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A Simple Method to Predict Regional Fish Abundance: An Example in the McKenzie River Basin, Oregon

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A Simple Method to Predict Regional Fish Abundance: An Example in the McKenzie River Basin, Oregon

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ABSTRACT: *Regional assessments of fisheries resources are increasingly called for, but tools with which to perform them are limited. We present a simple method that can be used to estimate regional carrying capacity and apply it to the McKenzie River Basin, Oregon. First, we use a macroecological model to predict trout densities within small, medium, and large streams in the McKenzie Basin. Next, we evaluate the reliability of the predicted trout densities by comparing them with field-measured densities. We then calculate the total surface areas of small, medium, and large streams within the basin and multiply these surface areas by the predicted trout densities to estimate regional carrying capacity. Predicted carrying capacity within the basin is approximately 2.1 million trout (median predicted abundance). Our method requires minimal input data, and much of this data can be compiled from literature sources. The method may therefore have broad utility.*

Propuesta de un método de predicción de abundancia regional de peces: la cuenca del Río McKenzie, Oregon, como caso de estudio

RESUMEN: si bien la demanda de evaluaciones regionales de recursos pesqueros ha incrementado, las herramientas para realizarlas aún son limitadas. En esta contribución se presenta un método simple que puede utilizarse para estimar la capacidad de carga en peces a nivel regional y se aplica a la cuenca del Río McKenzie, en el estado de Oregon. Primero, se utilizó un modelo macro-ecológico para predecir las densidades de trucha en cauces pequeños, medianos y grandes dentro de la cuenca McKenzie. Posteriormente se evaluó la confiabilidad de dichas predicciones mediante comparaciones con observaciones directas en campo de las densidades. Luego se calculó la superficie total de los cauces pequeños, medianos y grandes en la cuenca y se multiplicó por las densidades predichas de truchas para así estimar la capacidad de carga a nivel regional. Se proyecta una capacidad de carga de ~2.1 millones de truchas (la mediana de la predicción de abundancia). Este método requiere de un mínimo de información de entrada y muchos de los datos pueden ser compilados de la literatura disponible. Por lo tanto, este método posee amplia utilidad.

INTRODUCTION

Fisheries managers often seek to conserve or enhance fisheries resources at regional or landscape scales (e.g., Katz et al. 2007), and tools to estimate or predict fish abundances at these large scales are therefore needed. Habitat models can sometimes be used for this purpose. Habitat models use statistical correlations between fish data and suites of physicochemical habitat variables to predict fish abundances and/or distributions at sites where empirical fish data are not available or when habitat conditions change (Fausch et al. 1988; Rosenfeld 2003). For instance, Burnett et al. (2007) created a model of steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) rearing habitat in western Oregon streams and then used their model to prioritize land acquisitions and stream restoration activities.

However, habitat models can be difficult to build and calibrate. Large, spatially explicit data sets are needed to quantify the underlying fish–habitat correlations (e.g., Creque et al. 2005; Rashleigh et al. 2005). Geographic Information Systems and freely available geospatial data sets, such as National Hydrography Dataset Plus (NHDPlus 2010), can expedite the compilation and analysis of physicochemical habitat data, but the corresponding fish data must still be collected through traditional field methods, such as mark–recapture surveys. Highly complex models can also be more difficult for managers to apply (Adkison 2009).

Recently, McGarvey et al. (2010) presented a simple, macroecological model (sensu Brown 1995) that can predict fish abundance at regional scales. Macroecological models use robust statistical patterns to predict large-scale patterns and processes from relatively small-scale observations (Marquet et al. 2005). For example, McGarvey et al. (2010) created a trophic carrying capacity model that used the self-thinning relationship (i.e., the inverse relationship between population size and average body mass; Bohlin et al. 1994) to predict fish population density, given net primary production, in four cold-water and four warm-water systems. Their model (McGarvey et al. 2010) was relatively easy to build: it included only seven parameters and each of these was estimated with existing literature data.

In this study, we use the model of McGarvey et al. (2010) to estimate potential trout carrying capacity, expressed as total standing stock abundance, within the McKenzie River Basin

(MRB), western Oregon (Figure 1). We refer to this as "potential carrying capacity" because the model assumes that 100% of the available food resources will be consumed and converted to fish tissue. Our specific objectives are to (1) describe the model structure; (2) use the model to predict average trout densities within small, medium, and large streams in the McKenzie Basin; (3) assess model performance by comparing the predicted densities with empirical density estimates from comparable Pacific Northwest streams; and (4) extrapolate the predicted densities across the entire McKenzie Basin stream network to predict potential carrying capacity at the regional scale.

MODEL STRUCTURE—THE UNDERLYING CONCEPT

We used the self-thinning relationship

$$D = aM^{-b} \,, \quad (1)$$

to predict population density (D) from average body mass (M). The scaling exponent b is generally interpreted as the inverse of metabolism, which scales as M^b, and the coefficient a is thought to reflect trophic resources, or prey availability (Kerr and Dickie 2001; White et al. 2007). Thus, the self-thinning relationship (equation 1) is a model of ecosystem carrying capacity (Marquet et al. 2005). It predicts the numbers of organisms that can survive on a finite resource base, given that small species will, on average, be more abundant than large species because smaller species consume fewer per capita resources than larger species (Bohlin et al. 1994).

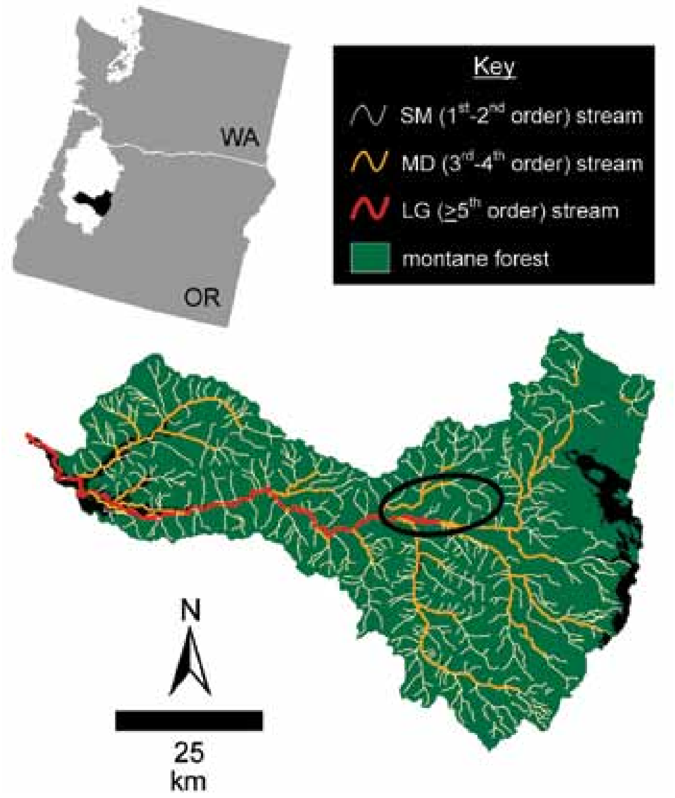


Figure 1. The McKenzie River Basin (MRB). Inset map shows the location of the MRB (black polygon) within the greater Willamette Basin (white polygon), in northwest Oregon. Main map shows the extent of montane forests (≥70% closed tree canopy, at or above 500 m elevation) within the MRB. The entire MRB stream network (1:100,000 scale) is shown and categorized by stream size: 'SM', 'MD', and 'LG' refer to small, medium, and large streams, respectively. Stream segments that overlap with montane forest were considered montane streams and included in the regional carrying capacity estimates; stream segments that did not overlap with montane forest (i.e., occur over black regions in the map) were not included. The black oval shows the location of H.J. Andrews Experimental Forest.

Estimates of M and b can be obtained directly with field measurements or inferred from literature values (e.g., Carlander 1969; Elliott 1993; J. W. A. Grant et al. 1998), but a standard method for measuring a does not yet exist (Bohlin et al. 1994; Fréchette and Lefaivre 1995; Cyr et al. 1997). Following Jennings and Blanchard (2004), we therefore used population biomass (B) as an estimate of a, as outlined below (see also Kerr and Dickie 2001; McGill 2008).

First, we assumed that trophic resource availability (i.e., food) is the primary determinant of trout carrying capacity in the McKenzie Basin (i.e., other factors such as habitat availability and life history requirements are secondary influences; see Poff and Huryn 1998; Jackson et al. 2001) and that trophic resource availability can be inferred from net primary production (NPP; Jennings and Blanchard 2004; McGill 2008). We then used a conceptual food web diagram (adapted from Macneale et al. 2010) to identify the major autochthonous (i.e., aquatic) and allochthonous (i.e., terrestrial) resources available to trout in the McKenzie Basin (see Figure 2A), as well as major competitors for these resources (primarily salamanders; see Net Primary Production and Salamander Consumption section), and calculated total NPP (NPP_{total}) as the sum of autochthonous (NPP_{auto}) and allochthonous (NPP_{allo}) production minus salamander consumption (NPP_{sal}):

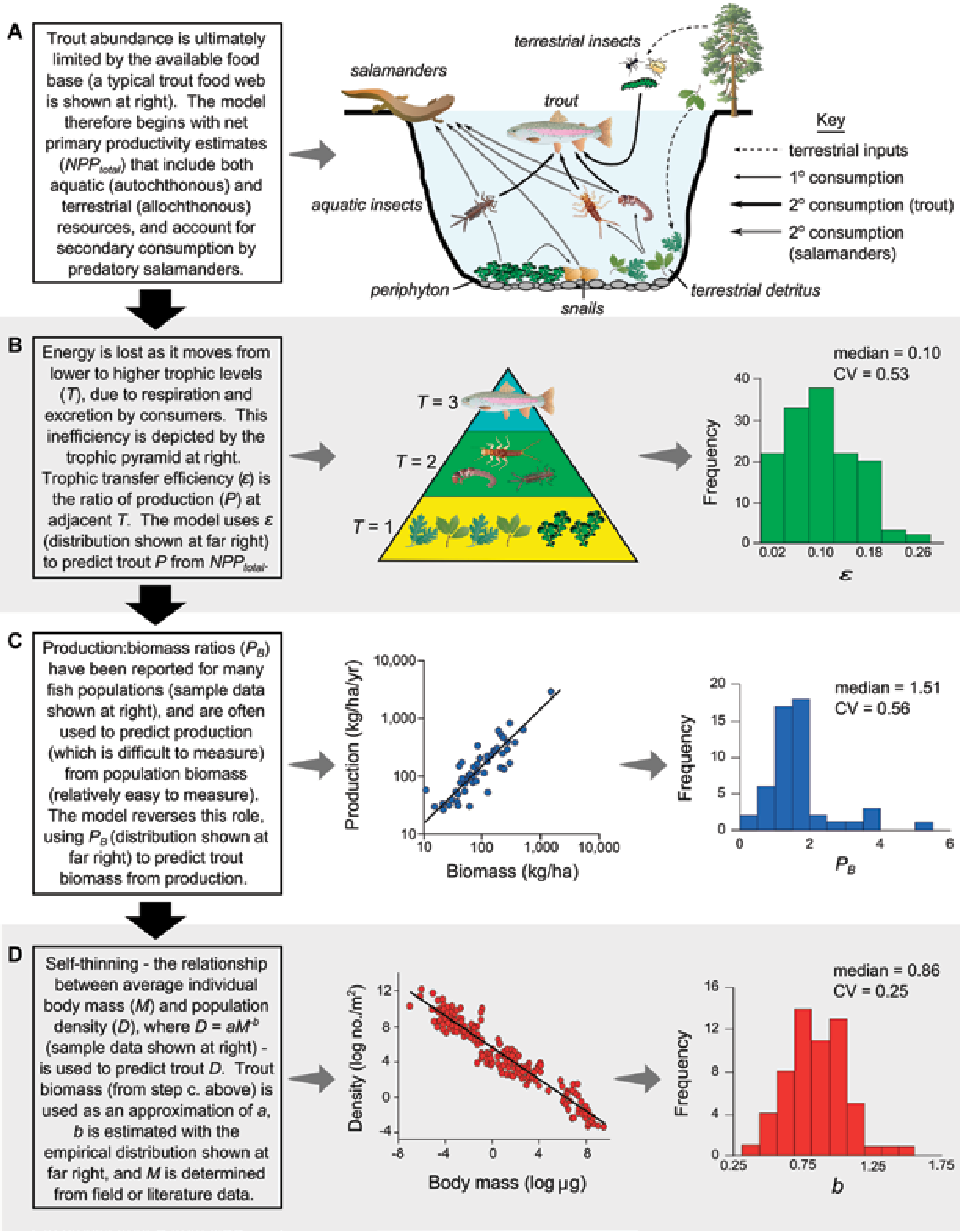
$$NPP_{total} = NPP_{auto} + NPP_{allo} - NPP_{sal} \,. \quad (2)$$

Second, we used trophic transfer efficiency (ε) estimates from the primary literature (see Figure 2B) to predict trout production (P), given NPP_{total}. ε is the ratio of production among two adjacent trophic levels and it is often approximately 0.1 (e.g., Lindeman 1942; Slobodkin 1960; Pauly and Christensen 1995; but see Barnes et al. 2010). P was modeled as

$$P = NPP_{total}\, \varepsilon^{T-1} \,, \quad (3)$$

where T is the average trophic level of an adult (age 1+) trout.

Third, we used the production:biomass ratio (P_B) to predict trout biomass (B) from P. Empirical P_B ratios are often used to predict P, which is difficult to measure *in situ*, from field estimates of B, which are relatively easy to obtain (Waters 1977).



A Trout abundance is ultimately limited by the available food base (a typical trout food web is shown at right). The model therefore begins with net primary productivity estimates (NPP_{total}) that include both aquatic (autochthonous) and terrestrial (allochthonous) resources, and account for secondary consumption by predatory salamanders.

B Energy is lost as it moves from lower to higher trophic levels (T), due to respiration and excretion by consumers. This inefficiency is depicted by the trophic pyramid at right. Trophic transfer efficiency (ε) is the ratio of production (P) at adjacent T. The model uses ε (distribution shown at far right) to predict trout P from NPP_{total}.

C Production:biomass ratios (P_B) have been reported for many fish populations (sample data shown at right), and are often used to predict production (which is difficult to measure) from population biomass (relatively easy to measure). The model reverses this role, using P_B (distribution shown at far right) to predict trout biomass from production.

D Self-thinning - the relationship between average individual body mass (M) and population density (D), where $D = aM^{-b}$ (sample data shown at right) - is used to predict trout D. Trout biomass (from step c. above) is used as an approximation of a, b is estimated with the empirical distribution shown at far right, and M is determined from field or literature data.

Figure 2. Flow diagram of the fish density model. Each of the basic concepts included in the model is shown in sequence and explained in the text boxes at left. Symbols used in the food web and trophic pyramid diagrams are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science. The ε distribution was reproduced from Pauly and Christensen (1995; *n* = 48 aquatic food webs) and is used with permission from the Nature Publishing Group. The PB data are from Randall et al. (1995; *n* = 51 stream/river samples) and are used with permission from NRC Research Press. The body mass vs. density plot was reproduced from Cyr et al. (1997) and is used with permission from John Wiley & Sons, Inc. The *b* distribution was compiled from: Egglishaw and Shackley (1977); Elliott (1993); Grant (1993); Bohlin et al. (1994); Cyr et al. (1997); Dunham and Vinyard (1997); Grant et al. (1998); Steingrímsson and Grant (1999); deBruyn et al. (2002); Knouft (2002); Rincón and Lobón-Cerviá (2002); Cohen et al. (2003); and Keeley (2003). Median values and coefficients of variation (CV) are shown for the ε, P_B, and *b* distributions.

However, the model reversed this role, using empirical P_B estimates (see Figure 2C) to predict trout B given trout P. B was then used as an estimate of the constant a in equation (1). Thus, a was calculated as

$$a \approx B = \frac{P}{P_B} \quad . \tag{4}$$

Whether B is an appropriate estimator of a is debatable. Mechanistic interpretation of a has been achieved for plants but not for aquatic animals (Begon et al. 1986; Hughes and Griffiths 1988). However, the assumption that $a \propto B$ is logical: in general, systems with higher NPP_{total} should support higher consumer biomass and higher consumer densities. This assumption is also consistent with studies that have demonstrated a positive relationship between a and NPP or consumer B (e.g., Bohlin et al. 1994; Cyr et al. 1997) and with other models that have applied the self-thinning relationship (e.g., Jennings and Blanchard 2004; McGill 2008).

Finally, we combined equations (2), (3), and (4) with equation (1) to obtain the final model

$$D = \left[\frac{NPP_{\text{total}} \varepsilon^{T-1}}{P_B} \right] M^{-b} \,. \tag{5}$$

The constant a is bracketed in equation (5) to emphasize that this is not a mechanistic bioenergetics model. It is a macroecological model that uses an estimate of standing stock B and the self-thinning relationship to predict D. Thus, when B (in g/m^2; equation 4) is multiplied by M (in g; equation 1) the units do not equate to fish/m^2. Rather, B is treated as a unitless value when it is used to estimate a.

MODEL APPLICATION — MCKENZIE RIVER BASIN EXAMPLE

Study Area

The MRB lies along the west slope of the Cascade Range, on the east side of the Willamette River Basin (Figure 1). It has a surface area of 3,466 km^2 and is covered primarily (>90%) by montane forest (Douglas fir, western hemlock, and western red cedar). Hydrology and geology are closely linked in the MRB and three distinct biogeoclimatic provinces are present: (1) a "High Cascades" zone (>1,200 m elevation) with porous, volcanic bedrock and extensive subterranean flow; (2) a "Western Cascades" zone (400–1,200 m elevation) with low permeability, volcanic bedrock and high surface drainage density; and (3) a "Cascade foothills and valley" zone (<400 m elevation) that is underlain by a combination of alluvium and sedimentary and volcanic bedrock (G. E. Grant 1997). We selected the MRB because an extensive database exists on the physical and biological characteristics of MRB streams (see Representative Streams Section).

Representative Streams

We focused exclusively on montane streams, because montane forests are the predominant land cover type in the MRB and trout are common within these systems (Waite and Carpenter 2000). We defined montane streams as those occurring within forested habitats (≥70% forest cover by area) at 500 m elevation or higher—the approximate elevation at which large stands of contiguous forest begin in the MRB (Figure 1). This constrained our analyses to the Western Cascades and High Cascades provinces. Land cover data were obtained from the Pacific Northwest Ecosystem Research Consortium (2009). We used the 1990 version of the Land Use/Land Cover digital data set.

The physical and biological characteristics of montane streams in the MRB were inferred from field studies in the H.J. Andrews Experimental Forest (see Figure 1), which is often used as a model of Pacific Northwest forest ecosystems (Geier 2007). For example, detailed studies of whole-stream metabolism have been conducted in Andrews Forest streams (Naiman and Sedell 1980; Cummins et al. 1983; Bott et al. 1985). These studies provided quantitative estimates of NPP_{auto} and NPP_{allo} (see Figure 3) and were instrumental in tests of the "River Continuum Concept": they demonstrated the longitudinal transition from small, heavily shaded, heterotrophic streams to large, open-canopy rivers with increasing autotrophic production (Bott et al. 1985).

Because Andrews Forest streams are broadly representative of montane streams in the MRB (Geier 2007), we used the three most intensively studied streams—Mack Creek, Lookout Creek, and the McKenzie River—as surrogates for all similarly sized streams within the MRB. Specifically, we assumed that Mack Creek is representative of small, perennial headwater streams in the MRB (see Figure 3). Mack Creek is typically classified as a third-order stream (e.g., Bott et al. 1985), but it is first order in the 1:100,000 scale NHDPlus (2010) data set, which we used to estimate the total size of the MRB stream network (see Regional Application of the Modeling Results section). We therefore labeled all first- and second-order montane stream segments in the NHDPlus data set as "small" (SM) streams and used Mack Creek data to estimate their physical and biological characteristics. This eliminated the smallest streams, which require 1:24,000 scale maps to detect, from our analyses. However, true first-order streams in the MRB (e.g., Devil's Club Creek; Bott et al. 1985) are often intermittent and rarely support resident trout populations (Murphy and Hall 1981). Next, we assumed that Lookout Creek is representative of "medium" (MD) streams (stream order = 3–4 in NHDPlus) in the MRB (Figure 3). Finally, we assumed that the McKen-

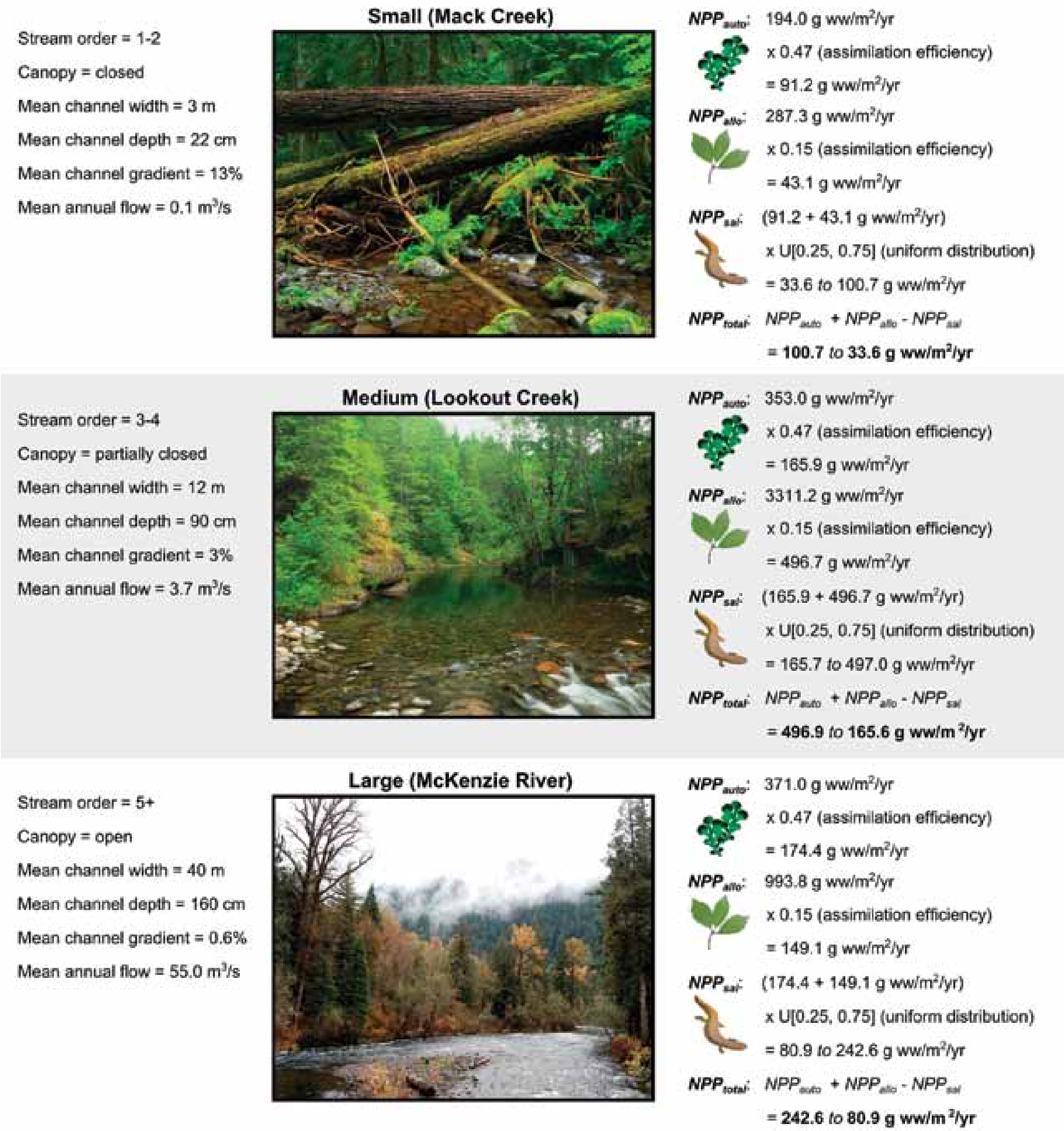


Figure 3. Physical and biological characteristics of small, medium, and large streams within the McKenzie River Basin. Stream order was interpolated from 1:100,000 scale digital maps (NHDPlus 2010). All physical habitat data are from Bott et al. (1985). NPP_{auto} data are from Webster and Meyer (1997). NPP_{allo} data are from Cummins et al. (1983). Assimilation efficiencies are from Pandian and Marian (1986). NPP_{sal} is represented by a uniform distribution ranging from 0.25–0.75 (U[0.25, 0.75]). Photos are courtesy of Al Levno© (Mack Creek and Lookout Creek) and Nora Waite© (McKenzie River).

zie River (near the Blue River confluence) is representative of "large" (LG) streams (stream order = 5–6 in NHDPlus; stream segments greater than sixth order did not occur above 500 m elevation) in the MRB (Figure 3).

Trout Distributions

Common montane fishes in the MRB include cutthroat trout (*Oncorhynchus clarkii*), rainbow trout (*O. mykiss*), and bull trout (*Salvelinus confluentus*); mountain whitefish (*Prosopium williamsoni*); mottled sculpin (*Cottus bairdii*), Paiute sculpin (*C. beldingii*), and torrent sculpin (*C. rhotheus*); and longnose dace (*Rhinichthys cataractae*) and speckled dace (*R. osculus*). We focused entirely on cutthroat and rainbow trout because they are the most abundant and widely distributed salmonids in the MRB (e.g., Murphy and Hall 1981). Cutthroat and rainbow trout were also treated as a single species in our simulations because we did not have sufficient data to distinguish cutthroat and rainbow trout habitats. However, this should not significantly bias our results, because the diets and body masses of cutthroat and rainbow trout are similar in Pacific Northwest streams (see (see Parameterizing, Running, and Evaluating the Model section).

Parameterizing, Running, and Evaluating the Model

Net Primary Production and Salamander Consumption

Bott et al. (1985) measured gross autochthonous production in Mack Creek, Lookout Creek, and the McKenzie River with recirculating oxygen chambers. These measurements were converted to annual *NPP* estimates (in g ash-free dry mass per m^2) following Webster and Meyer (1997). We then converted the *NPP* estimates from ash-free dry mass to carbon (C) with a conversion factor of 0.5 (i.e., 1 g ash-free dry mass = 0.5 g C; Waters 1977) and converted the C estimates to g wet weight (ww) with a conversion factor of 10 (i.e., 1 g C = 10 g ww of consumer tissue; Waters 1977). The resulting net production values were used as our NPP_{auto} estimates in SM, MD, and LG streams (Figure 3).

Allochthonous production was estimated with the annual litterfall data of Cummins et al. (1983; see their Table 9). We converted the litter data from tons C/stream order/year to g ww/m^2/year by first using the above C-to-ww conversion factor (1:10). We then divided the per stream order litter estimates by the total stream channel surface areas that corresponded to each stream order using surface area data in Cummins et al. (1983; see their Table 8) and used the resulting per square meter values for first-, third-, and fifth-order streams as our NPP_{allo} estimates in SM, MD, and LG streams (Figure 3).

On a per unit basis, autochthonous resources are more nutritious than allochthonous resources (Allan 1995). We accounted for this disparity by using mean assimilation efficiencies (47% vs. 15%) from Pandian and Marian (1986) as correction factors. Autochthonous production was multiplied by 0.47 to obtain the final NPP_{auto} estimates and allochthonous production was multiplied by 0.15 to obtain the final NPP_{allo} estimates. We then summed the resulting NPP_{auto} and NPP_{allo} values to estimate trophic resource availability in SM, MD, and LG streams (Figure 3).

Finally, we modified the *NPP* estimates to account for consumption by the Pacific giant salamander (*Dicamptodon tenebrosus*). The Pacific giant is the most abundant trout competitor in MRB streams (e.g., Antonelli et al. 1972), where salamander biomass often rivals or exceeds trout biomass (e.g., Hawkins et al. 1983). Unfortunately, direct measurements of salamander consumption rates (NPP_{sal}) were not available. In place of direct measurements, we assumed that salamanders consume between 25% and 75% of the available trophic resources. To do so, we used a uniform distribution ranging from 0.25 to 0.75 (i.e., U[0.25, 0.75]) and a Monte Carlo sampling routine. In each of 5,000 Monte Carlo simulations, we randomly selected an NPP_{sal} estimate from the uniform distribution and then estimated the total primary production (NPP_{total}) available to support trout production with equation (2), where $NPP_{sal} = (NPP_{auto} + NPP_{allo}) \times U[0.25, 0.75]$.

Trophic Transfer Efficiency and Trophic Level

We compiled a baseline ε distribution (Figure 2B) from the empirical ε data of Pauly and Christensen (1995). Monte Carlo simulations (×5,000) were then used to sample ε values at random from the baseline ε distribution.

We assumed that $T = 3$ for cutthroat and rainbow trout because insects generally occur at $T \approx 2$, and they are the primary food resource for both species of trout (Behnke 1992). Furthermore, most trout in MRB streams are too small (median fork length = 84 mm; see Average Body Mass and the Self-Thinning Exponent section) to be piscivores (see Mittlebach and Persson 1998). $T \approx 3$ has also been verified through gut content analyses (e.g., McHugh et al. 2008) and Fry's (1991) isotope study of Andrews Forest trout.

Production : Biomass Ratio

The empirical P_B data of Randall et al. (1995) were used to compile a baseline P_B distribution (Figure 2C) and Monte Carlo simulations (×5,000) were used to sample P_B values at random from this distribution.

Average Body Mass and the Self-Thinning Exponent

We used trout data from Andrews Forest streams (53 sampling events; 12,684 individuals sampled; see Gregory 2008) to estimate M. Length measurements (Figure 4A) were converted to body masses with a length–mass regression from Carlander (1969). Separate length–mass relationships were examined for cutthroat and rainbow trout, but they did not differ (Figure 4B). We therefore used a common equation ($\log_{10}$ weight $= -4.7 + 2.9 \times \log_{10}$ fork length) to estimate individual body masses for both species. The combined body mass distribution is shown in Figure 4C. The median body mass—7.5 g—was used as our M estimate. This weight is close to the median M reported in a regional survey of Pacific Northwest trout (Platts and McHenry 1988; median standing stock biomass ÷ median density = 7.1 g), and the length–frequency distribution for Andrews Forest trout (Figure 4A) is very similar to length distributions reported in other Pacific Northwest streams (e.g., House 1995; Mellina et al. 2005). Thus, we are confident that the Andrews Forest data were broadly representative of Pacific Northwest trout and that M = 7.5 g was a useful estimate of trout body mass in McKenzie Basin streams.

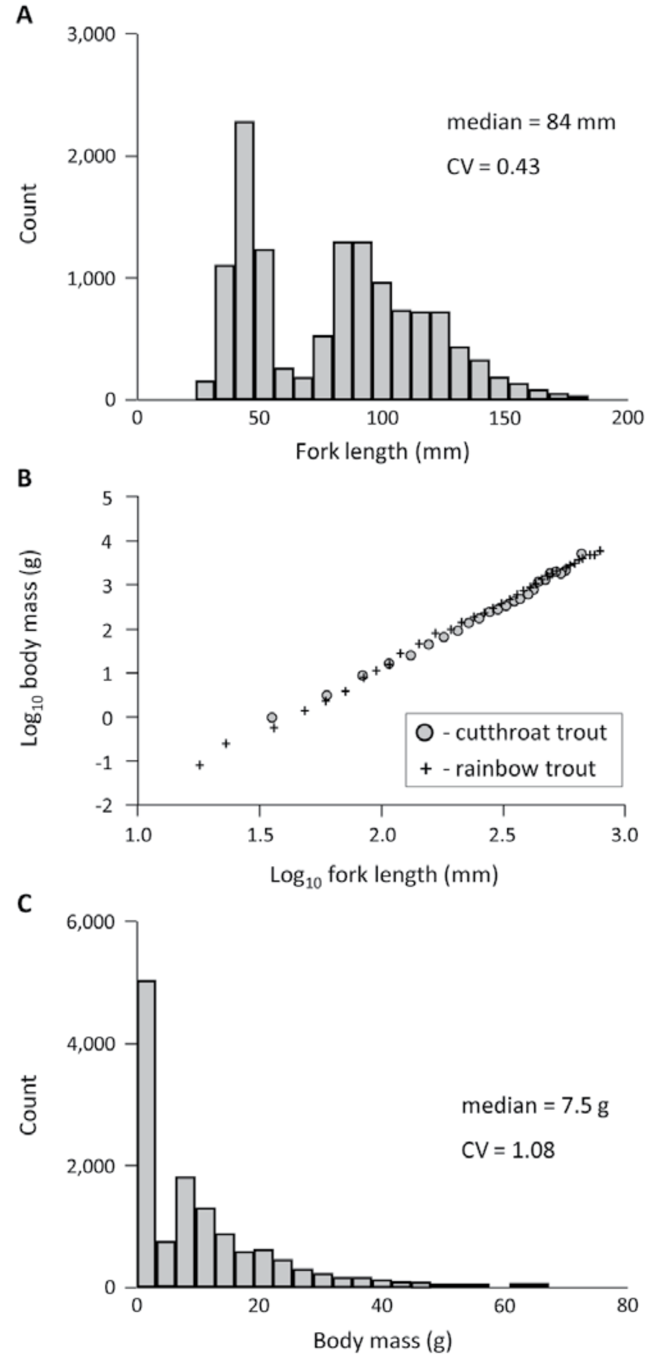


Figure 4. Representative body size data for cutthroat and rainbow trout in the McKenzie River Basin. (A) The length–frequency distribution for all trout collected by Gregory (2008) in H.J. Andrews Forest streams. (B) Length–mass relationships for cutthroat and rainbow trout (Carlander 1969) that were used to convert fork length to body mass. (C) The trout body mass distribution that resulted when all fork lengths were converted to individual body masses.

Note that when M = 7.5 g, the model is effectively predicting the *D* of age-1 trout: 7.5 g equates to approximately 84-mm fork length (Carlander 1969), which is typical of age-1 trout in the Pacific Northwest (e.g., House 1995). But the model does not explicitly account for age structuring nor does it currently predict the densities of multiple age-classes. This is important because the predicted *D* should not be interpreted as numbers of larval trout or of large, harvestable trout (see Prospects for Applying and Improving the Model section).

Finally, *b* data from the primary literature were used to compile a baseline *b* distribution (Figure 2D), and Monte Carlo simulations (×5,000) were used to sample from this distribution.

Model Performance and Sensitivity Analysis

Model performance was assessed by comparing the predicted *D* with the observed (OBS) trout density data of Platts and McHenry (1988). Their data, which were compiled from field studies of 50 small to large montane streams throughout the Pacific Northwest, provided a useful benchmark for testing whether the model-predicted *D* were comparable to estimates obtained with traditional surveying methods (e.g., mark–recapture). We compared the central tendencies of the predicted and OBS data as well as the precision (i.e., spread) of the data.

Sensitivity plots were then created for the model parameters NPP_{sal}, ε, P_B, and *b*. In each sensitivity plot, the predicted *D* were plotted against the complete range of potential NPP_{sal}, ε, P_B, or *b* values and the remaining parameters were held constant at their median values. Sensitivity plots were not created for NPP_{auto}, NPP_{allo}, *T*, or M because they were measured directly in Andrews Forest streams (Cummins et al. 1983; Bott et al. 1985; Fry 1991; Gregory 2008) and were not treated as variable parameters in the model.

Regional Application of the Modeling Results

We used the model to predict average trout *D* in SM, MD, and LG streams, but our final objective was to estimate the potential carrying capacity of all montane streams within the MRB. We therefore estimated the total surface areas of all SM, MD, and LG streams (see Estimating the Total Surface Area of the Stream Network section) and then multiplied these surface areas (m^2) by the model-predicted trout *D* (no./m^2) to obtain regional carrying capacity estimates.

Estimating the Total Surface Area of the Stream Network

We began by querying all montane stream segments (i.e., those occurring within contiguous forest ≥500 m elevation) in the MRB from the NHDPlus data set (see Figure 1) using ArcGIS, version 9. We then classified each of the queried segments as SM, MD, or LG using the stream size criteria described above in the Representative Streams section. Stream segment length and stream order were included in the NHDPlus attribute tables for all segments, but surface area was not. To estimate surface area, we first used a regression model to predict stream channel widths and then multiplied these widths by their corresponding segment lengths.

The stream width regression model was created with data from the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (Whittier and Peck 2008). We randomly selected 130 montane sample sites distributed throughout the Western Forested Mountains ecoregion (see Figure 1 in Whittier and Peck 2008) and used field-measured habitat data from these sites to test a variety of stream width models. The best overall model was

$$\log_{10} \text{stream width} = (0.30 \times \text{stream order}) - (0.00017 \times \text{elevation}), \quad (6)$$

where stream width and elevation were in meters and stream order was estimated at the 1:100,000 scale. This model fit the observed data well and was highly significant ($P < 0.01$; Figure 5).

Predicting Regional Trout Carrying Capacity

When the surface area of each montane stream segment had been estimated, we summed the total surface areas of all SM, MD, and LG streams within the MRB. We then multiplied the total surface areas of SM, MD, and LG streams by their respective model-predicted *D* values to estimate potential carrying capacity within the MRB. Results were also summarized by major watersheds (10-digit U.S. Geological Survey hydrologic units).

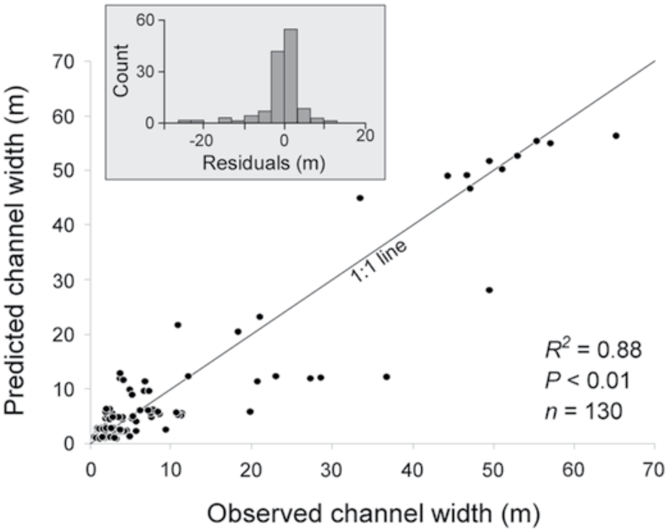


Figure 5. Relationship between observed (field-measured) and model-predicted stream channel widths. Plotted data points are randomly selected stream segments from the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program, Pacific Northwest region. Points near the 1:1 line indicate close fits between observed and predicted channel widths. The distribution of model residuals (i.e., prediction errors) is shown as an inset. Positive residuals are instances where the model predictions were greater than the observed widths and negative residuals are instances where the model predictions were less than the observed widths. Notably, most predictions are within ±5 m of the observed widths.

RESULTS AND DISCUSSION

Predicted Trout Densities

Model-predicted trout *D* were highest in MD streams and lowest in SM streams: the median predicted *D* were 0.11, 0.55, and 0.28 trout/m^2 in SM, MD, and LG streams, respectively (Figure 6). Overall, the model predictions were comparable to OBS trout densities. The predicted *D* were slightly lower in SM streams than the OBS densities, but the interquartile ranges exhibited considerable overlap (Figure 6). Predicted *D* in the MD streams exceeded the OBS densities by a relatively large margin. For example, the median predicted *D* in MD streams was approximately twice the median OBS density (0.24 trout/m^2). The median OBS density did, however, occur within the interquartile range of the predicted *D* in MD streams. And the predicted trout *D* in LG streams was very similar to the OBS densities: the median predicted *D* was 0.28 trout/m^2 (vs. 0.24 OBS) and the interquartile ranges exhibited substantial overlap. Also, 96% of all model predictions (i.e., SM, MD, and LG stream simulations combined) fell within the OBS minimum–maximum range (stars in Figure 6). We therefore conclude that the model-predicted trout *D* are realistic relative to OBS densities.

Model precision was generally low but comparable to the precision of the OBS trout density estimates. For instance, each

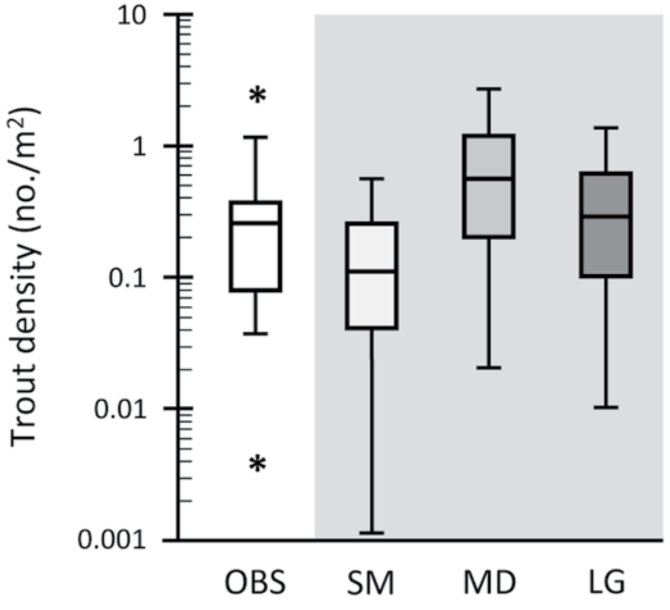


Figure 6. Observed (OBS) and model-predicted trout densities in small (SM), medium (MD), and large (LG) streams. All data are presented as box-and-whisker plots: boxes show the 25th, 50th, and 75th percentiles and whiskers show the 5th and 95th percentiles. Stars show the minimum and maximum OBS densities. Each of the model-predicted boxplots reflects 5,000 Monte Carlo simulations. The OBS data reflect empirical trout densities that were measured in a range of small to large streams distributed throughout the Pacific Northwest (Platts and McHenry 1988).

of the model-predicted interquartile ranges spanned approximately 0.75 orders of magnitude, whereas the interquartile range of the OBS densities spanned approximately 0.5 orders of magnitude (Figure 6). Model precision was also comparable with levels of precision reported in other regional-scale field studies. For example, Dauwalter et al. (2009) used a national database of trout densities to quantify natural variability within trout populations and reported an average coefficient of variation (CV) of 0.49. Petty et al. (2005) reported a similar CV (0.48) for eastern brook trout (*Salvelinus fontinalis*). The CVs for the interquartile ranges of the model-predicted D (calculated by removing the first and fourth quartiles) ranged from 0.49 to 0.50. Thus, the model predictions—particularly the interquartile ranges—may be well suited for estimating trout population densities at regional scales (see McGarvey et al. 2010).

Sensitivity plots showed that the model was least sensitive to changes in NPP_{sal}. Predicted D was a negative, linear function of NPP_{sal} and the slope of this relationship was relatively low, though it varied between SM, MD, and LG streams (Figure 7A). The model was much more sensitive to changes in ε, P_B, and b (Figures 7B–7D). Each of these parameters exhibited curvilinear relationships with predicted trout D, with D increasing more rapidly as ε increased or as P_B or b decreased. Using site- or region-specific data to narrow the range of potential ε, P_B, and b values should therefore be a priority in future research. In particular, one may wish to verify whether $\varepsilon \geq 0.15$ (the approximate inflection point in Figure 7B), $P_B \leq 1$ (see Figure 7C), or $b \leq 0.75$ (see Figure 7D). Doing so could greatly reduce the variability of the D predictions (i.e., increase model precision) shown in Figure 6.

Regional Carrying Capacity

We predict that the potential carrying capacity of all montane streams within the MRB is between 0.8 million (sum of 25th percentiles for all watersheds; see Figure 8) and 4.6 million (sum of 75th percentiles) trout. The median predicted carrying capacity is approximately 2.1 million trout. For individual watersheds, predicted carrying capacity is highest in the Lower McKenzie, due to the combined surface area of LG stream segments (93.3 ha). Predicted carrying capacity is lowest in the Blue River and Quartz Creek watersheds due to the lack of LG stream segments. However, we predict that all watersheds are capable of supporting large numbers of trout. For instance, the median predicted carrying capacities are more than 150,000 trout in all watersheds (Figure 8).

Prospects for Applying and Improving the Model

By substituting a simple, robust macroecological equation (i.e., the self-thinning relationship) for the more complex algorithms and data demands of traditional fish habitat models, we were able to predict regional trout carrying capacity in a highly efficient manner. Our model includes only eight parameters (see equations 2 and 5), and most can be estimated using

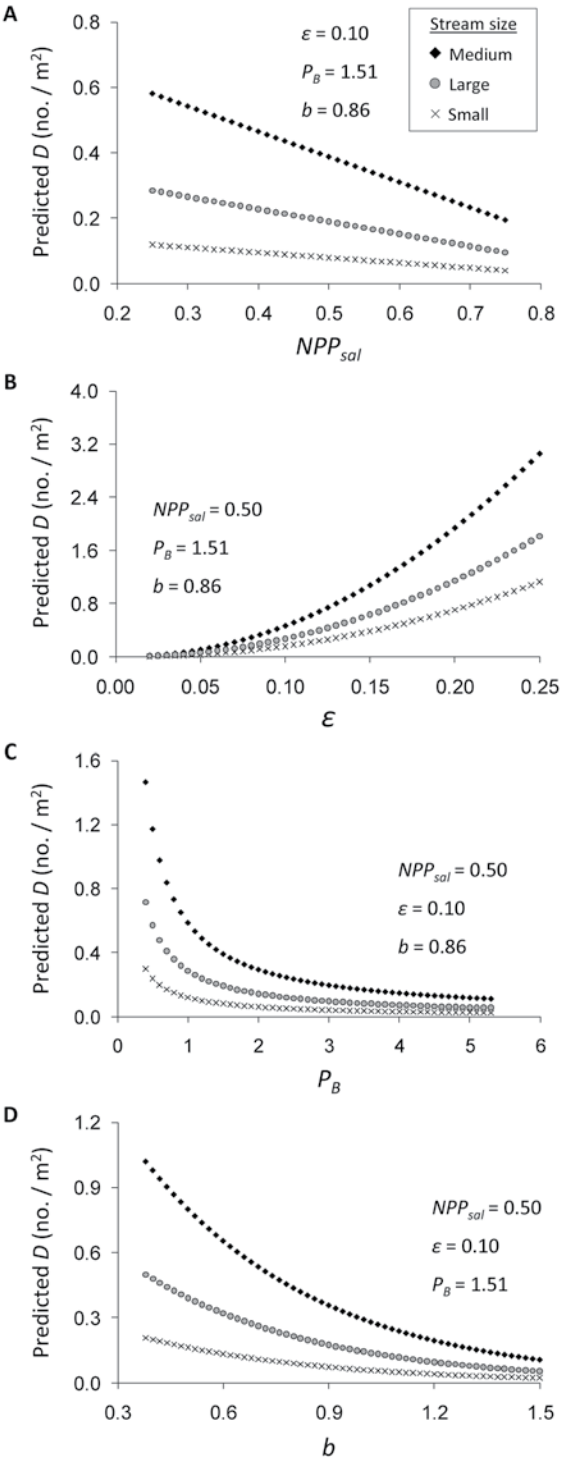
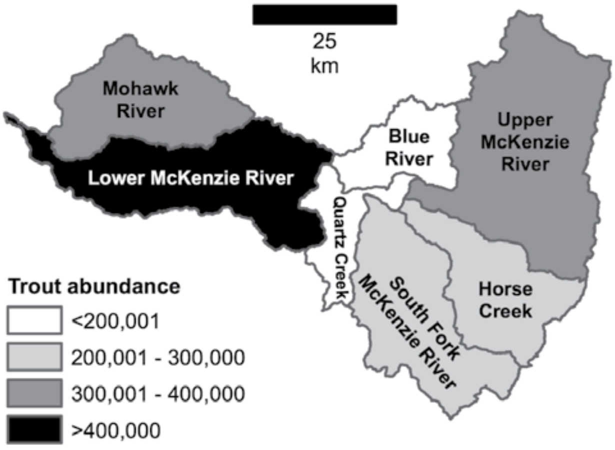


Figure 7. Sensitivity analysis results. Sensitivity plots are shown for the model parameters (A) NPP$_{sal}$, (B) ε, (C) P$_B$, and (D) *b*, when the trout density model was run in small, medium, and large streams. In each plot, the predicted trout densities are shown when the full range of potential parameter values (NPP$_{sal}$, ε, P$_B$, or *b*) is used in the model (equation 5), but the remaining parameters are held constant at their median values (shown on each plot).

data published in the primary or gray literature. For example, we have already compiled baseline distributions of ε, P_B, and b values (see Figure 2), and NPP_{auto} and NPP_{allo} have been quantified in many different types of systems (e.g., Bott et al. 1985; Webster and Meyer 1997). Thus, the model can potentially be used to estimate carrying capacity in many different regions.

Several caveats should, however, be considered when applying the macroecological model. First, the model cannot currently predict trout D within specific streams with a high level of precision. Variability in the model outputs reflected the overall sensitivity of the model; large changes in D were sometimes driven by relatively small changes in ε, P_B, and b (Figure 7). More precise parameter estimates may therefore reduce the variability in predicted D. That said, trout populations are naturally variable and the interquartile ranges of the predicted D (Figure 6) were comparable to observed rates of variation among years and among sites (e.g., Petty et al. 2005; Dauwalter et al. 2009). This suggests that high model sensitivity or variability is not a problem. Rather, it may be an efficient tool for modeling trout D at regional scales. We therefore recommend that the median predicted D be used to estimate average trout densities at the regional scale and the interquartile ranges be used to characterize natural variation within or among populations (see McGarvey et al. 2010).



Watershed	Trout carrying capacity (total abundance)
Blue River	
75th percentile	344,238
50th percentile	156,745
25th percentile	56,998
Horse Creek	
75th percentile	621,014
50th percentile	283,298
25th percentile	103,017
Lower McKenzie River	
75th percentile	1,144,629
50th percentile	522,272
25th percentile	188,222
Mohawk River	
75th percentile	666,173
50th percentile	303,265
25th percentile	110,278
Quartz Creek	
75th percentile	398,555
50th percentile	179,880
25th percentile	64,537
South Fork McKenzie River	
75th percentile	569,118
50th percentile	270,816
25th percentile	98,479
Upper McKenzie River	
75th percentile	862,071
50th percentile	392,900
25th percentile	142,873

Figure 8. Estimated trout carrying capacity within the McKenzie River Basin. The map shows the median predicted carrying capacity (50th percentile) in each of the Basin's major watersheds. The 25th and 75th percentiles of the predicted carrying capacities are also shown in the table for each watershed.

Second, by using common M and T values, we assumed that cutthroat and rainbow trout are functionally equivalent in montane streams. This assumption seemed reasonable, given that these species have similar diets and size distributions (see Parameterizing, Running, and Evaluating the Model section). But separate cutthroat and rainbow trout predictions will be necessary if managers have distinct objectives for these species. Thus, the ability to discriminate between cutthroat and rainbow trout could improve the model. For instance, a simple habitat differentiation rule that uses stream size as a predictor may be possible, given that cutthroat trout often occur in smaller, higher gradient streams than rainbow trout (Johnson et al. 1999).

Third, our carrying capacity estimates should not be construed as numbers of harvestable trout because the model used an average trout M of 7.5 g (or ~84 mm fork length), which is well below the minimum size limit for harvest in Oregon (≥203 mm; Oregon Department of Fish and Wildlife 2011). Harvestable trout abundances could be predicted if an algorithm to partition trophic resources among discrete age- or size-classes and independent M and T estimates for each size-class were available. Size-classes could then be modeled independently, effectively treating them as separate "species" (see McGill 2008). But for the moment, fisheries managers are advised that large, harvestable trout will comprise only a fraction of the predicted carrying capacities shown in Figure 8.

Fourth, the NPP_{total} estimates did not include terrestrial insect subsidies or marine subsidies (i.e., anadromous salmon carcasses and eggs), which can account for a large fraction of trout production (Wipfli and Baxter 2010). Marine subsidies should not significantly influence our results because dams now prevent migratory salmon from accessing much of their historical habitat in the MRB (Oregon Department of Fish and Wildlife 2005). However, terrestrial insect subsidies may be important, particularly in SM streams where aquatic–terrestrial linkages are strongest and terrestrial insect densities are highest (Wipfli and Baxter 2010). For instance, Romero et al. (2005) measured terrestrial insect subsidies in small streams along the Oregon coast. If their annual estimate (45.5 g ww/m^2/year, using C and ww conversions from Waters 1977) had been added to our NPP_{total} estimate in SM streams (at T = 2 because terrestrial insects are consumed directly by trout), our median predicted D would have increased to approximately 0.37 trout/m^2—a closer fit to the OBS density data than our original prediction for SM streams (Figure 6). Determining whether similar terrestrial insect subsidies are available to MRB trout should therefore be a priority in future research.

Fifth, we assumed that Andrews Forest streams are representative of all montane streams in the MRB. Strictly speaking, we know that this was incorrect and we acknowledge that site-specific data would improve the modeling results. But in the absence of a comprehensive, spatially explicit database, we submit that the Andrews Forest data were a good starting point for our regional simulations, noting that Andrews Forest is widely recognized as a model system for studying montane forest ecology in the Pacific Northwest (Geier 2007). We also emphasize that physical habitat and *NPP* data from other Pacific Northwest streams have generally corroborated the Andrews Forest data (e.g., Naiman and Sedell 1980).

Finally, our model did not account for nontrophic constraints on trout abundance, such as habitat quality or degradation. These secondary limitations may cause actual trout abundances to be lower than our predicted abundances in many streams (see Poff and Huryn 1998; Jackson et al. 2001). We did not consider this a problem because our objective was to estimate potential carrying capacity at the regional scale. Other models are better suited to predict fish abundance within disturbed habitats or at smaller scales (e.g., Burnett et al. 2007). In future applications, it may be possible to add nontrophic factors to our model. For example, if model parameter estimates were available from logged or agricultural streams, the model could be used to evaluate land use decisions (see Bernot et al. 2010), but doing so will add complexity and may ultimately blur the distinction between our simple model and conventional models. For now, we emphasize that the predicted abundances should be thought of as maximum carrying capacities within minimally impacted systems.

Methods similar to ours have been used in marine systems (e.g., Jennings and Blanchard 2004) but this study is, to the best of our knowledge, the first application in a freshwater environment. The data needed to run the model are, however, available in many freshwater systems (e.g., Webster and Meyer 1997). Our method may therefore be of help to anyone who wants to estimate regional fish abundances or carrying capacities but does not have the resources to build and calibrate more complex models.

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