

# Linking Stream Carrying Capacity for Salmonids to Habitat Features

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*Abstract.*—Stream carrying capacity for anadromous salmonids that rear to the smolting stage in freshwater can be predicted from a sequence of cause-response functions that describe fish preferences for macro-habitat features. The channel unit (e.g., pool, glide, riffle) is a useful stratum for quantifying rearing capacity for salmonids, and is a hydrologically meaningful unit for predicting the response of stream morphology to watershed processes. Thus, channel units are the natural link between habitat-forming processes and habitat requirements of salmonids. Maximum densities of juvenile salmonids that can be supported in a channel unit are related to availability of preferred habitat features including velocity, depth, cover, and substrate. Within channel unit types, maximum densities of salmonid parr will shift predictably as availability of cover from wood and boulders increases. Within stream reaches, additional variation in maximum rearing densities can be accounted for by light penetration and nutrient load. As salmonids grow, their habitat preferences change and the preferred habitat associated with their increasing size becomes less and less available. Further, territory size of salmonids increases exponentially with fish length, such that the demand for territory to support surviving members of a cohort increases at least through their first year of life. Changing habitat preferences and space demands, juxtaposed against shrinking habitat availability with the onset of summer low flows often results in a bottleneck to rearing capacity for age >1 salmonids in wadable streams. Habitat measurements in Oregon streams indicate that depths preferred by steelhead (anadromous rainbow trout) *Oncorhynchus mykiss* become scarce as parr exceed 15 cm in length, which coincides with the approximate threshold length for steelhead smolts. We present a generalized framework, called the Unit Characteristic Method, for accumulating effects of these habitat factors at the channel unit and reach-level scales to estimate carrying capacity for rearing salmonids in a basin. Our subsequent chapter in this book presents a demonstration of how this method can be applied to predicting salmonid production in streams.

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## Introduction

How many salmon or trout should a given stream be capable of sustaining, and how will human actions affect those production capabilities? This is an urgent and often debated question, especially when resource managers constrain harvest, choose a hatchery strategy, regulate land or water use, or propose habitat restoration. All strategies to manage human activities so as to sustain desirable fish populations share a need to understand the primary drivers of fish population trends. The traditional approach to determining carrying capacity for anadromous salmonids has been through stock–recruitment analysis (Ricker 1954; Beverton and Holt 1957). That approach arose from an era that focused on determining maximum sustainable yield (MSY) for harvest. However, traditional approaches to quantifying stock–recruitment relationships have proven to be imprecise, because they are often based on an inadequate range of population sizes (Walters 1997) and they incorporate variation in survival through both the freshwater and marine phases of life. In the present era of depleted salmonid stocks across much of North America, with a mandate under the Endangered Species Act (ESA) to design recovery plans for ESA-listed populations, we need habitat-based approaches for estimating salmonid stream production capacities to inform harvest and habitat decisions.

Stock–recruitment analysis requires a long time-series of data that includes a wide range of run sizes, but such data are lacking for the great majority of salmonid-producing basins. Even when data are available, the approach usually leaves a large share of recruitment variation unexplained (Figure 1), and leads to wide confidence intervals on estimated parameters of the curve (Cramer 2000). Some of the most robust data sets available appear as a cloud of data points when scattered against one another, without a clear pat-

tern to indicate the form of the stock–recruitment curve that should best fit them. Further, that approach is not helpful for identifying the specific habitat factors that are limiting the population, or for estimating the benefits from potential stream alterations in a small portion of the watershed.

If stream features change, those changes will influence the stream’s capacity to produce salmonids. Field studies of salmonids and their habitats have rapidly expanded over the last decade, and provide opportunities to develop more accurate and utilitarian approaches for parameterizing the stock–recruit function of salmonid populations. Promising methods have emerged and are being refined to estimate carrying capacity and productivity directly from measures of stream habitat (e.g., Bartholow et al. 1997; Cramer and Ackerman 2009, this volume; Blair et al. 2009, this volume). An ideal approach to predicting carrying capacity and survival rates of salmonids based on habitat features in a stream would offer the advantages of easily available data, and the potential to predict fish benefits from proposed habitat restoration or protection strategies.

A great challenge in determining the effects of land and water management on fish has been the inadequacy of efforts to quantify cause–effect relationships between watershed changes and changes in fish populations (Imhof et al. 1996). The key to quantifying this linkage is to first determine the specific stream features that substantially influence salmonid populations, and then use watershed process models to predict how those features will change due to watershed management actions.

In this chapter, we synthesize empirical evidence to link stream carrying capacity for salmonids to habitat features, and we explore possible cause–response relationships that determine the life stage of salmonids for which suitable habitat is most limiting. We show that channel unit types provide reliable

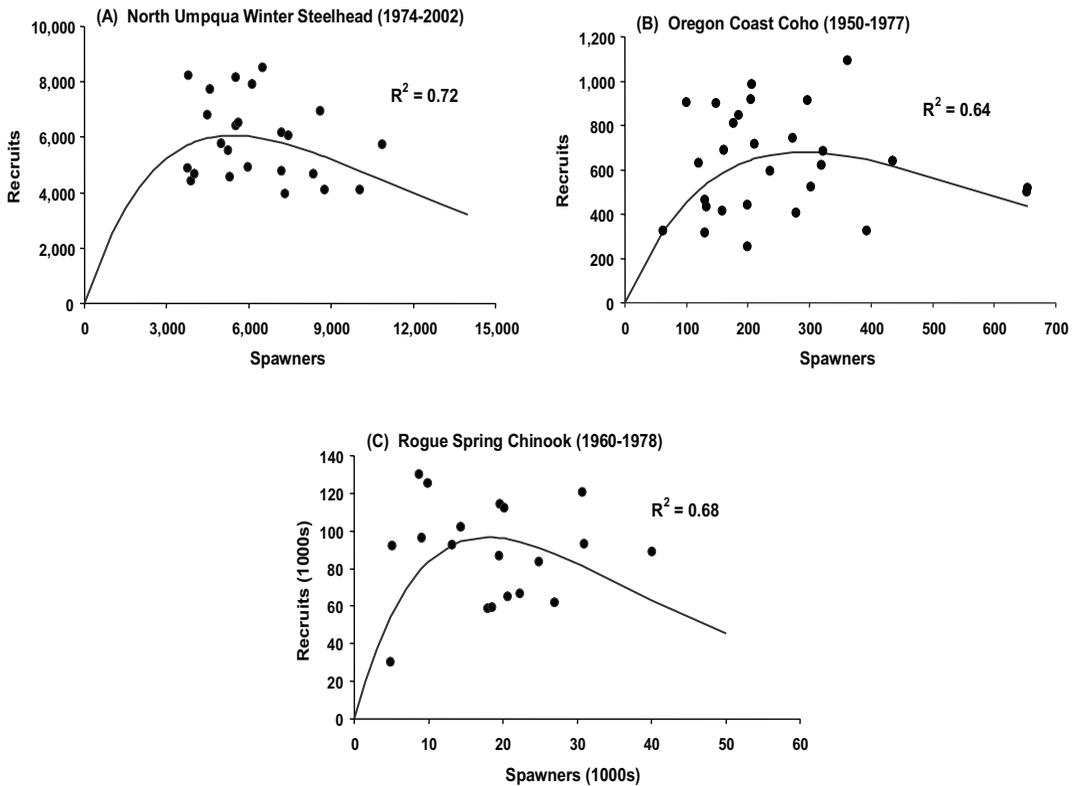


FIGURE 1. Examples of Ricker stock–recruitment curves fitted to a long time series of spawner and adult recruitment estimates, illustrating the typical wide dispersion of data. (A) North Umpqua Winter Steelhead (Mark Chilcote, Oregon Department of Fish and Wildlife, Portland, OR, personal communication), (B) Oregon Coast coho (Cramer 2000), and (C) Rogue Spring Chinook (Cramer 2000).

strata for predicting maximum rearing densities, and that these units can be used to link habitat-forming processes to stream carrying capacity for salmonids. In addition to the physical features of habitat, we also account for the influence of food supply on the capacity of streams to produce salmonids. We recognize that competition, predation, and water quality also influence carrying capacity, but these complex features are beyond the scope of this paper. High summer temperatures, for example, commonly restrict or reduce salmonid use from certain areas of basins where the habitat is otherwise suitable. The framework described here for determining habitat production potential was developed from studies

in salmonid-producing streams, and therefore will produce best results when applied to stream reaches having the typical range of conditions for streams that consistently support salmonids.

### Importance of Stream Area

At the broadest scale, the size of a basin constrains its capacity to produce salmonids. Correlations have been demonstrated between several measures of basin size and the run sizes of anadromous salmonids it produces (Figure 2). These correlations clearly indicate that salmonid production is a function of stream area or volume, but more detail

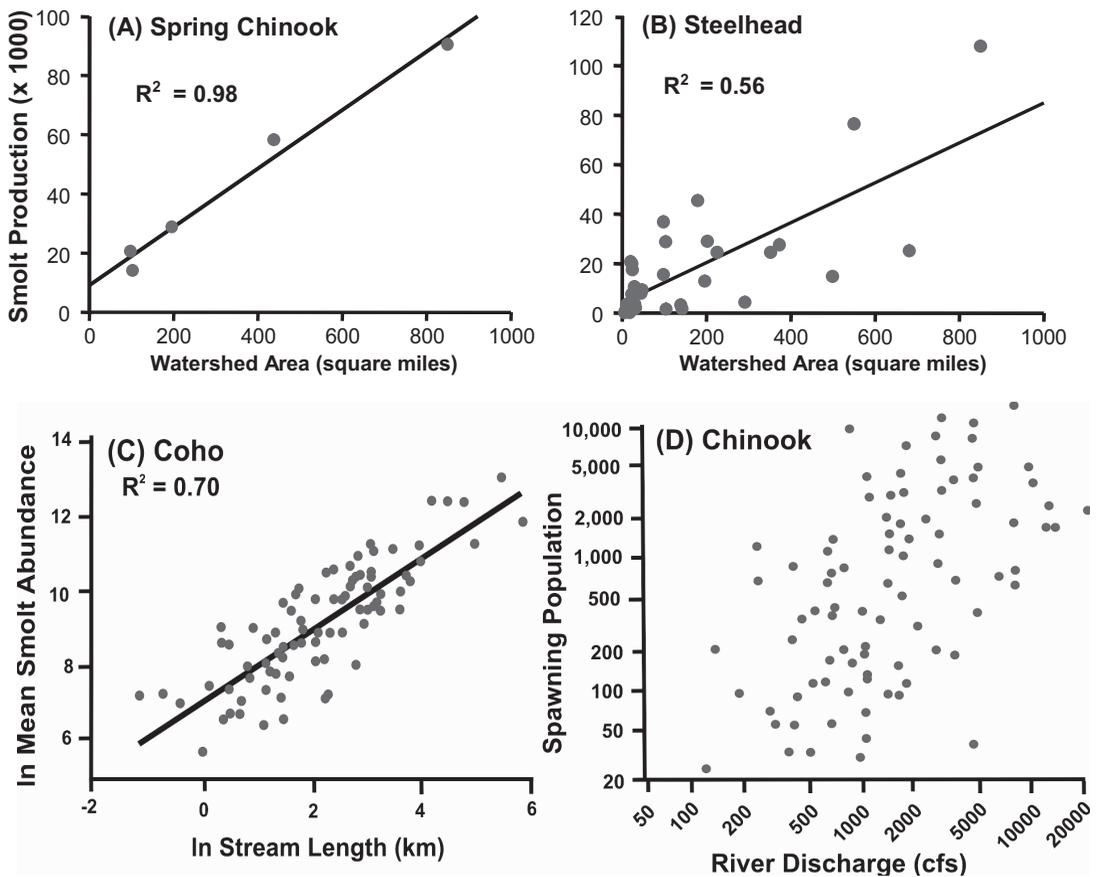


FIGURE 2. Example relationships of salmonids production to various measures of stream size. (A) maximum out-migration estimates of yearling spring Chinook in five watersheds of the Snake River Basin (Underwood et al. 2003); (B) maximum smolt estimates for steelhead in 39 watersheds of the Pacific Northwest (Underwood et al. 2003); (C) coho smolt production across 86 streams in western North America versus length of stream network with coho presence (Bradford et al. 1997), and (D) average spawning population of Chinook in British Columbia Rivers during 1952–76 (Healey 1991).

is needed about the specific habitat features that salmonids depend on before we can determine how human actions will influence salmonid habitat.

A fundamental concept in relating salmonid production to stream habitat is that stream-dwelling salmonids either defend, or rely on food from a characteristic area of territory (see Allen 1968 for an early review). Allen (1968) points out that territory requirements of individual fish of a given size vary little, whether fish are abundant or scarce, which

therefore leads to competition for space, and displacement when the sum of territory requirements for individual fish exceeds the area of available suitable habitat. Allen (1968) assembled data from 35 published studies on territory sizes of six salmonid species, and found a positive linear relationship between the logarithm of territory area and the logarithm of fish length across all six species. The data Allen assembled were measurements of area used by individual fish, not the area that a group of fish used. These areas of use

changed dramatically as fish length changed, but not as fish density changed (Allen 1968). This relationship was supported by the subsequent analysis and data of Grant and Kramer (1990). Allen (1968) concluded that densities of salmonids in streams had an upper capacity determined by the size of individual territories and “*the proportion of the bed accessible to and suitable for occupation by the fish.*” Further, he found that only 2–20% of stream area was used by the territories of salmonids at maximum observed densities in the 35 published studies and, therefore, there must be other stream features that limited the proportion of stream area suitable for salmonids of a given size. Similarly, Grant and Kramer (1990) found that density-dependent responses to competition were detectable in more than 50% of salmonid populations that exhibited greater than 27% of territory saturation. In a compilation of more recent studies in natural streams, Keeley (2003) found that reported densities rarely achieved the full saturation of territory sizes as reported by Grant and Kramer (1990). Keeley (2003) found through controlled manipulations of fish densities and food availability that, as fish grew over time, fish density decreased at a rate best predicted by the territory size function for individual fish as reported by Grant and Kramer (1990). This notion of carrying capacity is also implicit in stock–recruitment theory for salmonids (e.g., Ricker 1954; Beverton and Holt 1957), and in the Instream Flow Incremental Methodology (IFIM) methodology to assess effects of in-stream flow changes on salmonids (Bovee et al. 1998).

The finding that much of a stream remains unused by salmonids even when the population is at capacity leads to the question, “What are the features within a stream that determine the area suitable for salmonids to establish territories?” We now proceed through the evidence which indicates for juvenile anadromous salmonids that (1) territory size increases with fish length, (2) carrying capacity increases

with food availability, and (3) habitat preferences change with fish length. This generalization would not apply to chum and pink salmon that emigrate as swim-up fry, nor to sockeye that rear in lakes.

### *Territory size increases with fish length*

Grant and Kramer (1990) synthesized data from 10 studies that included observations of territory size for seven species of salmonids, and found that 87% of variation in territory size could be accounted for by fish length (Figure 3). The relationship they found is described by the following regression equation:

$$\log_{10} \text{Territory Area (m}^2\text{)} = 2.61 * \log_{10} \text{fish length (cm)} - 2.83 \quad (1)$$

Grant and Kramer (1990) established that this relationship was consistent with the predicted increase in food intake to satisfy the energetic requirements of fish. The breadth of data used by the authors demonstrates that this relationship is transferable to populations across species and regions for salmonids. This relationship makes it possible to determine the relative amount of rearing area that fish will require at progressive life stages. Further, the relationship can be rearranged to predict the maximum rearing density that should be expected for a given size of salmonid under average environmental conditions. When testing the relationship against an independent set of studies with salmonids, Grant and Kramer (1990) found that it correctly predicted the occurrence of density-dependent growth, mortality, or emigration in 81% of the cases. This indicates that the density limit predicted by the relationship is analogous to the carrying capacity parameter for a stock–recruitment relationship (at the stage studied).

Although length accounted for 87% of variation in territory size, Grant and Kramer

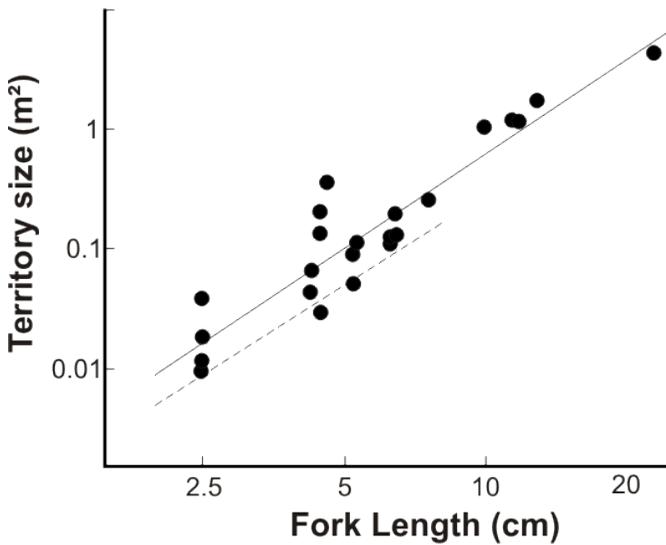


FIGURE 3. Relationship of territory size ( $\text{m}^2$ ) and fork length (cm) for stream dwelling salmonids (from Grant and Kramer 1990). Numbers with points identify data source given in Grant and Kramer (1990). Dashed line is regression for territory size of brook trout, and solid line is regression for other salmonids including rainbow trout, Atlantic salmon, brown trout, and coho salmon.

(1990) noted there was still an order-of-magnitude variation about the mean territory size for a given length of fish, and they presented evidence that some of that variation was related to environmental conditions. They cited specific studies within their data set that demonstrated territory size was influenced by food density and intruder pressure, which we consider later in this paper. Grant and Kramer (1990) also showed that salmonid densities in pools often exceeded the maximums predicted by territory size for fish length. They concluded that, in pools of sufficient depth, trout were vertically stratified, thereby increasing the density that could be sustained per surface area of pool relative to that of a riffle.

#### *Carrying capacity increases with food availability*

Data from several studies show that stream capacity for salmonids is related to fish size, food supply, and the factors affect-

ing that supply (Grant and Kramer 1990; Grant et al. 1998; Slaney and Northcote 1974; Keeley 2001). Juvenile salmon and trout in streams feed primarily on drift invertebrates, and studies show that the invertebrates most likely to occur in the drift are the species produced in riffles (Rader 1997). Field and laboratory studies indicate that production of invertebrate drift is strongly determined by at least four factors: (1) availability of riffles, (2) amount of light penetrating to the stream, (3) percentage of fines in the riffle substrate, and (4) nutrient levels. Riffles provide the physical habitat (combination of substrate and velocity) that invertebrate taxa favored by salmonids are produced in, and sunlight and nutrients provide the energy and raw materials for the primary production (algae and plants) that serves as food for the invertebrates (Figure 4). In this chapter, we summarize evidence that demonstrates the role of each of these four factors in determining stream productivity, while Cramer and Ack-

erman (2009) describes how these factors are integrated into a functional relationship that quantifies their influence on productivity (an index of food availability).

*Importance of macroinvertebrates in riffles.*—Though aerial insects and spawned salmon carcasses are important food sources for juvenile salmonids during portions of the year (Bilby et al. 1996; Wipfli 1997), salmonids feed predominantly on drift invertebrates in streams (Rader 1997; Elliot 1973 as cited by Murphy and Meehan 1991). The primary source of drift invertebrates are riffle habitat types (Hawkins et al. 1983; Rader 1997). Hawkins et al. (1983) studied 13 coastal streams, and found that salmonid density was correlated to invertebrate density in riffles, but not to invertebrates typically found in pools. Further, most invertebrates in pools were in shells or protective casings, and did not drift, while invertebrates found in riffles were those most likely to drift.

Because riffles provide invertebrates upon which salmonids feed, it follows that low frequency of riffles will lead to a limitation in food supply for salmon and trout in streams. The percentage of area composed by riffles in a stream is largely a function of gradient (Hicks 1989). Hawkins et al. (1983) showed that salmonids were present at all sites in 13 coastal streams where gradients were greater than one percent, but were absent at eight of 10 sites with gradient less than one percent. Further, Hawkins et al. (1983) found the percentage of fines in the substrate was highly related to gradient, and that excess fines was correlated to reduced production of both invertebrates and juvenile salmonids.

*Influence of sunlight exposure.*—Several studies have demonstrated that the amount of sunlight penetrating the forest canopy limits primary production, the source of food for invertebrates, and therefore limits food production for salmonids. Such studies in

West Coast forests have evaluated streams where part or the entire forest canopy was removed and have shown that production of algae, aquatic invertebrates and salmonids increased in the affected stream reach (Carlson et al. 1990; Newbold et al. 1980; Murphy et al. 1981; Murphy and Hall 1981; Hawkins et al. 1983). In each of the studies, the authors related the increases in macroinvertebrates to an increased production of algae and vascular plants following the increased exposure of the stream to sunlight (Figure 4).

Combined results from field and laboratory studies demonstrate that primary production increases only up to a saturation level of light that is comparable to partial shade. If nutrients are sufficient, primary production can increase with increased light up to an optimum, or saturation level, of about 1–2 lumens/cm<sup>2</sup> (McIntire 1975), which is about 10–20% of full sunlight. McIntire (1975) found that primary production in laboratory streams was also influenced by temperature, and was about 50% greater at 20°C than at 10°C, apparently from the accelerating effect of temperature on chemical reactions.

The amount of sunlight reaching a stream is often estimated from measurements of angular canopy density in forested streams. Carlson et al. (1990) found in 11 undisturbed watersheds in northeast Oregon that 83% of variation in macroinvertebrate density was accounted for by regression on elevation and angular canopy density (%). This relation indicated that, as angular canopy density decreased from 80% to 40% (i.e., as light penetration doubled), invertebrate density doubled at an elevation of 1,500 m, and increased by 50% at an elevation of 1,000 m. The effect of elevation in this analysis probably reflected the combined influence of cooler temperatures and fewer nutrients in higher elevation streams. The data of Carlson et al. (1990) indicated that maximum effective sunlight for primary production occurred at angular canopy densities of ≤35%, which was the lowest value they sampled.

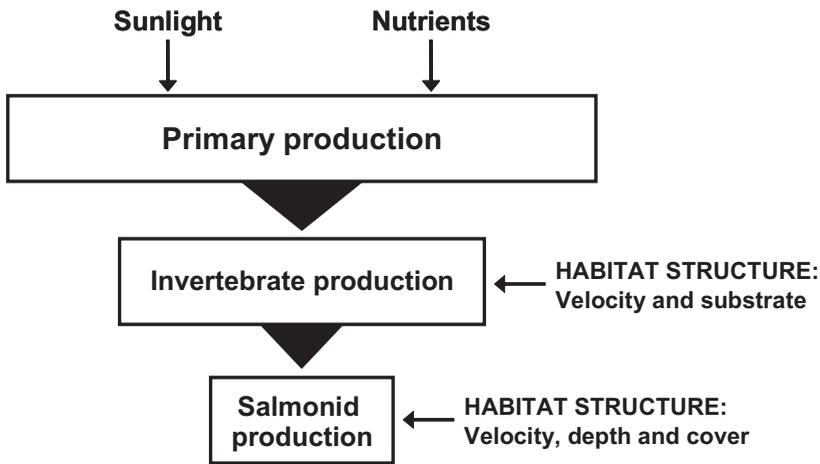


FIGURE 4. Diagram showing general pathways of influence by sunlight, nutrients, and habitat structure on salmonid production.

*Influence of turbidity.*—As sunlight penetration of the vegetative canopy influences stream production, so does light penetration into the water column. Rivers that are turbid experience a unique limitation to production in that light penetration is reduced. Lloyd et al. (1987) found that a turbidity level of only 5 NTUs can decrease primary production in shallow streams by 3–13%. An increase of 25 NTUs may decrease primary production by 13–50% in shallow streams. Primary production in streams deeper than 0.5 m would be reduced even further.

*Influence of fine sediment.*—Substrate embeddedness with fines is a key factor that influences both the production of invertebrate drift and the cover for juvenile salmonids. Hawkins et al. (1983) found that increasing percentages of fines in riffles across reaches in 13 coastal streams of Oregon was correlated to reduced production of both invertebrates and juvenile salmonids. Newly emerged fry can occupy the voids within gravel of 2–5 cm diameter, but psmolts need cobble (>7.5 cm) and boulder-sized rock to provide interstitial spaces they can occupy. These interstitial spaces can be filled by sediment, which

reduces available cover, availability of drift, and therefore rearing densities (Bjornn et al. 1977; Thompson and Lee 2000; Figure 5).

*Influence of nutrients.*—Invertebrate production generally increases as nutrient levels increase. Studies in British Columbia have shown that addition of fertilizer to a stream substantially increased production of invertebrates, and even increased the growth rate and density of juvenile salmonids (Ward et al. 2003; Wilson et al. 2003). Following addition of dry or liquid agricultural fertilizer to the Keogh River, British Columbia, benthic insects increased two- to seven-fold in a treatment area, mean weights of steelhead parr increased 30–130%, and smolt yield increased 62% (Ward and Slaney 1993).

Natural differences between streams in dissolved nutrient concentrations show strong correlation to the density of juvenile salmonids that can be supported. Bjornn and Reiser (1991) reported that standing crop of age-0 Chinook *Oncorhynchus tshawytscha* compared between streams in Idaho was 10 times higher in a stream reach with a 10-fold higher conductivity (40 versus 400  $\mu\text{S}/\text{cm}^3$ ). Several authors have shown a positive relation-

ship between stream alkalinity and salmonid production (Degerman et al. 1986; Scarnecchia and Bergerson 1987; Kwak and Waters 1997). Ptolemy (1993) found a positive relationship between total alkalinity and salmonid abundance across 226 streams in British Columbia ( $r^2 = 0.86$ ), and this relationship was valid when applied to 37 streams in six countries. Kwak and Waters (1997) showed that, at a broad geographic scale, alkalinity and salmonid biomass were positively and significantly related ( $P < 0.0001$ ).

**Habitat preferences change with fish length**

Chinook parr generally move to deeper and faster water as they increase in size (Lister and Genoe 1970; Everest and Chapman 1972; Hillman et al. 1987). They also, as a re-

sult of seeking deeper and faster water, move farther from shore (e.g., Everest and Chapman 1972; Don Chapman Consultants 1989). Everest and Chapman (1972) found a highly significant correlation between fish size and the depth or velocity at which juvenile Chinook and steelhead *O. mykiss* hold (Figure 6). Bjornn and Reiser (1991) found velocity so important to the preferences of salmonids that they concluded, “If velocities are unsuitable, no fish will be present.” Although most salmonid species that rear in streams are also well adapted to rearing in lakes, salmonids in streams feed primarily on invertebrate drift (Rader 1997) which tends to increase with velocity (Smith and Li 1983). Thus, foraging opportunities appear to drive their preference for velocity in streams. Studies by Rosenfeld et al. (2005) in experimental channels demonstrated that juvenile coho shifted to higher

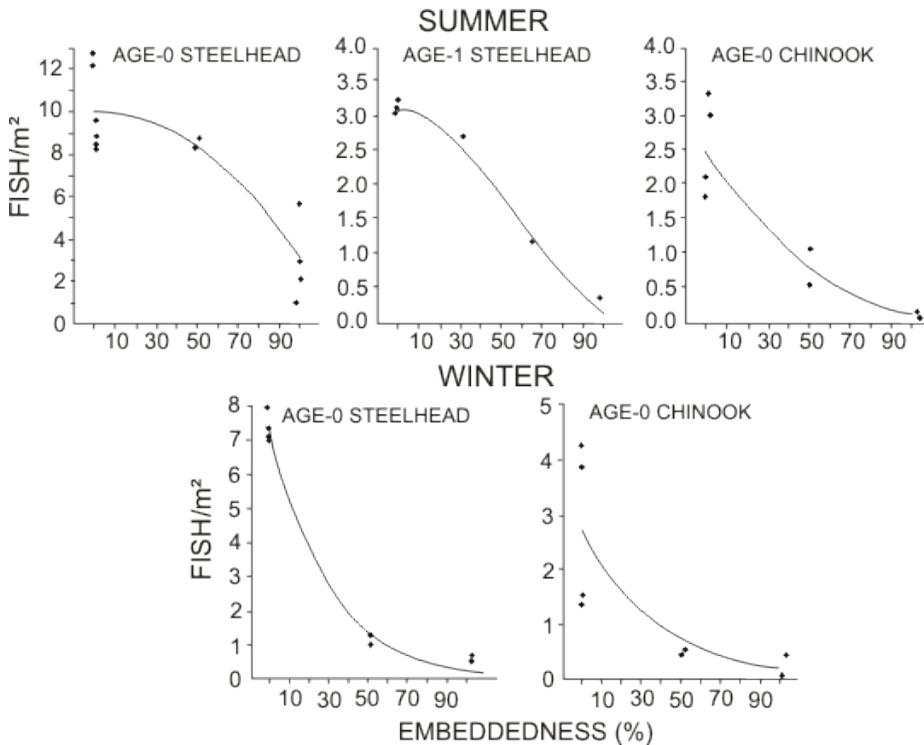


FIGURE 5. Densities of Chinook salmon and steelhead juveniles remaining after 5 d during summer and winter tests in laboratory stream channels with varying amounts of embeddedness by fines <6 mm. From Bjornn et al. (1977).

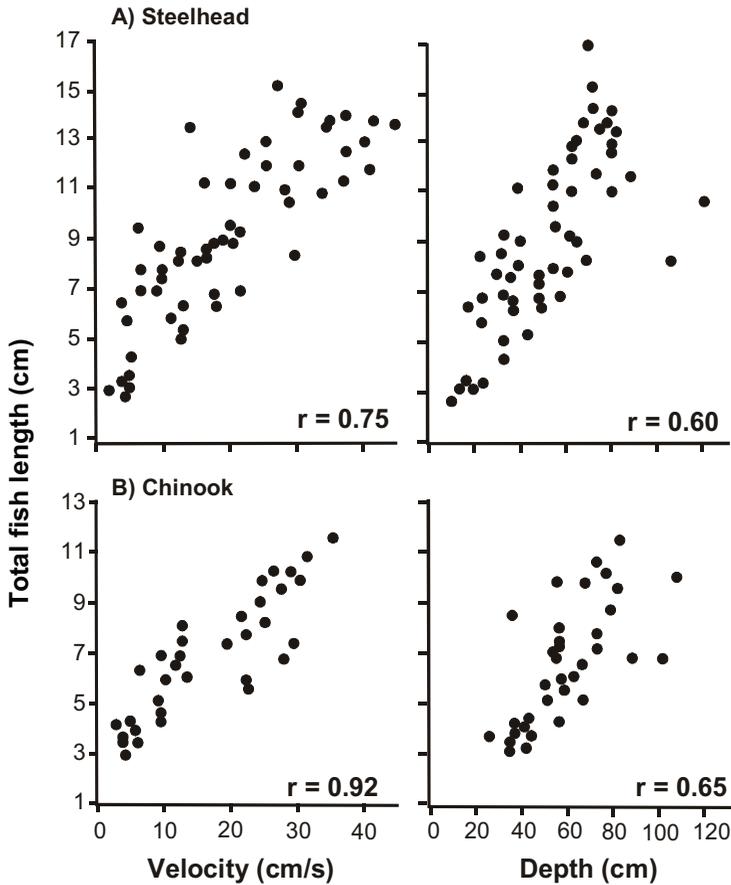


FIGURE 6. Scatter plot showing relationship between length of juvenile (A) steelhead and (B) Chinook and the depth and velocity of water at their focal point. From Bjornn and Reiser (1991), as redrawn from Everest and Chapman (1972).

average focal velocities as invertebrate drift was increased, and that growth rate was highly correlated to drift abundance.

At the typical length in late summer for age-1 steelhead parr (~12 cm) or age-0 Chinook parr (~9 cm), their preferred depth is roughly 0.8 m (Figure 6). The changing preferences of growing juveniles results in a reduction in the area of riffles and pools that are suitable to them. This is strikingly evident from the depth frequencies of pools and riffles in typical steelhead streams spread across Oregon. We assembled data from stream surveys by the Oregon Department of Fish and Wildlife and U.S. Forest Service from seven

watersheds that were important steelhead producers (see Cramer and Ackerman 2009). The surveys covered 528 km of stream and included measurements of over 10,000 channel units (pool, riffles, etc.). From these streams, we found that about 25% of riffles and 90% of pools have depths  $\geq 0.3$  m, but this availability drops to 10% of riffles and 60% of pools at 0.5 m, and to <1% of riffles and 25% of pools at 0.8 m (Figure 7). As juvenile salmonids grow beyond presmolt size, the data from Oregon streams show that the preferred steelhead stream habitat is rare. Thus, habitat availability at the parr stage in the summer is most likely to limit a watershed's carry-

ing capacity for salmonids that over-summer in streams because this life stage represents the convergence of increasing fish length and territory size requirements, and decreasing availability of water and suitable habitat.

The average stream area of suitable habitat required to raise a cohort of salmonids can be determined by combining the territory versus fish length relationship from Grant

and Kramer (1990) with survival between life stages reported in the literature. Although the type of habitat that is suitable for each life stage will vary, at least the relative area of stream required can be determined. For example, a pair of steelhead defends a territory of roughly 3–5 m<sup>2</sup> around their redd (Wydoski and Whitney 2003), spawn an average of 4,900 eggs (Quinn 2005), and an average

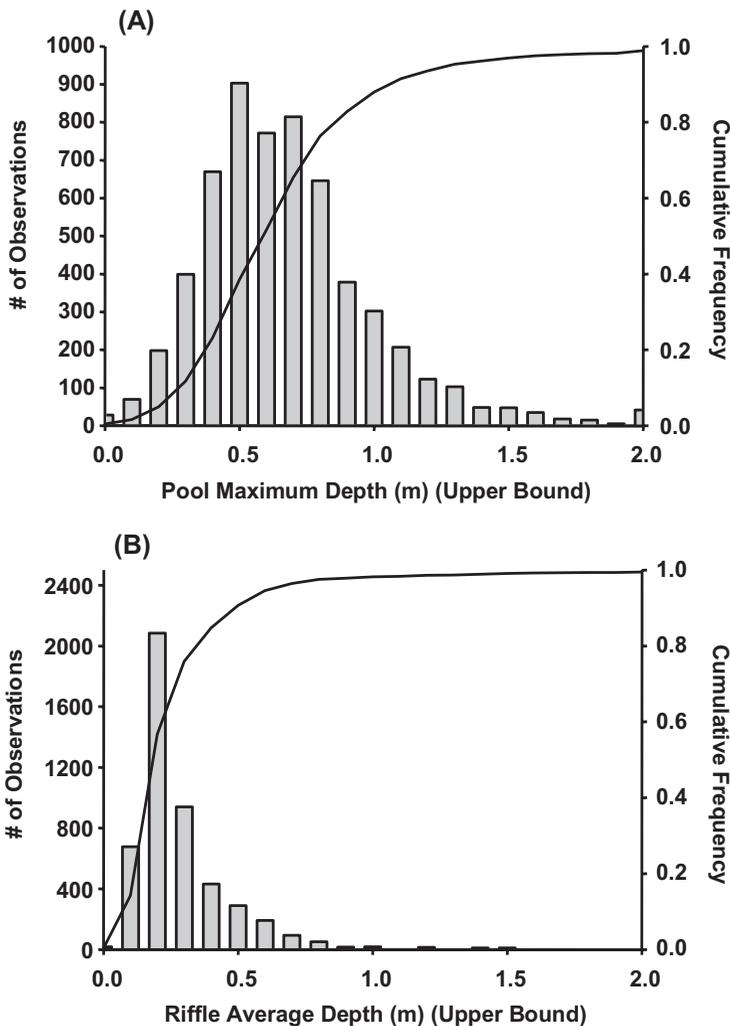


FIGURE 7. Frequency of (A) pool and (B) riffle depths throughout the channel networks used by steelhead in seven Oregon watersheds where steelhead smolt production has been monitored. See Cramer and Ackerman (2009) for a description of the watersheds. Channel unit data from U.S. Forest Service and Oregon Department of Fish and Wildlife Aquatic Inventories. Database available online at <http://oregonstate.edu/Department/ODFW/freshwater/inventory/habitgis.html>.

TABLE 1. Survivorship and predicted area required for a steelhead family cohort, based on the relationship of territory size to fish length (Grant and Kramer 1990). Fecundity and egg survival from Quinn (2005). Mid-range of parr survival from age 0 to age 1 reported by Bjornn (1978), Ward and Slaney (1993) and Johnson et al. (2005).

Parameter	Spawner	Fry	Age-0 Parr	Age-1 Parr
Length (cm)	72	3.5	8.0	12.0
Survival from previous stage	--	0.29	0.5	0.4
Survivors in cohort	4,900 eggs	1,421	711	294
Area needed (m <sup>2</sup> ) for cohort	5	55	239	276

29% survive to be fry (Quinn 2005). Using the values presented in Table 1, 50% of those fry survive to be parr at the end of summer, and 40% of those parr survive through the winter to become age-1+ parr the next summer. This means that a spawning pair of steelhead produce about 1,421 fry, of which 711 survive to the end of the first summer, and 284 survive to age-1+ parr the second summer (Table 1). Even though the number of survivors in the cohort rapidly declines over time, the total area of suitable habitat required for territories of the surviving individuals increases with age of the cohort (Figure 8). The 711 surviving age-1+ parr in combination require nearly five times the area needed by the 1,421 fry. Given the large increase in habitat area required with increasing age, coupled with a decreasing fraction of habitat that is suitable, it is likely that habitat availability will be most limiting when increasing fish size and flow-related decreases in habitat converge. This is typically the parr life stage rearing during low summer flows.

Territory dynamics are altered during winter when metabolic demands are lowest and refuge is the habitat priority. Due to the strong tendency of coho *O. kisutch* to seek off-channel and protected habitats during winter, their area required for winter habitat is often the factor limiting their carrying capacity (Nickelson 1998). However, there is evidence

that coho production is limited by low summer stream flows in some areas (Bradford et al. 1997). In contrast to coho, Chinook and steelhead do not seek off channel habitat for winter, and have a strong tendency to enter interstices of cobble and boulder substrates within the same channel types they occupy during summer (Hartman 1965; Bustard and Narver 1975; Hillman et al. 1987; Bjornn and Reiser 1991). Therefore, summer rearing habitat will determine the carrying capacity for yearling Chinook and steelhead. This concept has been illustrated for streams by multiple authors. Data from numerous studies suggests there is substantial density compensation after the age-0 rearing year (Bjornn 1978; Ward and Slaney 1993; Everest et al. 1987). Anadromous species that rear less than one year in freshwater (e.g., ocean-type Chinook) may experience habitat limitations for either spawning or rearing, depending on the species and stream-specific situation.

Now that we have substantiated that rearing habitat for the parr life stage is likely to be the most common bottleneck to salmonid carrying capacity in streams, we can describe a framework for quantifying that habitat. We find that channel units are a useful basal measure of habitat, and that variation in depth and cover can account for much of the difference in rearing density between units.

### Channel Units as the Basal Habitat Unit

A substantial body of evidence indicates that the channel unit is an appropriate and useful starting point from which estimates of stream carrying capacity should be constructed. A channel unit is an area of stream of relatively homogenous depth and velocity that is bounded by sharp gradients in depth and/or velocity. Fisheries biologists refer to these channel units by such terms as pools, riffles and glides (see Hawkins et al. for descriptions). The use of channel units as a basic metric for stream habitat largely grew out of the work of Bisson et al. (1982) who described a system of channel unit classification and related it to the hydraulic processes that formed them. The system was affirmed and updated by Hawkins et al. (1993), who pointed out that coho salmon, steelhead trout, and cutthroat trout segregate within stream segments by using different types of channel units. Further, Hawkins et al. (1993) noted that geomorphic units in a stream, as described by watershed process models, are equivalent to the habitat units measured in stream surveys

by fisheries biologists. Fluvial geomorphologists recognize pools and riffles as primary channel unit types. At low summer flow, pools have greater depth, finer substrate, and slower current than riffles. The biota inhabiting riffles and pools differs markedly, both in taxonomic composition and the morphological, physiological, and behavioral traits they possess (Hawkins et al. 1993).

Because the composition of channel units is the outcome of watershed processes, and fish production is strongly influenced by the composition of channel units, the effects of human actions in watersheds to the production of salmonids can be quantified through the common currency of habitat units (Figure 9). The three watershed processes that shape channel unit composition are sediment supply, transport capacity, and riparian vegetation (Montgomery and Buffington 1998). The surface geology influences sediment supply, while climate determines precipitation and snowmelt, which govern flow and the transport of material down the channel. The formation of these channel units can be related to hydraulic forces, sediment load, and resistance to flow provided by structural

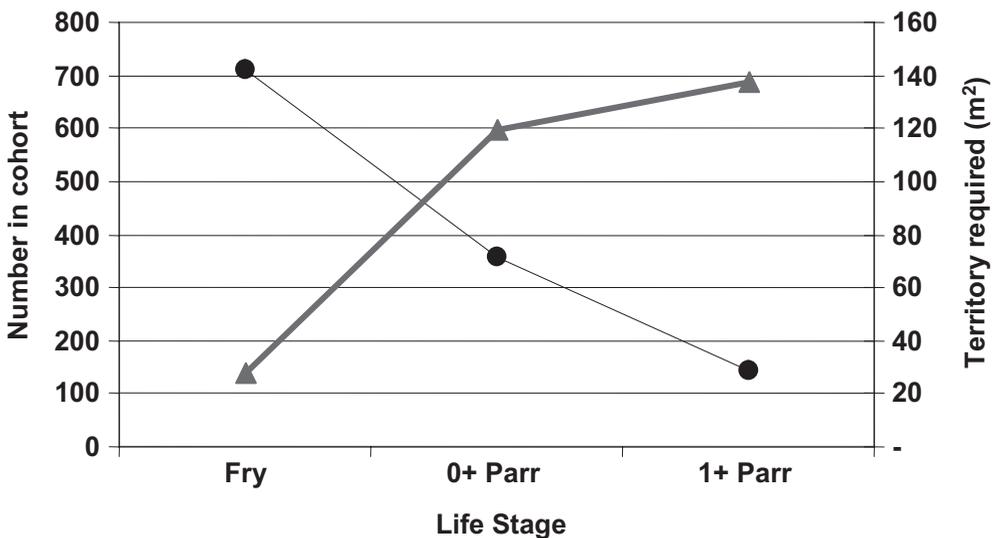


FIGURE 8. Change in abundance of fish (●) and their combined demand for territory (▲) for the survivors of a typical steelhead cohort produced by a single spawning pair (data from Table 1).

## Salmon Production in Streams

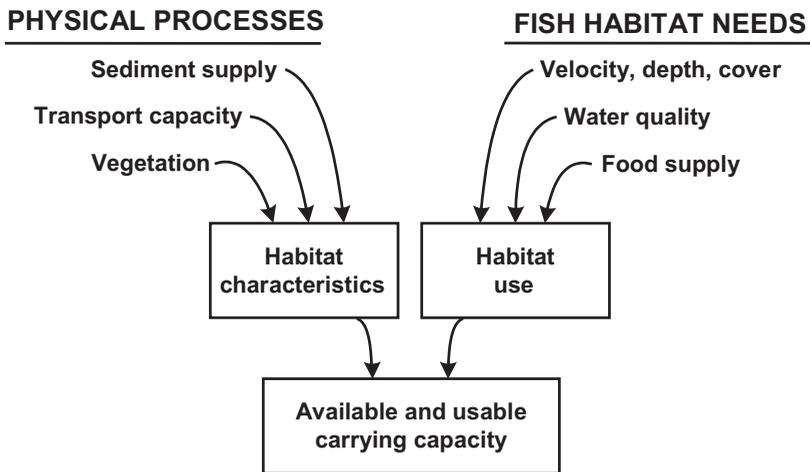


FIGURE 9. Average densities (points) and two standard deviation (lines) of (A) age  $\geq 1$  steelhead in 19 streams and (B) age  $\geq 1$  cutthroat trout in 30 streams thought to be fully seeded on the Oregon coast. Data from Johnson et al. (1993).

elements such as wood or rock (Leopold et al. 1964). Riparian vegetation influences bank stability and introduces large woody debris to the channel where it can be a forcing agent to guide flow and sediment deposition. Data and empirical functions have been developed to estimate how channel unit composition is affected by gradient and rock type (Hicks and Hall 2003), woody debris and channel width (Beechie et al. 2000), and sediment supply (Benda et al. 1998). See Naiman and Bilby (1998) for a review of watershed processes affecting fish habitat.

Classification and measurement of fish habitat should begin with units that are meaningful both to fish and to the physical processes that shape fish habitat. Although micro-habitat factors such as velocity, depth and cover have been widely used in the IFIM methodology as the starting point for classifying suitability for salmonid habitat, validation tests show that the method sometimes poorly predicts the distribution of fish densities. Several studies have shown that salmo-

nid rearing densities are more correlated to channel unit type than to velocity, depth and cover (e.g., Kershner and Snider 1992; Guay et al. 2000). Based on such evidence, Rosenfeld (2003) concluded, "Predicting fish density by habitat classes (e.g., riffle versus pool habitat units) is often more accurate than predicting density based on continuous variables (e.g., water depth), which suggests that discrete habitat classifications may characterize habitats in a more biologically meaningful way than continuous measurements."

Each channel unit type presents a characteristic suite of depths, velocities, and cover combinations available to fish, and these suites consistently differ between channel unit types. Field studies of salmonid behavior in stream habitats over a season, or even within a day, have shown that habitat preferences change with environmental circumstances, time of day, and degree of satiation. Bradford and Higgins (2003) found that most feeding activity by juvenile Chinook salmon and steelhead trout occurred at dusk and night

rather than day, even when temperatures were 10–14°C. Most fish were concealed in the substrate during day. Thus, the daytime holding positions of the fish that were out and active were not representative of the substrate interstices that most fish were choosing during the day. For this reason, juvenile salmonid densities should only be compared between channel unit types with data that is expanded to account for sampling efficiency (e.g., snorkel observations calibrated against mark–recapture population estimates in each channel unit type).

Habitat preferences can also change with environmental conditions. Juvenile salmonids change positions in a channel unit as temperature and day length change (Vondracek and Longanecker 1993). Velocity preferences change with food availability (Wilzbach 1985; Grant et al. 1998). Density of competitors and predators has been shown to dramatically influence habitat preference (Brown and Moyle 1991; Fausch and White 1986; Rosenfeld and Boss 2001). We deduce from these changing habitat preferences that fish choose to occupy a channel unit for an extended time (days to years), depending on the suite of desirable features available in the immediate area. Thus, fish would be more likely to choose a home territory first on the basis of a channel unit type than they would on the basis of a specific velocity or depth, although preferred velocities and depths must be present in the unit for it to be selected. Once a fish has chosen a unit type for its favorable suite of habitat opportunities, the fish then selects the specific depth, velocity and cover combination that it desires at the moment. Such a selection sequence would account for the observations, such as that of Rosenfeld (2003), showing that salmonid rearing densities are more related to unit type than to a microhabitat feature.

Numerous data sets in which densities of fish were measured for distinct channel units illustrate that each salmonid species exercis-

es consistent preferences for different types of channel units. Hankin (1984) and Hankin and Reeves (1988) showed that statistically stratifying fish population estimates according to channel unit types improved estimation accuracy and reduced variance. Hankin and Reeves (1988) concluded that extrapolation from data collected in only one of several “representative” reaches could give a highly biased and very misleading picture of true fish abundance, because variation was more aligned with differences between channel unit types than with reaches. Bjornn and Reiser (1991) present data on the densities of Chinook parr and yearling steelhead found within stream unit types averaged over 22 streams surveyed in Idaho during 1985 and 1986. They found that relative densities between unit types were consistent across streams and years. Chinook were most abundant in pools (21–22 fish/100 m<sup>2</sup>) and moderately abundant in runs (14 fish/100 m<sup>2</sup>), and least abundant in pocket water (5–10 fish/100 m<sup>2</sup>) and riffles (2–5 fish/100 m<sup>2</sup>). Age-1+ steelhead were most abundant in pocket water (2–5.5 fish/100 m<sup>2</sup>), and varied from 2.0 to 3.5 in pools, 1.5–2.5 in runs, and 0.5–2.0 in riffles. Don Chapman Consultants (1989) and Roper et al. (1994) report similar differences in habitat preferences of Chinook parr and steelhead age 1+. These differences indicate that Chinook have a greater preference for low velocity channel units, while steelhead prefer higher velocity channel units. In another study, Johnson et al. (1993) sampled numerous Oregon coastal tributaries and presented average density by unit type for 19 streams that satisfied their criteria for full seeding with steelhead, and 30 streams that satisfied their criteria for full seeding with cutthroat trout (Figure 10). Again, those data show strong preferences by both species for pools, and a much lower use of other unit types by cutthroat trout than steelhead.

### Framework for Habitat Capacity Estimation

We now describe a generalized framework, referred to as the Unit Characteristic Method (UCM), for estimating stream carrying capacity for salmonids. As the name implies, the channel unit is the basal building block for quantifying fish habitat. The most common channel units are referred to as pools, riffles and glides, and are defined as follows:

**pool:** a unit with no surface turbulence, except at the inflow, and has depth extending below the plane of the streambed.

**riffle:** a unit with discernable gradient and surface turbulence.

**glide:** a unit that has relatively uniform velocity down the channel, little surface turbu-

lence, and no depth below the plane of the streambed.

The UCM assigns a standard density for each fish species to each unit type (Table 2), and then increments or decrements that density according to the amount that substrate, depth, and cover deviate from average. The magnitude of incremental change in fish density per increment of a habitat feature is derived from preferences demonstrated by each fish species for each habitat feature, as we will describe. The UCM predicts a stream's carrying capacity under average conditions by multiplying fish density by surface area in each unit, and then adjusts for differences between stream reaches in factors that influence food supply, as described in the section below. The general form of the predictor for a given species in a specific stream reach is:

$$Capacity_i = (\sum area_k \cdot den_j \cdot chnl_{jk} \cdot dep_{jk} \cdot cvr_{jk}) \cdot prod_i \tag{2}$$

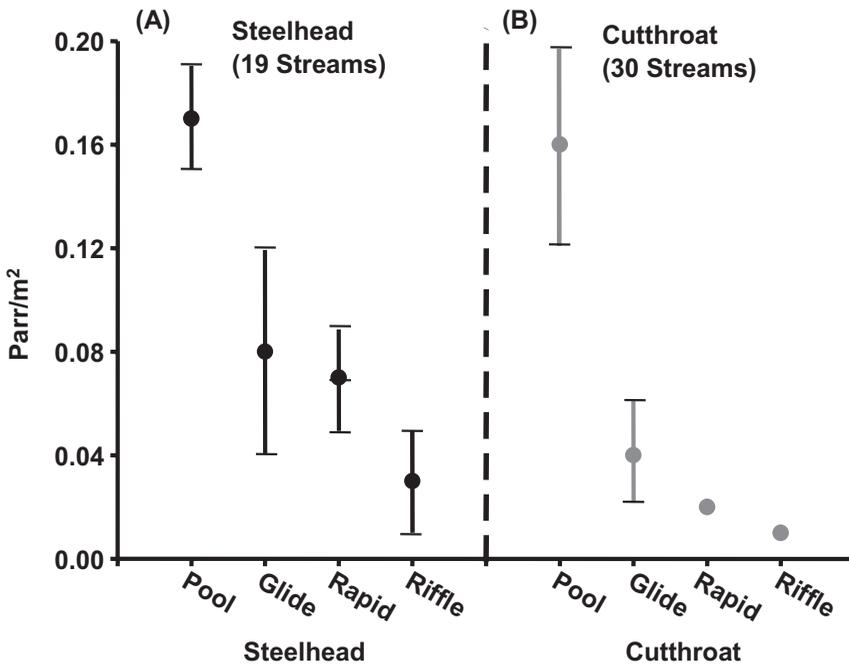


FIGURE 10. Linkage of watershed processes and salmonid preferences for habitat that together determine stream carrying capacity for salmonids.

TABLE 2. Relative density of juvenile salmonids, by channel unit type, determined from typical streams where these species are abundant. Densities scaled relative to densities in pool units. Data sources: spring Chinook from personal communication, D.B. Lister, British Columbia; coho from Solazzi et al. (1998); steelhead and cutthroat from Johnson et al. (1993).

Unit Type	Spring Chinook	Coho		Steelhead	Cutthroat
		Summer	Winter		
Pool	100%	100%	100%	100%	100%
Beaver Pond	79%	106%	450%	41%	24%
Backwater	54%	71%	150%	29%	12%
Glide	29%	47%	25%	47%	24%
Riffle	10%	6%	3%	18%	6%
Rapid	10%	6%	3%	41%	12%
Cascade	10%	12%	0%	18%	0%

Where;

$$prod_i = turb_i \cdot drift_i \cdot fines_i \cdot alk_i \quad (3)$$

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

Where;

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

$j$  = channel unit type,

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

$k$  = individual channel unit,

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

$area$  = area (m<sup>2</sup>) of channel unit  $k$ ,

$alk$  = alkalinity during summer low flow (measured as mg/l CaCO<sub>3</sub>).

$den$  = standard fish density (fish/m<sup>2</sup>) for a given species in unit type  $j$ ,

$dep$  = depth scalar with expected value of 1.0,

$cvr$  = cover scalar with expected value of 1.0,

$chnl$  = discount scalar for unproductive portions of large channels 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 (3).

The several variables that are represented as scalars having mean of 1.0 must each be defined by a separate function that relates that variable to fish density and must be determined by the average value for the data set from which the standard fish density was determined. For example, the standard densities for steelhead parr presented in Cramer and Ackerman (2009) are taken from a set of Oregon coastal streams, so the scalar value for  $dep$  would be set to 1.0 at the average value of depth in the Oregon coastal streams that were sampled. The scalar would then take on values >1.0 if  $dep$  was greater than average,

or values  $<1.0$  if *dep* was less than average. The rate of change in each scalar per change in the represented variable is unique for each variable, and is the subject of further evidence presented in this paper. Mathematical functions to describe these scalars specifically for steelhead parr are presented in Cramer and Ackerman (2009).

Salmonids in streams show clear preference for a set range of water velocities, but velocity is not explicitly included in the framework described by this equation. Velocity is a microhabitat feature, and the base scale of our framework is the channel unit, a macro habitat feature. Different channel unit types offer different ranges of velocity, as acknowledged in the classification of channel units into fast-water and slow-water types (Hawkins et al. 1983). We assume that the UCM accounts for fish velocity preferences through the differences in densities it assigns to the channel unit types.

We assembled sufficient data from various field studies of four species of salmonids (spring Chinook, coho, steelhead, and coastal cutthroat trout *O. clarkii*) to establish expected densities of parr at full seeding in different channel unit types. Unit-specific densities for spring Chinook were derived from observations in the fully seeded Coldwater River, British Columbia (data provided by D.B. Lister & Associates). Relative coho densities from summer and winter sampling of fully seeded Oregon coastal streams were derived from the Habitat Limiting Factors model (HLFM) described by Solazzi et al. (1998). Both steelhead and cutthroat trout densities were derived from the study of Johnson et al. (1993), who sampled numerous, fully seeded Oregon coastal tributaries and presented average density by unit type for each species.

Although there were consistent differences in juvenile densities between channel unit types, densities within each unit type were strongly influenced by depth and cover. To predict how fish will choose habitat, it is

important to understand the priority order of preferences they display if some preferred factors are lacking. For example, combined observations from several experiments indicate that steelhead exercise habitat preferences in the priority order of depth first, velocity second, and cover third. In a study where effects of cover were held constant, Beecher et al. (1993) compared depth and velocity preferences of steelhead parr (75–200 mm) in a fully seeded Washington stream that was uniformly lacking in cover; large boulders accounted for less than 1% of surface area and there was no LWD. The authors found that steelhead parr strongly avoided shallow habitats, but once depth was sufficient, velocity preference influenced habitat selection. Parr of all salmonid species strongly avoided areas with depths  $<0.2$  m, and steelhead and cutthroat parr showed increasing densities as unit depths increased up to at least 1 m (Figure 11). Beecher et al. (1993) found that most parr were observed at velocities of 27.4–33.2 cm/s, but velocities most preferred were less available and were 21.3–27.1 cm/s. Similar preferences by steelhead parr for depth and velocity were found in an Idaho stream by Everest and Chapman (1972) (see Figure 6), and have been confirmed in an experimental setting by Fausch (1993).

A variety of field and laboratory studies have demonstrated that increasing cover in a habitat unit leads to greater densities of juvenile steelhead and Chinook in summer or winter. Cover can be provided from above, laterally, or below in the substrate, and each type is used to varying degrees by different species. Cover provided by woody debris is often noted as important to salmonid parr, and a study by Johnson et al. (1993) was able to quantify the benefit of cover by assigning a cover complexity score to the pools in which fish were sampled. Parr density in pools for both steelhead and cutthroat increased about three fold as woody debris complexity increased from none to high complexity (Figure 12).

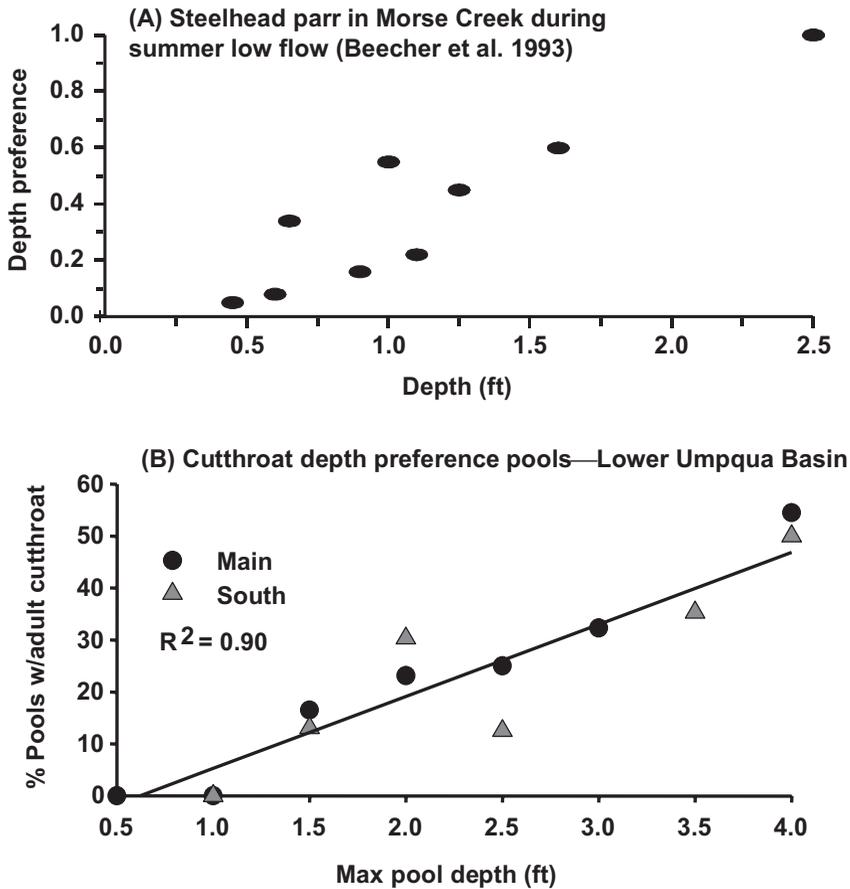


FIGURE 11. Examples of salmonid preference for depth in streams. (A) Upper graph is steelhead parr in a stream nearly devoid of wood or boulder cover, adapted from Beecher et al. (1993). (B) Bottom graph is snorkel observations of adult cutthroat presence within pools of tributaries to the main and South Umpqua Basin, author's data.

Boulders provide a form of cover in streams, particularly in riffles. Don Chapman Consultants (1989) found that steelhead parr in high gradient reaches (>5%) of the Wenatchee River, Washington, generally selected stations where adjacent velocities were six to eight times their nose velocity and were usually stationed individually behind boulders where surface turbulence provided cover. Ward and Slaney (1993) found that placement of boulders resulted in about one steelhead parr rearing per boulder where none had reared previously. Dambacher (1991) found, in the Umpqua River Basin, Oregon, that stream channels with relatively

high ( $0.02/m^2$ ) and low abundances ( $<0.02/m^2$ ) of age >1 steelhead were separated, with some overlap, by the relative amount of large boulder substrate. Johnson (1985) used snorkel surveys to estimate parr densities in a number of western Washington rivers, and his data show over a 10-fold variation between reaches in average parr densities within riffles. We obtained and examined his data and found that parr densities in riffles where boulders were the most prevalent substrate size-class averaged about five times greater than in riffles with other substrate size classes (e.g., cobbles, gravel) as most prevalent (Figure 13).

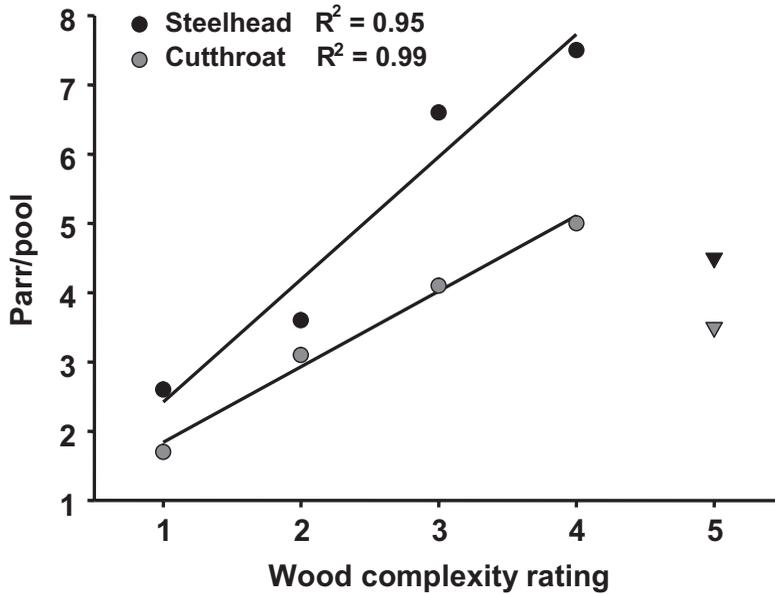


FIGURE 12. Relationship of steelhead and cutthroat parr densities in pools to wood complexity within Oregon coastal streams (redrawn from Johnson et al. 1993). Values for the complexity rating of 5 (triangles) omitted from the regressions, because sampling effectiveness was impaired.

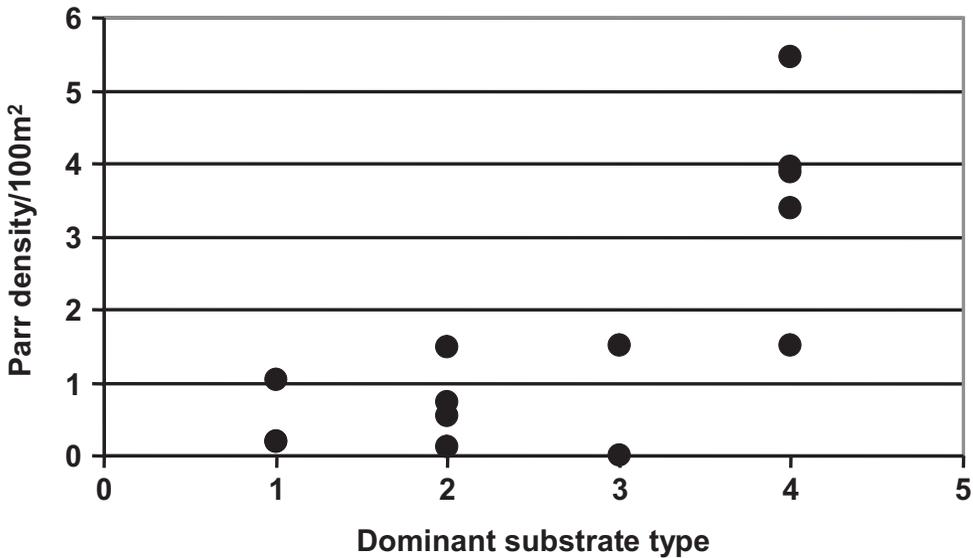


FIGURE 13. Relationship of steelhead parr density in riffles to the dominant substrate type in those riffles of western Washington rivers. Data from Johnson (1985). Substrates are: 1 = large gravel; 2 = small cobble; 3 = large cobble, and 4 = boulders.

## Discussion

### *Potential uses of UCM*

We have found that the UCM has a credible basis for applying stream habitat measurements to estimate a basin's capacity for rearing stream-dwelling anadromous salmonids. Because the territory size needed for each salmonid increases exponentially with fish length, the total area of suitable habitat needed to support a cohort generally increases at a faster pace than mortality thins the population, at least through the first two years of rearing in a stream. Thus, the availability of suitable habitat during low flow in the summer prior to smolting will typically determine the carrying capacity of a stream for salmonids that over-summer in streams. Exceptions can certainly arise in streams with little spawning gravel or where preferred winter habitat is in short supply, such as is often the case for coho. However, habitat measurements in typical steelhead-producing streams show the preferred depths of steelhead rapidly become scarce as parr approach the length of smolts (15–20 cm). The increasing mismatch between territory requirements and availability of suitable habitat in typical steelhead streams suggests that lack of habitat for larger fish may be a key reason that such streams support anadromous rather than resident *O. mykiss*.

Equation (2) provides a generalized framework for predicting salmonid rearing capacity in streams. This equation then provides the quantitative link between stream habitat features and the population dynamics of anadromous salmonids. Maximal rearing densities differ between types of channel units, and observations of fish densities in numerous streams make it possible to establish the mean maximum densities and their confidence intervals that can be expected in typical channel units. Within a specific unit type, field observations have also established that

juvenile salmonid densities vary as a function of depth and cover. Thus, maximal densities can be predicted by first assigning the expected average density for a given unit type, and then incrementing or decrementing that density according to the amount that depth or cover deviate from the average for that unit type. Dissolved nutrients in the stream, turbidity, and fine sediment also influence the density of salmonids that can be supported, so rearing capacity for a given stream reach must also be decremented or incremented to the extent that these factors deviate from average.

Cramer and Ackerman (2009) tested the fit of UCM predictions for steelhead parr to observed smolt production in seven watersheds dispersed across Oregon with widely differing environmental conditions. They found that observed smolt production corroborated the UCM carrying capacity predictions. Further, they found that habitat quality and the habitat factors most limiting to steelhead production varied widely both within and between basins, which suggests that basic habitat surveys conducted by fisheries agencies provide sufficient information to distinguish production bottlenecks and predict fish benefits of proposed habitat restoration or enhancement actions.

The use of channel types as a starting point for estimating stream carrying capacity offers substantial advantages to natural resource managers. First, measurements of channel units and their basic features are widely available from the standard habitat surveys performed by state and federal agencies to inventory the state of fish-producing streams. Unit type, area, depth, substrate composition, and some score of cover are recorded as part of the standard protocol by state and provincial fisheries agencies and federal land management agencies. Secondly, the surface area of natural channel units provides a means to quantitatively link the effects of human activities on land or in wa-

ter to the production of salmonids. Channel units (also known as geomorphic units) are a predictable output from models of watershed processes that shape streams. The formation of channel units can be related to the combination of physical forces and structure from discharge, sediment load and structural elements that resist flow, such as wood or rock (Leopold et al. 1964). Because channel units are output quantities from watershed process models, and inputs to models of salmonid carrying capacity, future efforts to link the two model types could make it possible to predict fish benefits from proposed habitat restoration strategies, land use activities, and flow alteration.

The number of fish predicted by equation (2) estimates the potential maximum production that would be achieved with full seeding of fish under average conditions. Salmonid populations vary substantially between years in response to variable spawner abundance and environmental conditions. As a consequence, estimated abundance falls below the predicted capacity in most years and only exceeds the average capacity in years with sufficient spawners and beneficial environmental conditions. Thus, the capacity value estimated by equation (2) is useful as the estimate of the upper bound on stock-recruit curves in which the recruits are parr rather than adults. In the case of a Ricker curve, the expected number of recruits ( $R$ ) is expressed as a function of the number of parent spawners ( $P$ ) that produced them:

$$R = \alpha P e^{(-\beta P)} \tag{4}$$

where;

$\alpha$  = parameter defining maximum value of  $R/P$ , and

$\beta$  = parameter defining maximum value of  $R$ .

The parameter values of this function

are typically estimated from a least squares regression of  $\ln(R/P)$  on  $P$  from a long-term data set of adult recruits and spawners. However, if  $\beta$  were estimated separately from habitat measurements as we described here, the value of  $\alpha$ , which is the recruitment rate at low population density, would need to be determined separately. This might be based on a meta-analysis of estimates for  $\alpha$  in comparable populations. Most values of  $\alpha$  reported in the literature, however, are expressed in terms of adult recruits per adult spawner. In order to convert an  $\alpha$  value expressed as adults per adult to one expressed as parr per adult, the former must be divided by the average parr-to-adult survival rate ( $S$ ):

$$\alpha_{(parr/spawer)} = \alpha_{(adults/spawner)} \div S \tag{5}$$

This conversion assumes that mortality after the parr stage is independent of population density. Parr-to-adult survival is certainly variable between years, but if the parr stage is the final density bottleneck to survival, then the form of the stock–recruitment relationship will not be altered by the variation in density-independent mortality.

The Ricker equation can be rearranged, and the value of  $\beta$ , can be calculated in two steps. In the first step, we estimate the abundance of parents that exactly replaces themselves with recruits,  $P_r$ , and in the second step,  $\beta$  is estimated. Ricker (1975) demonstrated that the maximum number of recruits,  $R_{max}$ , is given by:

$$R_{max} = (e^{a-1})(P_r)/a \tag{6}$$

where,

$a = \ln(\alpha)$ , and

$P_r$  = Number of parents at the level of replacement (the level where  $R = P$ ).

We proceed by choosing an independent

estimate of  $\alpha$ , converting its units of measure to parr per spawner, and then substituting  $a = \ln(\alpha)$  into equation (6).

The only remaining unknown in equation (6) is  $P_r$ , which can then be solved. Once we have solved for  $P_r$ , we can calculate  $\beta$  based on the relationship of Ricker (1975):

$$\beta = a/P_r \quad (7)$$

### Example applications

The UCM has been applied in several basins of Oregon to help resolve specific issues relating to stream potential for producing salmon and steelhead. We describe two of these applications, one in the Hood River Basin and one in the Deschutes River Basin, as examples of the different uses for UCM.

The 10-year progress evaluation of the Hood River Production Program in Oregon (Underwood et al. 2003) provides an example of these calculations and their application. That program, first implemented in 1992, provided extensive supplementation of spring Chinook, summer steelhead, and winter steelhead with hatchery fish in the three main forks of the Hood River basin, and also implemented a variety of habitat restoration measures to improve natural production of anadromous salmonids. The combination of hatchery supplementation and habitat restoration was intended to raise natural production to the full potential of the basin. However, program goals for the natural production that could be achieved had been based on sketchy information. Underwood et al. (2003) used the UCM to estimate carrying capacity for steelhead and spring Chinook parr, based on more extensive and recent habitat surveys completed by natural resource agencies. Underwood et al. (2003) were able to use the UCM capacity estimates to derive the capacity parameter in stock–recruitment relationships for each species, and with those stock–recruitment relationships determine how the

populations were performing compared to their production potential.

In the Hood River example, the UCM estimate of winter steelhead capacity was 49,827 parr for the entire basin. Further, survival of parr to smolting was estimated to be 35% and the survival of smolts to adult recruits was estimated to be 3.9%. Thus, we have

$$(R_{max, parr}) = 49,827$$

Expected survival ( $S$ ) of these parr to adults would be

$$S = 0.3500 \cdot 0.0390 = 0.0137$$

Because there was no estimate of adult recruitment rate, a review of stock–recruitment analyses for steelhead in other Columbia Basin streams then led to the decision that  $\alpha = 6$  (adult recruits/adult spawner) was a reasonable assumption for the maximum recruitment rate among Hood River winter steelhead. This provides the information needed to convert the  $\alpha$  value for adult recruitment rate to a parr recruitment rate and then convert the parr capacity to the  $\beta$  parameter for the Ricker function. From equation (4) we have:

$$\alpha \text{ (parr/spawner)} = 6 \div 0.0137 = 439$$

$$P_r = \ln(439) \cdot 49,827 \div e^{(\ln(439)-1)} = 1,881$$

$$\beta = \ln(439) \div 1,881 = 0.00324$$

And thus,

$$\text{parr recruits} = 439 \cdot P \cdot e^{-0.00324 \cdot P}$$

The Ricker function for parr could then be combined with estimates of density-independent survival from parr to adult to estimate harvestable surpluses for the fisheries that the Hood River Production Program was intended to support.

Separate from their use to derive the stock–recruitment function, the UCM estimates of parr carrying capacity revealed that Hood River Basin’s capacity for natural smolt production was far less than the rough estimate used in the 1992 planning to determine appropriate rates of supplementation with hatchery fish. The UCM prediction of natural production capacity was only 24% of the 1992 planning target for steelhead and 37% of the target for spring Chinook, as can be seen from the following data derived from Underwood et al. (2003).

monies. Further, they illustrate the utility of the UCM framework as an objective basis for benefit-to-cost predictions to be used by decision makers as they prioritize investment in habitat restoration or enhancement actions.

The Hood River example also illustrates that habitat measurements included in the UCM clearly distinguish where and how serious the habitat conditions are that limit natural production of steelhead and Chinook salmon. Glacial turbidity, fine sediments (glacial sand), and a low percentage of area composed by pools were the primary habitat

Species	Planning target rearing capacity	UCM estimate of Capacity	Maximum observed production (1994–2001)
Steelhead	101,968 smolts	25,337 smolts	24,488 smolts
Spring Chinook	120,500 parr	44,835 parr	11,745 parr

Actual production of smolts, estimated from expanded catches in screw traps during 1994–2001 (a period of supplementation and habitat restoration) was even less than the UCM-predicted capacity. The maximum observed production for spring Chinook in any year reached only 26% of the UCM capacity, and averaged less than 10% of predicted capacity. The maximum number of steelhead smolts leaving the basin (24,488) only approached the UCM-predicted capacity (25,337) above the trap location in one of seven years, and averaged about half of capacity. The observed smolt production indicated that the UCM capacity estimates were more reasonable than those originally used as planning targets, and the corroborating examples presented by Cramer and Ackerman (2009) further confirm reliability of the UCM estimates. These large discrepancies between planning targets for a major fish enhancement project and the carrying capacities predicted from habitat measurements may reflect the human tendency to subjectively over-estimate potential benefits of proposed projects when attempting to justify expenditures of public

characteristics responsible for a lower production potential than had been assumed at the Program outset. Glacial turbidity was estimated by the UCM to reduce parr production by up to 50% in reaches of the Middle Fork Hood River, and up to 20% in many reaches throughout other portions of the basin. Parr production begins to decrease when fines in riffles exceed 15% (Figure 5), and values for fines (dominantly glacial sand) were generally 25–30% in the main stem and West Fork, and were 38–44% in the East Fork. Further, channel morphology was not favorable for salmonid production as gradient was typically high (>2.5%), and led to a low proportion of surface area composed by pools (generally <20%). The variation in percentage of surface area composed by pools had over a two-fold effect on predicted parr capacity between reaches.

The case of the Hood River Production Program also illustrates the utility of the UCM as a tool to assist with hatchery reform. Repeated findings that hatchery programs have unintended negative consequences on natural production of salmonids have led to

the development of new guidelines for hatchery practices (Mobrand et al. 2005). The Hatchery Scientific Review Group (HSRG) was tasked by Congress to determine how hatcheries could be managed to continue supporting sustainable fisheries while, at the same time, assisting with the conservation and recovery of naturally spawning populations. The HSRG concluded that supplementation programs, such as that on Hood River, should, “necessarily be limited by the habitat available to the natural populations with which it is integrated” (Mobrand et al. 2005). The UCM analysis of fish habitat in the Hood River basin demonstrated that use of professional judgment to define natural production goals for hatchery supplementation has low reliability. However, the UCM provides a relatively rapid assessment method to develop realistic predictions of habitat carrying capacity, and these can be used to design hatchery strategies that are compatible with sustainable natural production.

Habitat-based estimates of salmon or steelhead carrying capacity can be used to assess cost effectiveness of restoring passage to streams above barriers. The UCM was used in the Deschutes River Basin of Oregon to determine the population size of steelhead that could be supported above Pelton and Round Butte dams if passage were restored. The dams blocked effective fish passage after their construction in 1958. Prior to construction, the distribution of steelhead spawning in various tributaries had been well established, but the abundance of steelhead had not been estimated. We used existing data from stream habitat surveys by various agencies to apply the UCM and predicted that 41,059 age-1+ steelhead parr could be produced in the entire basin upstream of the Pelton-Round Butte complex (Cramer and Beamesderfer 2002). These predictions were compatible with adult run sizes that arrived at the base of the dam during its construction. Further, the UCM was also applied to habitat surveys in the Trout

Creek watershed of the Deschutes Basin below the Pelton-Round Butte complex, and direct sampling of smolt production from that watershed corresponded with the UCM estimate of carrying capacity (Cramer and Ackerman 2009). The UCM prediction of carrying capacity above the Pelton-Round Butte complex was split between 17,346 age-1+ parr in the Whychus Creek watershed, and 23,613 produced in the Crooked River watershed. This split was important to the planning process, because access to the Whychus Creek watershed was unimpaired, but passage into the Crooked River would require the removal of an additional dam at substantial cost. Achieving successful passage of steelhead smolts downstream through Pelton and Round Butte reservoirs was highly uncertain, so the estimated parr capacities were used further in the development of a steelhead life cycle model for the Deschutes Basin. It was then possible to simulate the abundance of wild steelhead that could be sustained above the Pelton-Round Butte complex, given different rates at which parr might residualize in the reservoirs (Cramer and Beamesderfer 2002).

### *Needs for further development of UCM*

Additional work is needed to expand the UCM framework to include special circumstances that strongly influence salmonid production in some streams. One such circumstance is interaction with abundant competitors or predators, which may alter habitat usage by rearing salmonids (Brown and Moyle 1991; Fausch and White 1986; Rosenfeld and Boss 2001). Brown and Moyle (1991) showed on the Eel River that habitat use by salmonids substantially shifted after northern pikeminnow *Ptychocheilus oregonensis* were introduced to the basin. Bradford and Higgins (2003) found that densities and behaviors of age-0 steelhead and Chinook salmon differed between two reaches of the same river where risk of predation from bull

trout *Salvelinus confluentus* differed. In the lower reach where the risk of predation was greater, juveniles were less dense and feeding behavior was almost exclusively nocturnal. The effect on rearing capacity of these behavioral responses to predators has not been quantified and warrants further study.

Estimates of rearing capacity in a basin based on the UCM framework are likely to be most accurate when the actual limits of rearing distribution for juvenile salmonids in a stream network are established by field observations. Distribution of fish presence in remote headwater streams must sometimes be predicted from environmental attributes of the area. Other workers have developed such predictive approaches that rely on factors such as gradient, watershed area, rainfall, and temperature (Fransen et al. 2006). Given that rearing capacity for salmonids in streams is typically limited by demands for habitat during the last summer or winter they spend in freshwater, it is important that all channels in a network with suitable habitat for that life stage be included in any estimate of a basin's carrying capacity. Although spawning may occur in only portions of the stream network, juveniles may disperse both up and downstream to find suitable rearing areas. Thus, the full range of rearing opportunities accessible to mobile juveniles should be included in estimates of rearing capacity.

Future work is also warranted to determine how functions can be included in the UCM framework to account for variable factors such as the availability of marine nutrients and stream temperatures. Nutrients from spawned salmon carcasses enhance food supply, and thus rearing populations of juvenile salmonids (e.g., Bilby et al. 2001; Wipfli et al. 1999). Salmonids are coldwater fishes, and stream temperatures frequently restrict salmonid use in portions of a basin. Most salmonids show preference for temperatures cooler than about 18°C, but temperature heterogeneity in a stream channel can provide opportunities for

juveniles to find satisfactory habitat within restricted areas of the channel, perhaps even in the same channel unit where they have been rearing (e.g., Ebersole et al. 2003). Thus, temperatures above optimum for salmonids would likely act to progressively reduce rearing density (Bovee 1978; Isaak and Hubert 2004) until the point is reached that thermal refuges are completely eliminated. Factors that vary substantially between years, such as the supply of marine nutrients, stream temperatures, and even flow, might be best accounted for as separate factors in a stochastic or year-by-year simulation combined with a base-level capacity predicted by the UCM.

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