson River, and deviations from predicted capacity were greatest there for any of the test basins (Table 5).

Distinction of Habitat Quality

The UCM provided a quantitative measure of habitat quality by predicting the density of parr or smolts that a given basin, or stream reach within the basin, could support. Although basin area was highly correlated to observed smolt production, the UCM predicted that four of the seven test watersheds had widely differing habitat quality between reaches. Only the three coastal watersheds had consistent habitat quality, as indicated by the low variability in predicted density among reaches, compared to the interior basins (Figure 8). All of the interior and glacial basins had some low quality reaches that would support less than 0.01 smolts/m², and high quality reaches that would support greater than 0.06 smolts/m². Median values of smolt density at capacity were about 50% higher in interior basins than those for coastal basins.

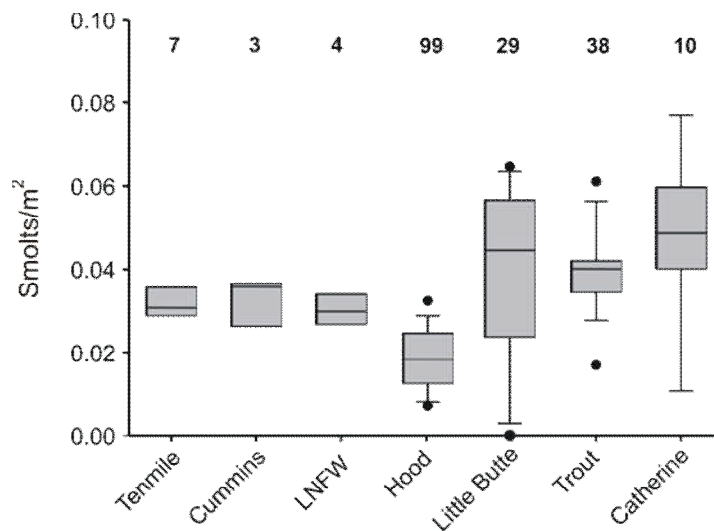


Figure 8. Predicted smolt capacity densities among reaches within each basin. Sample size (n) is labeled above each box. Box is defined by 25th 50th, and 75th percentiles, whiskers represent the 10th and 90th percentiles, and points represent 5th and 95th percentiles

Prediction Sensitivity to Habitat Factors

Differences between basins.—Alkalinity (*alk*) had a greater effect on capacity predictions than any other model term (Figure 9). Alkalinity strongly distinguished watersheds in dry, interior climates from those in wet, coastal climates. The adjustment for alkalinity substantially increased predicted capacities for Trout, Catherine, and Little Butte creeks, while slightly decreasing capacities in the other four basins. Predictions of basin capacity were moderately influenced by *dep* and *cvr*, with *dep* having more influence (Figure 9). The depth scalar for all basins exceeded 1.0, indicating that depths in the test basins were generally greater than in the standard streams. The cover scalar had mixed effects on model outcomes. Cover quality was better in Cummins Creek, Trout Creek, and Catherine Creek, but lower in other test basins than for the standard streams (Figure 9).

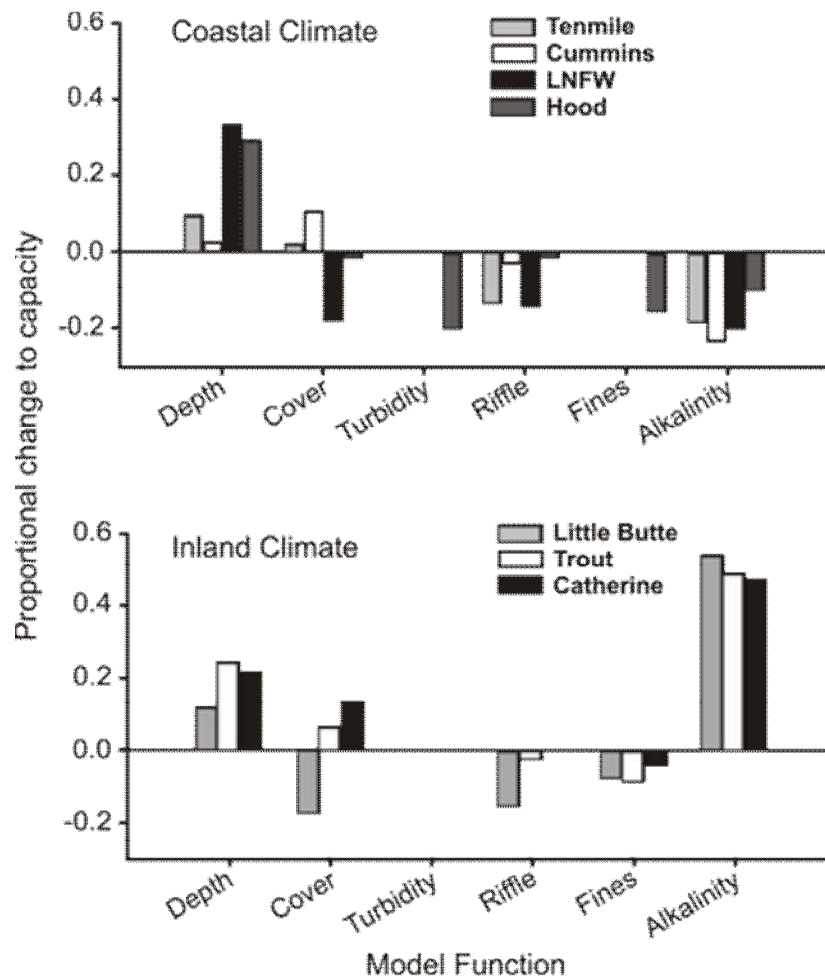


Figure 9. Response of UCM predicted capacity within each test basin to each habitat attribute.

The attributes, *turb*, *drift*, and *fines*, generally had small effects on most predictions, but notable effects in specific watersheds. The Hood River was the only glacially turbid stream tested, and the

predicted effect of turbidity there was to reduce capacity by 21% (Figure 9). The largest effect of *drift* on capacity predictions was to reduce capacity approximately 10% for three of seven watersheds (Figure 9). The proportion of fines in the substrate was only high enough in the Hood River Basin to have a notable negative effect (-15%) on predicted capacity (Figure 9). Fines averaged 26% in riffles in the Hood River basin, but only ranged from 2 to 17% in other test basins (Table 6).

Table 6. Habitat attributes of test basins. Note: In some reaches, habitat substrate was surveyed as dominant and subdominant substrate types. Those classifications are not included in this table, but were included in model scenarios.

Basin	Depth (m)		Wood	% Fines in	% Boulders	Alkalinity
	Pools	Riffles	Complexity (1–5)	Riffles	in Riffles	(mgCaCO ₃ /l)
Tenmile Creek	0.6	0.1	1.9	2%	22%	18
Cummins Creek	0.6	0.1	2.2	8%	10%	16
Little N. Fk. Wilson	1.2	0.3	1.3	8%	14%	17
Hood River ²	1.3	0.5	1.1	26%	19%	23 ¹
Trout Creek	0.6	0.1	— ³	17%	15%	68
Catherine Creek	0.5	0.2	1.7	2%	11%	66
Little Butte Creek	0.7	0.2	1.4	14%	7%	891

1. Several streams within the basin were assigned different values based on available data. Value is mean from streams included in the model. In other watersheds, a single value was applied to all streams within the basin.
2. Estimate represents value from dominant steelhead producing reaches. Reaches listed in Table A12 of Underwood et al. (2003).
3. No wood complexity data available for Trout Creek. Assumed no adjustment for wood complexity.

Differences between reaches.—More variation in habitat features was expressed between reaches than between basins, so we examined the effect of reach-level attributes on predictions of smolt capacity and density in 137 reaches where all, or nearly all, habitat attributes were evaluated in surveys. Stream surface area within a reach had the greatest influence on predicted reach capacity, but was not related to habitat quality (parr capacity/m²). Reach surface area ranged from under 5,000 m² to over 270,000 m², a 50-fold difference, among all reaches studied. Predicted habitat quality (parr/ m²) varied substantially by 15-fold between reaches, but the range of predicted capacities was still driven by the 50-fold range in stream surface area between reaches.

In the first calculation step of the UCM, the surface area for each type of channel unit is multiplied by the standard parr density for that unit type. We refer to this initial stage of calculations as the “base capacity” predicted by the model. The base capacity density (parr/m²) in

test reaches increased as a function of the percentage that pools composed of the stream surface area (Figure 10). The expected parr density at base capacity approached 0.04 parr/ m² as the proportion of pools in a reach approached zero, and increased up to 0.13 parr/m² at 70% pools, the highest percentage observed. This is a three-fold range in the densities predicted at this initial calculation step. Baseline capacity densities were higher in coastal Oregon watersheds, where pools comprised 40 to 41% of habitat, compared to 13 to 38% of the habitat in interior and glacial basins (Table 4).

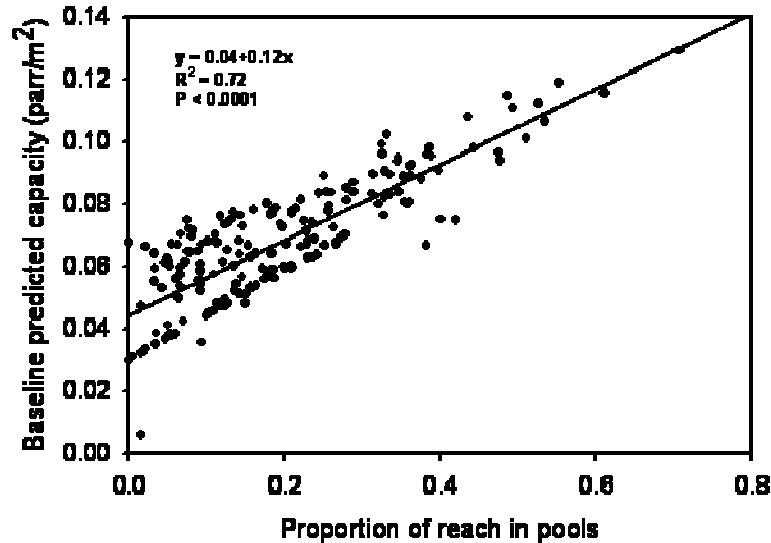


Figure 10. Relationship between the proportion of pools within a reach and the predicted base capacity in terms of parr/m². n = 190. The straight-line relationship among a large number of the observations in the lower left of the data array are reaches where only the pools were deep enough to support age >1 steelhead parr.

Sensitivity of capacity density predictions to functions within the UCM were determined by adding each UCM factor in stepwise fashion to the UCM calculation, and computing the proportionate change in the fish density prediction with each new factor added (Figure 11). We refer to this accumulating product of scalars as the cumulative density multiplier. The median value of this multiplier accumulated for all habitat factors in the UCM was 1.09 (little different than the base density of $(\sum area_{jk} \cdot den_j) / \sum area_k$), but ranged up to 3.0 for the 90th percentile of reaches and down to 0.2 for the 10th percentile (Figure 11). Alkalinity produced the greatest difference in the density multiplier between reaches, ranging from 0.8 to over 2.0 (Figure 11). The percentage of fines was the second most influential factor, and generally reduced the density multiplier, ranging from 1.0 down to 0.5. Lesser effects from pool and riffle depths tended to increase the multiplier, while channel width, wood cover (lack thereof), and fines tended to reduce it. Boulder cover, drift availability and turbidity usually produced scalars near 1.0, and only had notable effects in a few reaches. The multiplier for winter cover had no effect in any of the reaches surveyed.

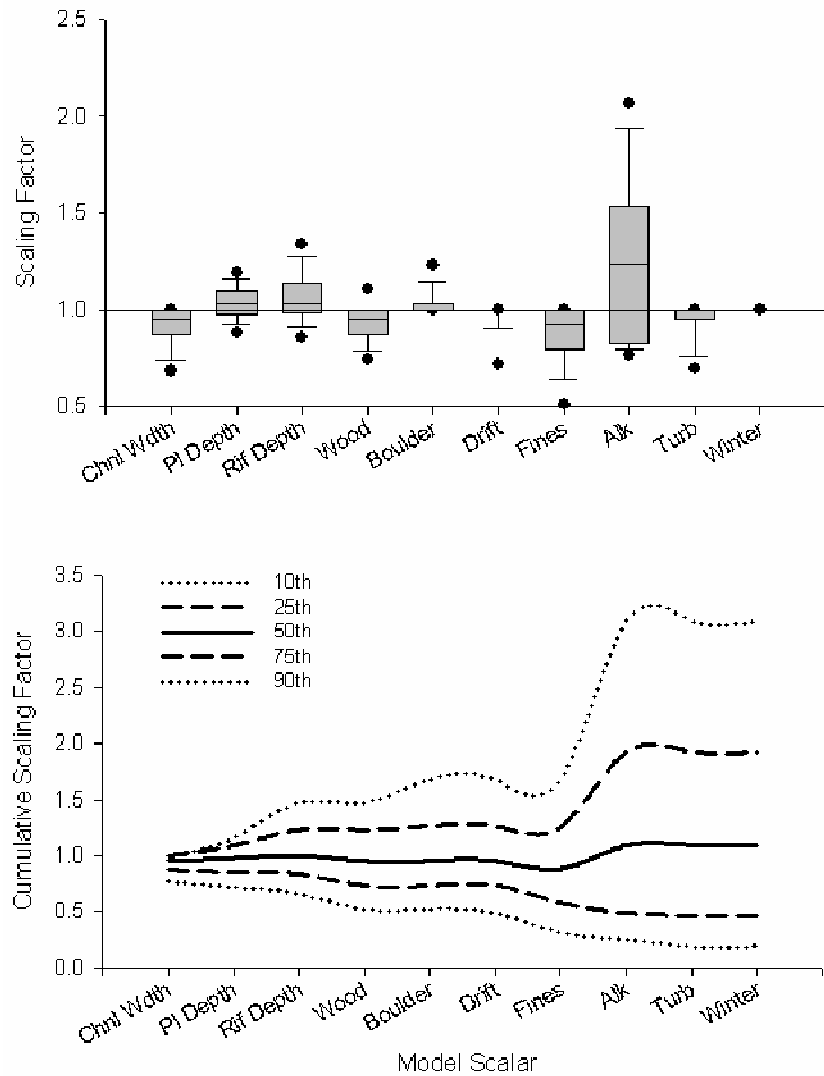


Figure 11. Effects of individual scalars on model outcomes. Top graph: Each box represents the effect of that scalar on model outcomes independent of other scalars. Plot constructed by pooling data from all basins and all reaches where full suite of habitat data were available (n = 137). Box is defined by 25th 50th, and 75th percentiles, whiskers represent the 10th and 90th percentiles, and points represent 5th and 95th percentiles. Bottom graph: plot constructed from data in top graph by compounding 10th to 90th percentile scaling factors across all model scalars.

DISCUSSION

Accuracy of Prediction

Parr capacities predicted with the UCM using habitat measurements at the channel unit level showed a high correlation ($R^2 = 0.88$) to direct estimates of smolt production in six test watersheds of widely different size and habitat characteristics. This finding suggests that the UCM predictions of smolt capacity are reasonably accurate at the basin scale, but we also found that basin area by itself was similarly correlated to observed smolt production ($R^2 = 0.88$). Thus, the high correlation of predicted and observed smolt capacities should not be regarded as validation of the UCM. Such validation will require comparison of predicted and observed parr or smolt per unit area (i.e., fish densities) between reaches representing a wide range of predicted capacity densities. Data on parr densities in each reach were not available for four of our six test basins. Though statistical procedures might be helpful to account for the separate effect of basin size on the fit of predicted to observed smolt capacity, our limited sample size of six basins with direct estimates of smolt production provides little statistical power to account separately for the effects of basin size.

However, by expressing these predictions in a per-unit-area scale, the overriding influence of reach area on basin predictions can be eliminated. Application of UCM to the test reaches demonstrated that the method could sharply distinguish habitat quality throughout the basin in terms of carrying capacity per unit area. The cumulative density multiplier in the UCM after all habitat factors were included ranged over 15-fold between reaches, from a high of 3.0 for the 90th percentile of reaches and to a low of 0.2 for the lower 10th percentile of reaches (Figure 11). Cramer and Ackerman (2008) presented the evidence from a number of studies that demonstrate steelhead parr densities are strongly related to the habitat factors included in the UCM, and the habitat data from the test basins indicate that those factors important to steelhead were substantially different between some of the reaches in nearly every basin. In spite of the wide range of these habitat factors and the large differences they produce in predicted parr capacity between the 190 reaches analyzed in this study, the sum of these reach-level predictions still reflected the observed smolt production from the basin. Thus, the UCM prediction appeared to have accurately expressed both the heterogeneity of habitat quality in a basin, and the combined potential of those different habitat qualities to produce smolts from throughout the basin.

The results of our study support the notion that basin area is a reasonable predictor of carrying capacity for steelhead similar to that reported for other species (Underwood et al. 2003). Our results also demonstrate that much additional information about limiting factors and likely

distribution of fish production in the basin can be gained from habitat measurements collected during typical state and federal stream surveys. Apparently, the averaging of a wide range of habitat qualities that exists between reaches within a basin leads to a central range of smolt densities that can be expected between basins. The predictions of the UCM for the test streams confirm this interpretation. As shown in Figure 11, the cumulative density multiplier, although ranging widely between reaches within a basin, still had a median value of 1.09; quite close to the 1.0 level that would indicate no difference compared with habitat quality in the streams from which standard parr densities were derived.

Sources of Error

The correlation of predicted to observed parr capacity ($R^2 = 0.88$) was surprisingly high given the substantial source of error introduced by back-calculating of summer parr capacity from estimates of smolt outmigration in four of the six validation streams. Predicted parr capacity was most consistently near the observed parr production in the two streams, Cummins and Tenmile creeks, where parr abundance was estimated directly from sampling of parr. In those two streams, observed parr abundances were slightly above or below the predicted capacity in a balanced number of years (Figure 5).

In addition to sampling variation, there are at least two sources of error that enter into the back-calculation to parr from smolt abundance. First, immigration or emigration of parr during fall is a common behavior among juvenile salmonids in pursuit of winter habitat (Cederholm and Scarlett 1981, Leider et al. 1986; Bramblett et al. 2002). Either event confounds our ability to determine actual parr capacity based on smolt population estimates. Second, differences in flow stability between streams can lead to substantial differences in over-winter survival, with peak flows reducing survival (Seegrist and Gard 1972), and stable flows allowing high survival (Mundie and Trabor 1983). We assumed a constant 50% overwinter survival in all years sampled, and in all test streams except Hood River, where we assumed a 35% overwinter survival. Overwinter survival was estimated annually during field studies in two of the test streams, Tenmile and Cummins creeks, and found to vary by two to threefold (32% to 59% in Cummins Creek and 18% to 48% in Tenmile Creek; Solazzi et al. (2002)). Clearly, this variation contributed to error in estimation of annual parr production in the test streams for which only smolt production was sampled.

Our analysis suggests that the UCM may slightly over-predict capacity in the larger basins ($> 900 \text{ km}^2$), such as Trout Creek, Little Butte Creek, and Hood River, or in highly alkaline basins such as Trout Creek and Little Butte Creek. In each of these basins, the observed smolt production for most sampled years fell below the predicted smolt capacity (Figure 5). The deviation of predicted

from observed was not large in these streams (18% to 34%), but the consistency of the pattern warrants scrutiny as further data are gathered. It may simply be that capacity is fully reached in large basins less frequently, because the larger stream network increases the probability due to random variation that some of the reaches will not be fully seeded. However, two of the three larger test basins were also assigned large increases in predicted capacity (about 150%) due to high alkalinity (Figure 9). It is possible that the high correlation found by Ptolemy (1993) for salmonid densities to alkalinity across 226 streams may have been influenced by correlations of alkalinity to stream morphology. Alkalinity tends to increase as runoff per km² watershed area decreases, and such differences in water yield may influence the formation of channel morphology. For example, pools comprised 40 to 41% of habitat in coastal basins, compared to 13 to 38% elsewhere for our test streams. These possible confounding factors warrant further study, but the results from our test streams suggest that little increase in prediction accuracy will be achieved by improvements to the basin size and alkalinity functions.

Smolt yield in the Little North Fork Wilson was anomalously high compared to the capacities predicted by both the UCM and watershed size (roughly four times the expected yield), and may have been influenced by immigration of parr from the main stem Wilson River in the fall. Substantial immigration would result in over-prediction of summer parr abundance when back-calculated from the abundance of smolts departing the stream the following spring. The Little North Fork Wilson enters the mainstem Wilson River near the upper end of tidewater, where it is a last-chance opportunity for non-natal rearing of juveniles that arrive in tidewater before they are ready to smolt. Local biologists have found no unusual habitat morphology in the Little North Fork to account for exceptional production of anadromous salmonids in that stream (pers. comm., Tim Dalton, ODFW).

A clear understanding of the distribution of steelhead rearing within a basin network of channels is important in determining juvenile production potential. The distribution of salmonids within a watershed varies seasonally and annually. These variations are driven in part by flow, temperature, and competition (Welsh et al. 2001; Jacobs et al. 2001; Bramblett et al. 2002). Greatest accuracy in applying the UCM can be achieved by excluding channels that may be used for migration or spawning, but not for rearing. For example, the uppermost reaches where steelhead spawn within a basin may provide an insufficient water supply during summer for parr rearing, in which cases parr move further down in the stream network to rear. Likewise, lower reaches that serve only as migration corridors should also be excluded from assignment of rearing capacity. Lack of rearing in lower reaches of a basin may result from the influences of factors such as high stream temperature or an abundance of predators, which are not included in the UCM.

UCM Sensitivity to Habitat Factors

The variation in reach scalar values for each habitat factor in all seven test basins provided a realistic and practical context for examining model sensitivity to the factors included. The wide range of values for each habitat factor between basins (Figure 4) provided a useful test for how the model responds to combinations of habitat features found in steelhead streams. Although the values for scalars ranged widely (with the exception of winter cover) the effect of averaging multiple factors across multiple reaches within a basin proved to be a strong homogenizing force on predicted density at capacity for a basin. Though scalar values for each of the eleven habitat factors ranged up to seven fold between reaches within a basin, the density multiplier accumulated across all factors had a median value of 1.09 and ranged only fourfold between the 25th and 75th percentile of reach values (Figure 11). As a result, the median reach value for predicted smolt density ranged only 2.5-fold between the seven test basins. Alkalinity had a greater effect on capacity predictions than any other model term, and its primary effect was to distinguish watersheds in dry, interior climates from those in wet, coastal climates (Figure 9). The percentage of surface area in pools accounted for up to a three fold range in the base parr densities between reaches, and up to 50% difference between basins. The factor of depth in pools and riffles tended to increase capacity densities by 20 to 30% in large basins compared with those in the smallest coastal basins, Cummins and Tenmile creeks (Figure 9).

Data from the test streams illustrate that specific habitat factors may only cause anomalies in habitat quality predictions in specific basins, while having little effect in others. As one example, the Hood River was the only glacially turbid stream tested, and the predicted effect of turbidity there was to reduce capacity by 21% (Figure 9). In another example, boulder cover had little effect in most streams, and had its largest effect in Catherine Creek, despite the low average proportion of boulders in riffles (11%). However, a high value of boulder cover in a small number of riffles (7% of the stream's habitat area) accounted for a 20% increase in the capacity prediction for the Catherine Creek basin. This second example illustrates the importance of applying model functions at the unit scale rather than using average habitat values at the reach or stream scale to estimate capacity. Even though a particular habitat factor may have little effect in most basins and reaches, it can still have an important effect in specific areas.

No specific measurements of velocity were included in the UCM, because velocity is not typically measured on stream surveys. Steelhead show strong velocity preferences related to their size, so the absence of specific velocity information undoubtedly contributes to error in the UCM prediction of carrying capacity. However, some effect of velocity is captured in the predictor through the densities assigned to different channel unit types. For example, steelhead are typically

found in riffles at higher densities than juvenile Chinook (Bjornn and Reiser 1991), or coho (Nickelson 1998). Thus, higher densities for steelhead than other salmonids in riffles reflects in part their unique velocity preferences, in combination with their preferences for other habitat features.

Applications of the UCM

Whether a proposed restoration strategy focuses on expanding stream habitats, improving fish passage, reducing the harvest fraction, or altering the use of hatchery fish, all of these strategies share a common need for accurate knowledge of a stream's capacity to produce the species of interest. The UCM offers the means to obtain such knowledge for many steelhead-bearing streams for which spawner abundance has not been monitored over the long term.

Both the UCM and basin area appear to offer rapid, accurate means to predict a stream's carrying capacity for steelhead. Traditional approaches to estimating carrying capacity have required 10 to 20 years of monitoring catch and spawner escapement, to statistically fit a stock-recruitment function such as the Ricker (1954) or Beverton and Holt (1957). Fits to these functions are generally mediocre, producing R^2 values in the range of 40 to 60%. For example, Chen and Holtby (2002) fit Ricker parameters for 83 populations of coho in British Columbia, and found the average model R^2 was 41%. While that approach will always remain useful, because it confirms real production of adult fish, basin area can be used to predict carrying capacity at least equally well with less than a few hours effort, and the UCM can be used with a few days to a few weeks of effort to distinguish habitat quality between reaches within a basin.

The novel information provided by the UCM about carrying capacity for steelhead in a stream is the present habitat value and limiting factors at specific locales throughout the basin. Further, the UCM quantifies stream carrying capacity in terms of stream features that can be targeted by habitat conservation/restoration actions, and makes it possible to predict changes in fish production that would result from changes to habitat features, even at the level of a single channel unit. Such an approach has been applied to coho by Nickelson and Lawson (1998) who used the habitat-based model of Nickelson (1998) to predict carrying capacity for coho in streams across the Oregon coast. Nickelson and Lawson (1998) then used a life-cycle model to predict the future change in coho populations that would result from habitat improvements versus that which would result from allowing continued habitat degradation. They found that the fine-grained habitat information included in their model of coastwide populations, "provided insights into the dynamics of coho salmon population and the mechanisms controlling their distribution within a basin." Similarly, the UCM is well suited for application in life-cycle modeling as a means to link

habitat features and their modifications, even at the channel unit scale, to the performance of an entire population.

The UCM can be used to provide a common currency for expressing the effectiveness of various kinds of habitat conservation or restoration activities. Restoration effectiveness has often been expressed in terms of specific habitat features that have changed, such as pool surface area or wood complexity (e.g. Crispin et al. 1993; Johnson et al. 2005). The UCM would enable these changes to be expressed as predicted changes in parr rearing capacity. Restoration actions may cause gradual change in habitat characteristics, and some changes will be eliminated by floods or channel changes (Roni et al. 2002), so these factors must also be accounted for by explicit assumptions when using the UCM to predict probable future benefits of a restoration project. While monitoring of restoration success should include sampling of fish response, wide variation in salmonid abundances from year to year and out-of-basin influences pose significant statistical hurdles for detecting the magnitude of effects on fish (House 1995). Monitoring of stream habitat change can be used in conjunction with the UCM to provide earlier and reliable feedback on benefits realized from an action.

Additional uses of the UCM may include predicting the change in production potential that would be realized with elimination of man-made barriers, or with the addition of artificial side channels. At a larger scale, changes in watershed management could affect turbidity, fines, channel width, or channel complexity, and each of these changes can be specifically accounted for in the UCM to determine their effect on steelhead carrying capacity.

The UCM may also be used, in conjunction with other tools, to identify areas within a watershed where preservation or restoration may be targeted. For example, when paired with an approach such as that taken by Burnett et al. (2006), areas within a watershed can be compared in terms of both their intrinsic and current potential. Those areas where intrinsic potential is high and there is great divergence of intrinsic and current potential could be considered for restoration. Areas where current potential is near its intrinsic potential may be considered for conservation.

Possible Enhancements to UCM

The UCM was developed for streams in which water quality and species composition were in the range typical of steelhead streams. Further studies may provide the data needed to derive scalars that would adjust for violation of these assumptions and broaden the set of streams for which UCM would be applicable.

Many water quality factors such as temperature, dissolved oxygen, pH, etc. are not included in the model, but can have significant impacts on habitat capacity. For example, high summer

temperatures may totally exclude steelhead from certain areas where the habitat is otherwise suitable. Incorporation of this into the understanding of stream capacity is important and should be dealt with when establishing the distribution of steelhead rearing. Additionally, increased nutrient levels beyond those accounted for in the alkalinity adjustment, such as nutrients derived from carcass additions, may offer improvement to capacity predictions.

Although the model assumes that summer habitat for parr limits steelhead production, recent studies have found that stream restoration techniques, particularly the addition of large wood, can enhance over-winter survival and increased production of steelhead smolts (Johnson et al. 2005). The UCM attempts to account for winter habitat through the inclusion of cobble availability, but the dynamics that determine winter capacity or survival are certainly more complicated than the availability of cobble. Further studies on winter habitat use and survival of juvenile steelhead may reveal a means to improve the accounting for differences in winter habitat.

Interspecific competition is an important phenomenon that is not accounted for in the UCM, and may substantially affect steelhead carrying capacity in some situations. Harwood et al. (2002) noted that interspecific competition for shelter (Gregory and Griffith 1996) can result in density-dependent use of refuge habitat (Armstrong and Griffiths 2001) and thereby have important implications in terms of carrying capacity. This may have specific implications to a stream's steelhead carrying capacity as competition with coho (*O. kisutch*) for summer habitat has been shown to cause steelhead to re-distribute themselves (Hartman 1965; Allee 1982). However, McMichael et al. (2000) found that competition between fish in the Yakima Basin was strongest between individuals of the *O. mykiss* species, but competition of steelhead with juvenile Chinook and coho was negligible. Interspecific competitive interactions are highly complex, and whether or not they influence capacity depends partly on the life stage at which competition occurs. The streams used to test the UCM included varied species assemblages that covered the typical range for steelhead streams throughout Oregon. Thus, we expect that separate accounting for inter-species competition or predation may only lead to substantial change in predicted rearing capacity in a small fraction of steelhead-producing streams.

The UCM does not distinguish between capacity utilized by the different life-histories of *O. mykiss* that may rear and compete with one another in the same reach. Non-anadromous rainbow will compete with anadromous fish, and thus would share the available capacity when rearing in the same reach. Further, McMichael et al. (2000) found in the Yakima River that agonistic interactions were substantial between individual *O. mykiss*, regardless of whether they were resident or anadromous, and that the larger individuals were behaviorally dominant in over 80% of contests observed. Thus, larger resident rainbow will be competitively dominant, and will defend more habitat per individual than steelhead parr (Grant and Kramer 1990). To account for

capacity consumed by non-anadromous *O. mykiss*, it will be necessary to account for additional habitat factors, and perhaps racial abundance.

CONCLUSIONS

The UCM provides estimates of basin carrying capacity for steelhead that are consistent with observed smolt yields for basins widely different in size and character. The UCM predictions indicate that habitat quality ranges widely between stream reaches within a basin, and the method provides specific metrics to identify factors most limiting and most beneficial for steelhead capacity. Such predictions can be used to prioritize and justify investments in habitat restoration or conservation. Factors that limit production are often quite different between stream reaches and even between basins. Given the range of habitat characteristics observed in the test basins, the predictions of steelhead capacity are most affected by the percentage of stream area in pools, alkalinity, and percentage fines in the substrate. Further validation of the model should be pursued at the stream reach level to compare predicted and observed parr densities across a wide range of habitat quality.

ACKNOWLEDGEMENTS

Much of the data we used on fish and habitat in test streams was collected by dedicated staff of ODFW and the USFS. We owe special thanks to Steve Johnson of ODFW who helped us obtain detailed data from their studies and answered our many questions about interpretation of their data. The Oregon Building Industry Association funded initial work on model development, and subsequent development was partially funded by both Bonneville Power Administration and Portland General Electric.

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