Hierarchical analysis of relationships between brook trout (Salvelinus fontinalis) density and stream habitat features

Article *in* Canadian Journal of Fisheries and Aquatic Sciences · April 2007

DOI: 10.1139/f07-053

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Hierarchical analysis of relationships between brook trout (*Salvelinus fontinalis*) density and stream habitat features

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Abstract: We used hierarchical linear regression to examine relationships between brook trout (*Salvelinus fontinalis*) density and habitat features nested at three levels: sections within reaches, reaches within streams, and streams within a basin. Brook trout density and environmental variables were quantified at 600 stream sections distributed among 120 reaches and 22 streams in the Cascapedia River basin, Quebec, Canada. Decomposition of variance showed that variation in density among streams was small relative to that among sections or reaches and not statistically significant. Density was influenced by habitat variables at both the section (current velocity, woody debris, cover) and reach (subbasin area, height increment at flood, valley width) levels. A cross-level interaction between current velocity and subbasin area pointed to a "contextual" effect: density showed stronger decline with current velocity in larger subbasins than in smaller subbasins. This result suggests that there was no single "best scale" for examining fish–environment relationships. Accounting for contextual effects by use of hierarchical models can enhance our understanding of how habitat features influence fish densities at multiple spatial scales.

Résumé : La régression linéaire hiérarchique nous a permis d'examiner les relations entre la densité d'ombles de fontaine (*Salvelinus fontinalis*) et les caractéristiques environnementales emboîtées à trois niveaux hiérarchiques : les sections à l'intérieur des tronçons, les tronçons à l'intérieur des tributaires et les tributaires à l'intérieur d'un bassin. Nous avons échantillonné les poissons et les variables environnementales dans 600 sections réparties sur 120 tronçons et 22 tributaires de la rivière Cascapédia (Québec), Canada. La décomposition de la variance montrait que la variation de la densité entre tributaires n'était pas significative et était plus faible que celle entre sections ou entre tronçons. La densité était influencée par des caractéristiques environnementales aux niveaux des sections (vitesse du courant, débris ligneux, couvert) et des tronçons (superficie du sous-bassin, augmentation de la hauteur à la crue, largeur de la vallée). L'interaction entre la vitesse du courant et la superficie du sous-bassin suggérait l'existence d'un effet contextuel : l'influence négative de la vitesse du courant sur la densité était plus forte dans les grands sous-bassins que dans les petits sous-bassins. Les résultats indiquent qu'il n'y avait pas d'échelle « optimale » pour l'analyse des rélations poissons–environnement. L'examen des effets contextuels à l'aide des modèles hiérarchiques peut améliorer notre compréhension des relations poissons–environnement à plusieurs échelles spatiales.

Introduction

Ecological data often have clustered or nested structure that arises from observations made on sampling units grouped at different hierarchical levels. Because sampling levels can be chosen to correspond to spatial scales of analysis, nested sampling designs can be useful in examining fish–habitat relationships at multiple spatial scales. The hierarchical structure in data from such designs can be exploited to address questions about the scale dependence of patterns and responses, e.g., do environmental features influence fish distribution similarly across channel units nested within reaches, reaches nested within streams, or streams nested within a basin? (Dunham and Vinyard 1997; Inoue et al. 1997; Watson and Hillman 1997).

By explicitly considering hierarchical structure, one can also examine potential "cross-level" interactions between environmental variables characterising units at different spatial scales. Such interactions may result in contextual effects in which the influence of a local environmental variable is contingent upon the level of another, larger-scale variable. For example, in Japanese streams, the influence of cover on the abundance of masu salmon (*Oncorhyncus masou*) within a small-scale channel unit (pool, riffle, glide, cascade, or rapid) differs across large-scale geomorphic channel types comprising groups of 60 to 70 channel units (Inoue et al. 1997). At the scale of a pool–riffle sequence, salmon density is positively related to the abundance of cover, but at the scale of stream reaches (10 pool–riffle sequences), this relationship only holds when cover is rare (Inoue et al. 1997).

Received 7 July 2006. Accepted 26 March 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 12 June 2007. J19405

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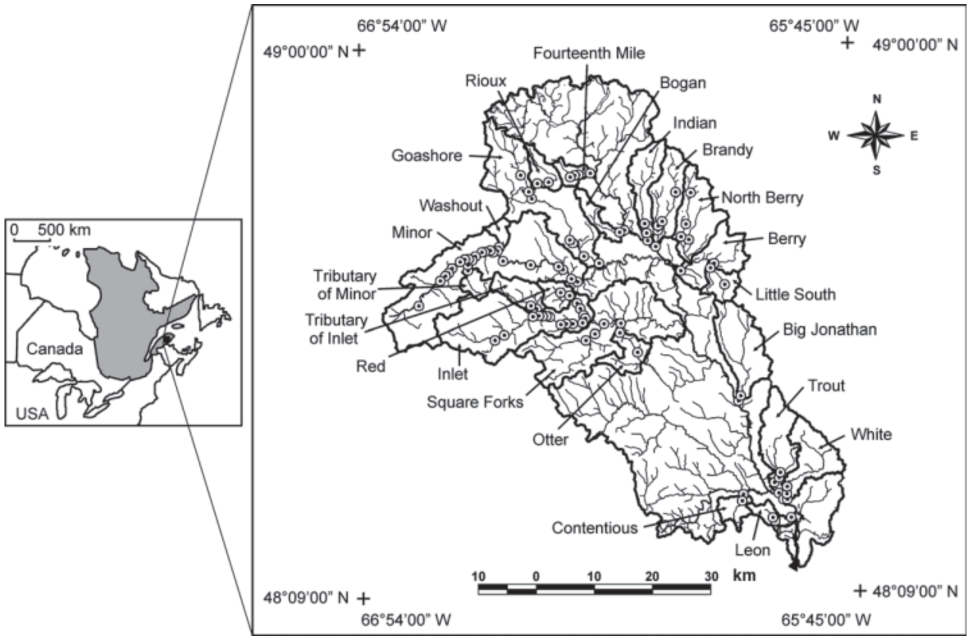
 doi:10.1139/F07-053

Fig. 1. Location of the 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin, Québec, Canada.



Patterns and processes detected at local spatial scales do not necessarily also apply at larger scales (Inoue et al. 1997; Folt et al. 1998; Schneider 2001). Examples of apparent inconsistencies in patterns and processes across scales include differences in habitat preference of fish species across river sections or reaches (Poizat and Pont 1996), fish response to environmental features across basins (Dunham and Vinyard 1997; Watson and Hillman 1997), and longitudinal distribution of mesohabitats across hydro-ecoregions (Cohen et al. 1998). These examples hint at potential outcomes of cross-level interactions and suggest that the above inconsistencies may be resolved by explicitly considering such interactions.

Nested sampling designs can yield useful insights into processes operating at multiple spatial scales, yet few studies in stream ecology seem to have fully exploited this potential. One technical obstacle has been that in nested samples, units within a group usually tend to be more similar to other units within their group than to units in other groups. Thus, individual observations are not entirely independent as required by conventional regression models.

This potential drawback is addressed by hierarchical regression modelling, a statistical approach that copes effectively with nested data structures and allows for inclusion of effects operating at several levels, as well as cross-level interactions, in a single model (Hox 2002; Goldstein 2003). In this study, we use hierarchical linear (HL) regression to examine the relationships between brook trout (*Salvelinus fontinalis*) density and environmental features nested at three spatial scales: across sections within reaches and streams, across reaches within streams, and across streams within a basin.

Materials and methods

Fish sampling and environmental measurements

Brook trout density and environmental variables were quantified at 600 sections distributed among 120 sampling sites and 22 tributary streams in the Cascapedia River basin (3179 km^2), Québec, Canada (Fig. 1). Sites were selected to maximize spatial coverage of the basin subject to accessibility constraints. Sites were visited in random sequence during low flow from mid-June to late August in 2000 (24 sites), 2001 (48 sites), and 2002 (48 sites). At each site, samples were collected from a 75-m stream reach comprising five adjacent sections, each approximately 15 m in length. No attempt was made to position sampled reaches to coincide with habitat boundaries. The nested sampling design therefore spanned three spatial scales: sections within reaches (maximum fluvial distance between sections ≈ 0.075 km), reaches within streams (maximum fluvial distance between reaches averaged across streams ≈ 8 km), and streams within the basin (maximum fluvial distance between stream mouths ≈ 82 km).

Sampled areas covered the entire stream width in completely wadable reaches and ranged 5 m from one bank, chosen randomly, towards the opposite bank otherwise. Fish were sampled by single-pass electrofishing (Smith-Root D-15) in an upstream direction within open stream sections (Lobón-Cerviá and Utrilla 1993; Crozier and Kennedy 1994; Jones and Stockwell 1995). All captured fish were identified, measured, weighed, and returned to their point of capture. Brook trout density was calculated as total captures divided by section area (numbers·100 m^{-2}). Because capture efficiency is not 100%, this measure underestimates true density but should be proportional to it if efficiency is comparable across sampling units, an assumption that seems tenable given that all sites were sampled under base flow conditions.

In all, 21 environmental variables were quantified at the section, reach, or stream scales (Table 1). For each section, water depth and substratum size (modified Wentworth scale) were measured at five equidistant points along each of four equidistant transects perpendicular to stream flow. Current

Table 1. Hierarchical level (HL), median, and quartiles (25%–75%) for 21 environmental variables describing fish habitat in 600 sections distributed among 120 reaches and 22 streams of the Cascapedia River basin.

Variable name	HL	Median	Quartiles (25%–75%)
Overhead opening (°)	Section	95.7	75.4–113.5
Cover index	Section	2.4	1.4–3.0
Mean depth (cm)	Section	24.6	18.8–29.4
Mean current velocity ($cm\cdot s^{-1}$)	Section	34.9	26.0–48.9
Mean substratum size index	Section	5.3	4.9–5.8
Mean wetted width (m)	Section	9.3	6.3–14.1
Large woody debris (number)	Section	3.5	1.0–8.5
Vegetation abundance index	Section	1.0	1.0–1.8
Accessibility index	Reach	0.8	0.3–1.0
Altitude (m)	Reach	240.0	167.5–315.0
Distance to mainstem (km)	Reach	9.1	2.5–21.7
Entrenchment (%)	Reach	10.0	5.0–15.0
Height increment at flood (m)	Reach	0.5	0.4–0.7
Mean temperature (°C)	Reach	10.5	9.0–12.0
Stream slope (°)	Reach	1.0	0.6–1.3
Stream gradient (°)	Reach	2.1	0.6–3.3
Stream order	Reach	3.0	3.0–4.0
Valley width (m)	Reach	180.0	95–350
Subbasin area (km^2)	Reach	70.1	25.5–151.0
Width increment at flood[a] (m)	Reach	2.6	1.9–4.0
Distance to mouth (km)	Stream	75.5	52.8–82.4

Note: The hierarchical level indicates the scale at which measurements varied among sampling units.
[a]Sum of measures from right and left margins.

velocity (pygmy-type meter, Scientific Instruments 1205) was measured at five equidistant points along the second transect from the downstream end. Wetted width was measured at each transect. Abundance of submerged vegetation (moss or macrophytes) and overall availability of structural cover (rocks, woody debris, undercut bank, and overhanging vegetation) were estimated visually and assigned ordinal values reflecting areal coverage (1, ≤5%; 2, 6%–15%; 3, 16%–45%; 4, >45%). Overhead opening (angle between riparian canopy or hilltops blocking incident sunlight at the centre of the stream; Table 1) and slope over the stream reach were measured with a handheld clinometer (Suunto MP-5). The increment in stream height and width at flood (from annual flood marks) were measured on site for each section and averaged by reach. Water temperature was measured at each section (handheld thermometer, Barigo). Entrenchment (mean gradient ≤100 m away from stream bank), valley width (distance between piedmonts on each side of the stream), stream order (Strahler scale), and altitude were obtained from 1:20 000 topographic maps, as were distances by waterway from each section to the Cascapedia River (“distance to mainstem”) and from the mouth of each stream to the mouth of the Cascapedia River (“distance to mouth”) (planimeter, Calculated Industries 6125). Subbasin surface area and stream gradient (mean slope from sampling reach to source) were obtained from 1:20 000 maps (Ministère des Ressources naturelles du Québec) by use of a geographic information system (ArcView 3.2, ESRI, Redlands, Calif.). Units of large woody debris (>10 cm diameter) and pools were counted within each section. Physical barriers potentially affecting upstream migration of fish along a tributary were assessed from field observations and topographic maps, and their effectiveness was coded as an integer value, B, ranging from 0 (no visible barrier) to 4 (insurmountable barrier), reflecting the height, type (beaver dams, log jams, culverts, falls), and configuration of the barrier. An index of accessibility combining multiplicatively all potential barriers for each site was calculated:

$$\text{accessibility} = \prod_{i=1}^{N} \left(1 - \frac{B_i}{4}\right)$$

where N is the number of visible barriers and B_i is the effectiveness of barrier i downstream from the site. Accessibility was assigned the value 1 in the absence of visible barriers. The index thus ranged from 0 to 1, taking a value of 0 if at least one barrier was insurmountable (B_i = 4).

Quantitative analyses

The relationships between brook trout density and habitat features nested at different hierarchical levels were examined by use of HL regression (program MLwiN, version 2.0; Rasbash et al. 2004), a model known as linear mixed effects in the statistical literature and multilevel regression in the social sciences. The description that follows is largely drawn from Hox (2002) and Goldstein (2003). The HL model relates observations made on I units clustered within J groups to one or more predictor variables (X_{ij}). For a single predictor,

$$Y_{ij} = \beta_{0j} + \beta_{1j} X_{ij} + \varepsilon_{ij}$$

where β_{0j} is the intercept and β_{1j} is the group-specific slope for the predictor. Departure of observation i from the predicted regression line of group j is represented by the random term ε_{ij}, the level-one residuals. In contrast to ordinary least-squares (OLS) regression, HL regression assumes that groups are randomly sampled from a larger population of groups, and sampling units within groups need not be independent. Variation among groups in the intercept β_{0j} and slope β_{1j} is characterized as

$$\beta_{0j} = \beta_0 + u_{0j}$$

$$\beta_{1j} = \beta_1 + u_{1j}$$

where the random effects u_{0j} and u_{1j} represent departures of the intercept and slope of group j from the fixed terms β_0 (overall mean intercept) and β_1 (overall mean slope), respectively. The random effects u_{0j} and u_{1j}, which represent level-two residuals, explicitly allow for the hierarchical structure of the data and constitute a fundamental difference between OLS and HL regressions. The terms u_{0j}, u_{1j}, and ε_{ij} are assumed to follow normal distributions with zero mean and variances to be estimated ($\sigma^2_{u_0}$, $\sigma^2_{u_1}$, and σ^2_ε). The random effects u_{0j} and u_{1j} are assumed to be independent from the level-one residuals ε_{ij} but generally not from each other.

The intercepts and slopes of the HL regression are weighted averages of OLS estimates for each group and the overall regression estimate for all similar groups. As a result, residuals are shrunken back towards the overall mean. The amount of shrinkage depends on the reliability of the estimate for a group, which is determined by the number of units within the group and the difference between the estimate for the group and the overall mean. Therefore, less reliable estimates are shrunken closer to the mean.

Among-group variation in both intercept and slope can be accounted for by introducing level-two predictors (Z_j):

$$\beta_{0j} = \beta_0 + \beta_{01} Z_j + u_{0j}$$

$$\beta_{1j} = \beta_1 + \beta_{11} Z_j + u_{1j}$$

The full model, including fixed and random terms, is then

$$Y_{ij} = \beta_0 + \beta_1 X_{ij} + \beta_{01} Z_j + \beta_{11} X_{ij} Z_j + u_{0j} + u_{1j} X_{ij} + \varepsilon_{ij}$$

where $X_{ij}Z_j$ is a cross-level interaction between level-one and level-two predictors.

The regression model was produced by a forward selection procedure in which individual terms were selected according to the significance of changes in deviance between models (log-likelihood ratio tests, $\alpha = 0.05$). A stepwise sequence similar to that proposed by Hox (2002) was followed in building the final model. In the first step, the total variance in brook trout density was decomposed and apportioned among hierarchical levels by use of the classical model for variance components:

$$Y_{ijk} = \beta_0 + u_{0jk} + \nu_{0k} + \varepsilon_{ijk}$$

where $u_{0jk} \sim N(0, \sigma^2_{u_0})$, $\nu_{0k} \sim N(0, \sigma^2_{\nu_0})$, and $\varepsilon_{ijk} \sim N(0, \sigma^2_\varepsilon)$ and the σ^2 terms represent variances at the stream ($\sigma^2_{\nu_0}$), reach ($\sigma^2_{u_0}$), and section (σ^2_ε) levels. To determine whether random intercepts were needed at the reach and stream levels, we examined whether brook trout density varied significantly at those levels by using one-sided tests for the corresponding variance terms (Snijders and Bosker 1999; Hox 2002). Because brook trout density did not vary significantly at the highest level, across streams (Table 2), only two-level models reflecting variation at the section and reach levels were considered in subsequent analyses. In the second step, section-level (level-one) predictors were tested one at a time, and the predictor accounting for the greatest change in deviance was added to the model if the change in deviance was significant. This procedure was repeated until no significant reduction in deviance could be attained by including any of the remaining potential predictors. In the third step, the slope coefficients of the selected predictors were tested for significant reach-level (level-two) variation to determine whether random slopes were required for those predictors. In the fourth step, reach-level predictors were tested similarly to the section-level predictors in step 2. In the fifth step, all first-order interaction terms between section- and reach-level predictors already in the model were tested and included in the model if significant.

Table 2. Random-effects decomposition of the total variance in brook trout (*Salvelinus fontinalis*) density, by hierarchical level (HL).

HL	Variance term	Estimate (SE)	Total variance (%)	p
Sections	σ^2_ε	0.349 (0.023)	34.9	
Reaches	$\sigma^2_{u_0}$	0.597 (0.096)	59.7	<0.001
Streams	$\sigma^2_{\nu_0}$	0.051 (0.060)	5.1	0.102

Note: HL (variance term): section (σ^2_ε), reach ($\sigma^2_{u_0}$), streams ($\sigma^2_{\nu_0}$). Variance among sections corresponds to the error term and has no associated p value. SE, standard error.

To account for serial correlation potentially arising between first-level residuals because of the proximity between sections within a reach, a first-order autoregressive (AR1) covariance structure with equal spatial intervals was included in the model:

$$\mathrm{cov}(\varepsilon_{ij}, \varepsilon_{i-s,j}) = \sigma^2_\varepsilon e^{-\alpha s}$$

where s is the standardized distance between two sections in the same reach and α is a decay coefficient for the spatial autocorrelation, which is given by $e^{-\alpha s}$ (Yang et al. 2001; Hox 2002; Goldstein 2003). The section-level R^2 was obtained by squaring the Pearson correlation between observed values and values predicted by the full model.

Before analysis, brook trout density was transformed as $\ln(X + 1)$; environmental variables were transformed by use of logarithmic or power functions when necessary to reduce the influence of extreme points and better fit statistical assumptions of linearity, normality, and homoscedasticity. All variables were standardized to their grand mean to avoid nonessential colinearity between predictors and facilitate the interpretation of the intercept (Hox 2002).

Results

Brook trout were found in 89% of sections, 98% of reaches, and all streams. The decomposition of variance showed that variation in brook trout density among streams was small (5.2% of total variance) in relation to that among sections (35.3%) or reaches (59.5%) and not statistically significant (Table 2). The 21 potential predictors were not strongly intercorrelated: only 8 of 210 pairwise correlations were >0.5 in absolute value and all of the tolerances were

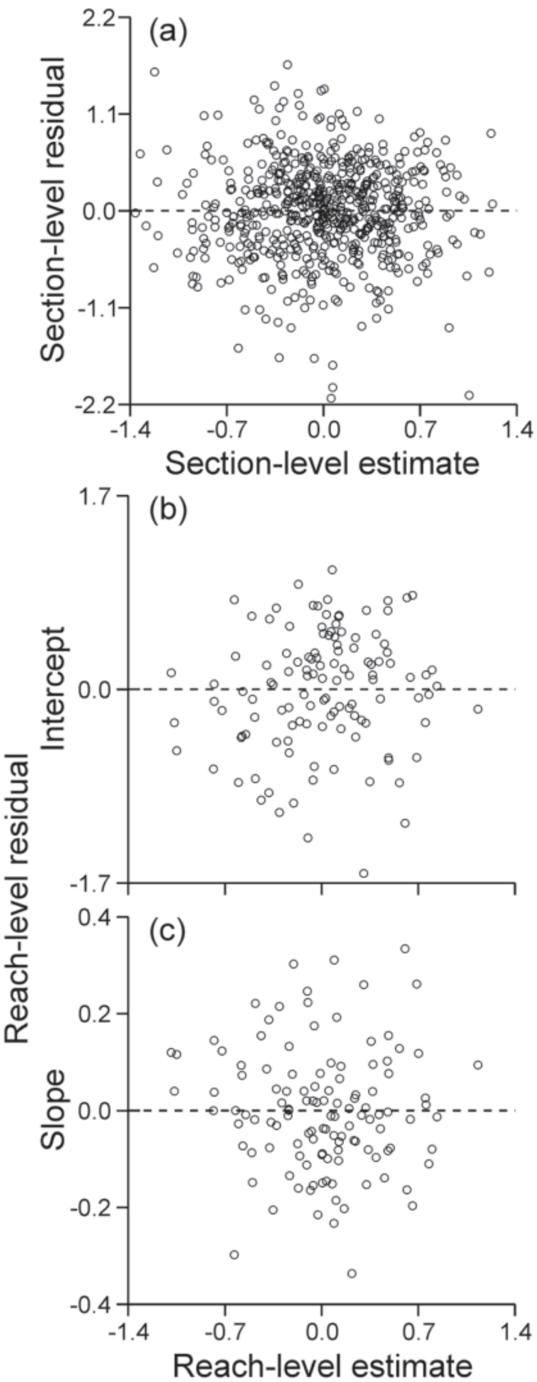


Fig. 2. Residual plots for section-level and reach-level residuals. (*a*) Section-level residuals are the differences between observed values and values predicted by reach-level regressions. (*b* and *c*) Reach-level residuals refer to the regression parameters for current velocity. (*b*) Reach-level residuals for the intercept are the differences between the estimated intercepts for each reach and the overall mean intercept. (*c*) Reach-level residuals for the slopes are the differences between the estimated slope for each reach and the overall mean slope. Residuals are plotted against the standardized density predicted by the fixed-effects part of the model.

≥0.06. The final regression model included three section-level predictors (current velocity, units of woody de-

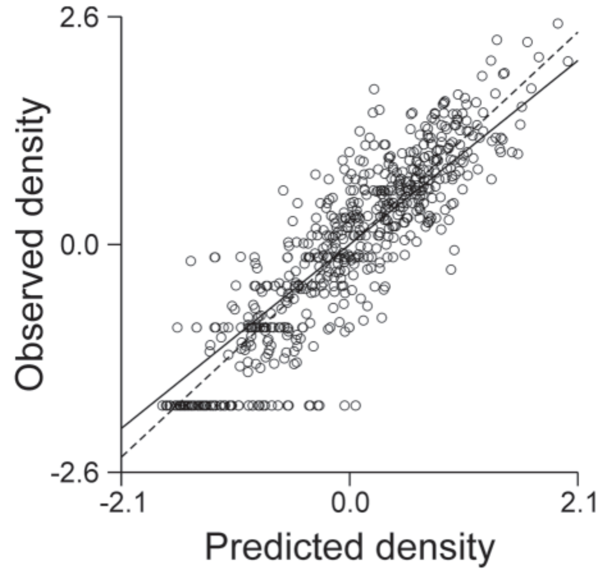


Fig. 3. Scatterplot of observed vs. predicted densities of brook trout (*Salvelinus fontinalis*). Densities are standardized to zero mean and unit variance. Predicted values are from the full model including both fixed and random effects. One-to-one (solid) and regression (broken) lines are also shown. The horizontal row of values at the bottom of the figure represents sections where no fish were captured.

bris, and cover index), three reach-level predictors (subbasin area, valley width, and height increment at flood), and a cross-level interaction between current velocity and subbasin area. Although the spatial autocorrelation term was not statistically significant (p = 0.075), it was nevertheless kept in the model to adjust for the spatial relationship between sections. The tolerance for predictor variables in final models was always ≥ 0.75, indicating only mild colinearity among the predictors. Graphical analyses showed no apparent deviations from the assumptions of normality, homogeneity of variance (residual plots for the section and reach levels; Fig. 2), and linearity (scatterplot of observed vs. predicted values; Fig. 3).

Brook trout density was positively related to woody debris and cover and negatively related to height increment at flood, valley width, and current velocity, but the relationship between brook trout density and current velocity varied markedly across reaches, as shown by the variation in the slope coefficients for current velocity (Fig. 4). This variation was related systematically to subbasin area, as revealed by the significant cross-level interaction between current velocity and subbasin area (Table 3). A graphical display of the cross-level interaction showed stronger decline with current velocity in larger subbasins than in smaller subbasins (Fig. 5).

Discussion

In the Cascapedia River basin, brook trout density did not vary significantly among streams, but varied substantially both among sections within reaches and among reaches. Although multiscale studies often examine the proportion of variation explained by environmental features at different

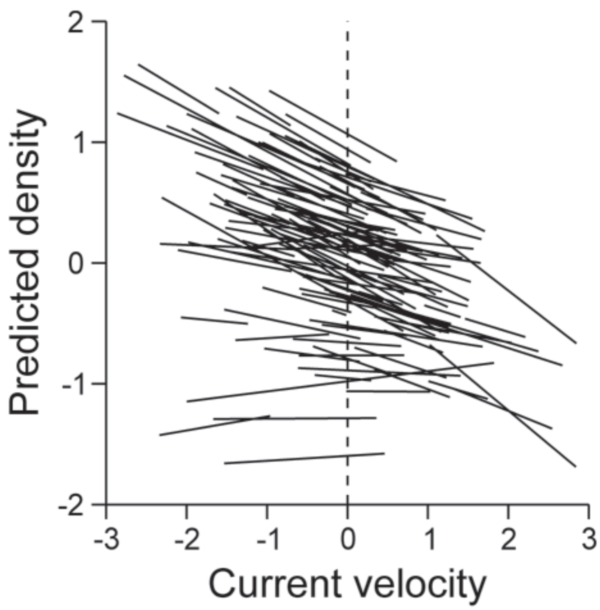
Table 3. Coefficient estimates, standard errors, and *p* values for the fixed and random components of the hierarchical linear model.

Model term	Estimate	SE	*p*
Predictor variable (fixed coefficient)			
Intercept (β_0)	0.018	0.063	
Current velocity (β_1)	–0.221	0.044	<0.001
Large woody debris (β_2)	0.16	0.034	<0.001
Cover index (β_3)	0.103	0.042	<0.001
Subbasin area (β_4)	–0.164	0.069	0.008
Height increment at flood (β_5)	–0.226	0.07	<0.001
Valley width (β_6)	–0.129	0.068	0.003
Current velocity × subbasin area (β_7)	–0.093	0.043	0.032
Random components			
σ_{ε}^2	0.325	0.046	
$\sigma_{u_0}^2$	0.36	0.066	<0.001
$\sigma_{u_1}^2$	0.054	0.026	0.034
$\sigma_{u_{01}}$	–0.05	0.028	0.034
Decay coefficient for spatial autocorrelation			
α	2.378[a]	0.521	0.075

Note: The coefficients for the intercept and current velocity have a fixed and a random part, i.e., $\beta_{0j} = \beta_0 + u_{0j}$, $\beta_{1j} = \beta_1 + u_{1j}$, with $u_{0j} \sim N(0,\sigma_{u_0}^2)$ and $u_{1j} \sim N(0,\sigma_{u_1}^2)$. The covariance between u_{0j} and u_{1j} is $\sigma_{u_{01}}$. The autocorrelation decay coefficient is α. SE, standard error.

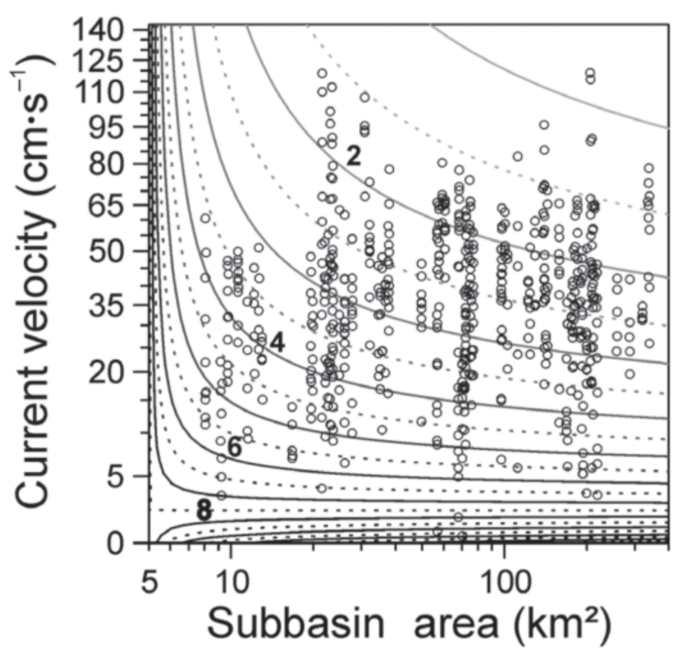
[a]Implies a spatial correlation of 0.186 between adjacent sections.

Fig. 4. Plot of predicted densities of brook trout (*Salvelinus fontinalis*) vs. current velocity at each of the 120 reaches. Densities and current velocity are standardized to zero mean and unit variance. Predicted values are from the model including both fixed and random effects for the intercept and current velocity.



spatial scales (Milner et al. 1995; Watson and Hillman 1997), only a few of these studies have specifically quantified variation in fish abundance at each scale (e.g., Dunham and Vinyard 1997). Yet, the decomposition of variation in fish abundance can identify those scales at which populations vary most and can therefore guide the choice of environmental features and measurement grain needed in an

Fig. 5. Contour plot illustrating the effect of the cross-level interaction between current velocity, a section-level predictor, and subbasin area, a reach-level predictor, on density of brook trout (*Salvelinus fontinalis*). Contour lines represent density of brook trout (numbers·100 m^{-2}) as predicted by the fixed-effects part of the hierarchical linear model. The circles represent observed combinations of current velocity (cm·s^{-1}) and subbasin area (km^2) at individual sections; the dispersion of the circles reflects the joint variability in these two variables.



analysis. In the present study, the results from the decomposition of variation motivated the use of a simplified hierarchical model focused on variation only at the section and reach scales.

The relationship between brook trout density and current velocity varied across reaches as a function of subbasin area. Brook trout density was weakly related to current velocity in reaches within smaller subbasins but declined markedly with current velocity in reaches within larger subbasins. This contextual effect may be linked to stream size, because subbasin area was positively related to stream width (Spearman rank correlation, $r_s = 0.85$) and stream order ($r_s = 0.63$), two measures of stream size. Velocity refugia are used by stream salmonids to maximise energy intake and minimise swimming costs (Grant and Noakes 1987; Fausch 1993; McLaughlin and Noakes 1998). Instream structures that create velocity refugia, such as boulders, provide energetically suitable locations for salmonids, resulting in greater population density (Fausch and Northcote 1992; McLaughlin and Noakes 1998). Structures such as boulders and woody debris tend to be less abundant in larger streams (Benke and Wallace 1990; Jowett et al. 1998; Wing and Skaugset 2002). Because of their greater depth, larger streams also have lower relative roughness, and thus smoother flow near the streambed, than smaller streams (Leopold et al. 1964). Water velocity may therefore have had greater influence on brook trout density in larger streams as a result of the lower availability of velocity refugia in those streams.

Within reaches, brook trout density was greater in sections with more woody debris and cover. Large woody debris and cover are thought to enhance the habitat suitability of streams for salmonids by providing low-velocity refugia during floods, profitable feeding positions of low velocity next to high-velocity patches, and visual isolation that reduces interference competition and risk of predation (McMahon and Hartman 1989; Fausch 1993; Inoue et al. 1997). Woody debris acts as additional substratum for macroinvertebrates, usually resulting in higher food abundance for fish (Dolloff 1986; Harmon et al. 1986). Large woody debris is also associated with the development of pools (Andrus et al. 1988; Carlson et al. 1990), a preferred habitat for brook trout (Gibson et al. 1993; Rodríguez 1995; Bélanger and Rodríguez 2002).

Brook trout density was negatively related to height increment at flood and valley width. Negative effects of high flows on stream fish abundance are well documented (Freeman et al. 2001; Roghair et al. 2002; Lobón-Cerviá and Rincón 2004). High flows may increase egg and yearling mortality or displace juvenile and older fish (Erman et al. 1988; McMahon and Hartman 1989; Carline and McCullough 2003). Brook trout displaced experimentally in a natural stream tended to settle in preferred habitats away from their home site (Bélanger and Rodríguez 2001); in the absence of effective homing, population density may remain low for extended periods in stream reaches where brook trout are displaced by high flow events. The negative relation between brook trout density and valley width may be mediated by geomorphic processes related to longitudinal variation. Valley width was related negatively to entrenchment ($r_s = -0.57$) and stream gradient ($r_s = -0.38$). Other studies have found greater fish density (Rabeni and Sowa 1996) or better spawning substratum (Coulombe-Pontbriand and Lapointe 2004) in narrower, more entrenched, upstream segments than in wider downstream segments, which have shallower slopes, a greater proportion of gravel and sand, and a smaller proportion of cobbles and boulder in the streambed (Rabeni and Sowa 1996; Isaak and Hubert 2000). This result suggests that large-scale fluvial dynamics contributed to determining brook trout density at the reach scale.

Hierarchical models account for the intragroup correlation inherent to nested sampling designs and can therefore properly assess the statistical significance of potential predictors, hence improving the reliability of these models relative to conventional approaches such as multiple regression based on ordinary least squares. In many studies, the problem of intragroup correlation has been dealt with by aggregating observations at the higher levels and working with group means, examining small-scale (lower-level) patterns separately for each higher-level group, or a combination of both (e.g., Inoue et al. 1997; Watson and Hillman 1997; Angermeier and Winston 1999). However, these approaches usually leave among-group differences in small-scale patterns unexamined and can also lead to loss of information and statistical power (Hox 2002; Goldstein 2003).

Although hierarchical models are often used in aquatic ecology to account for spatial or temporal correlation between sampling units, their potential to enhance our understanding of patterns of species distribution at multiple spatial scales still remains largely untapped. The relationships between brook trout density and individual environmental features in this study are broadly in agreement with findings from previous studies; however, the hierarchical modelling approach additionally allowed for detection and proper statistical treatment of the effect of reach-level variables and the contextual effect of section-level variables on brook trout density. By accounting for the nested sampling design and simultaneously using the information available at all spatial scales, the hierarchical model allowed us to detect a cross-level interaction between environmental predictors at the section and reach levels that by definition would not have been detectable had we aggregated the data by averaging observations from individual sections. The presence of a cross-level interaction illustrates that patterns uncovered at smaller scales cannot always be extrapolated to larger scales and supports the notion that there is no single "best scale" at which to examine the relationships between fish distribution or abundance and environmental features (Schneider 2001).

Acknowledgements

We thank V. Bérard, K. Brassard, C. Cossette, M.-J. Gagnon, E. Racicot, and C. Sauvé for expert field assistance, M.-A. Bernard, M. Gauthier, and la Société de la faune et des parcs du Québec for logistic support, and M. Lapointe for advice on site selection. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, le Fonds Québécois de la recherche sur la nature et les technologies, la Société Cascapédia, le Centre interuniversitaire de recherche sur le saumon atlantique (CIRSA), and le Syndicat des professeurs et professeures de l'UQTR. This paper is a contribution to the CIRSA program.

References

Andrus, C.W., Long, B.A., and Froehlich, H.A. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Can. J. Fish. Aquat. Sci. **45**: 2080–2086.

Angermeier, P.L., and Winston, M.R. 1999. Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. Ecol. Appl. **9**: 335–349.

Bélanger, G., and Rodríguez, M.A. 2001. Homing behaviour of stream-dwelling brook charr following experimental displacement. J. Fish Biol. **59**: 987–1001.

Bélanger, G., and Rodríguez, M.A. 2002. Local movement as a measure of habitat quality in stream salmonids. Environ. Biol. Fishes, **64**: 155–164.

Benke, A.C., and Wallace, J.B. 1990. Wood dynamics in coastal plain streams. Can. J. Fish. Aquat. Sci. **47**: 42–49.

Carline, R.E., and McCullough, B.J. 2003. Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. Trans. Am. Fish. Soc. **132**: 1014–1020.

Carlson, J.Y., Andrus, C.W., and Froehlich, H.A. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, U.S.A. Can. J. Fish. Aquat. Sci. **47**: 1103–1111.

Cohen, P., Andriamahefa, H., and Wasson, J.-G. 1998. Towards a regionalization of aquatic habitat: distribution of mesohabitat at the scale of a large basin. Regul. Rivers Res. Manag. **14**: 391–404.

Coulombe-Pontbriand, M., and Lapointe, M. 2004. Geomorphic controls, riffle substrate quality, and spawning site selection in two semi-alluvial salmon rivers in the Gaspé Peninsula, Canada. Rivers Res. Appl. **20**: 577–590.

Crozier, W.W., and Kennedy, G.J.A. 1994. Application of semi-quantitative electrofishing to juvenile salmonid stock surveys. J. Fish Biol. **45**: 159–164.

Dolloff, C.A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southwest Alaska. Trans. Am. Fish. Soc. **115**: 743–755.

Dunham, J.B., and Vinyard, G.L. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. Trans. Am. Fish. Soc. **126**: 323–329.

Erman, D.C., Andrews, E.D., and Yoder-Williams, M. 1988. Effects of winter floods on fishes in the Sierra Nevada. Can. J. Fish. Aquat. Sci. **45**: 2195–2200.

Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. Can. J. Fish. Aquat. Sci. **50**: 1198–1207.

Fausch, K.D., and Northcote, T.G. 1992. Large wood debris and salmonid habitat in a small coastal British Columbia stream. Can. J. Fish. Aquat. Sci. **49**: 682–693.

Folt, C.L., Nislow, K.H., and Power, M.E. 1998. Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research. Can. J. Fish. Aquat. Sci. **55**: 9–21.

Freeman, M.C., Bowen, Z.H., Bovee, K.D., and Irwin, E.R. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecol. Appl. **11**: 179–190.

Gibson, R.J., Stansbury, D.E., Whalen, R.R., and Hillier, K.G. 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 53–69.

Goldstein, H. 2003. Multilevel statistical models. Oxford University Press, New York.

Grant, J.W., and Noakes, D.L.G. 1987. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. J. Anim. Ecol. **56**: 1001–1013.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302.

Hox, J.J. 2002. Multilevel analysis: techniques and applications. Lawrence Erlbaum Associates, Inc., Mahwah, New Jersey.

Inoue, M., Nakano, S., and Nakamura, F. 1997. Juvenile masu salmon (*Oncorhynchus masou*) abundance and stream habitat relationships in northern Japan. Can. J. Fish. Aquat. Sci. **54**: 1331–1341.

Isaak, D.J., and Hubert, W.A. 2000. Are trout populations affected by reach-scale stream slope? Can. J. Fish. Aquat. Sci. **57**: 468–477.

Jones, M.L., and Stockwell, J.D. 1995. A rapid procedure for the enumeration of salmonine populations in streams. N. Am. J. Fish. Manag. **15**: 551–562.

Jowett, I.G., Hayes, J.W., Deans, N., and Eldon, G.A. 1998. Comparison of fish communities and abundance in unmodified streams of Kahurangi National Park with other areas of New Zealand. N.Z. J. Mar. Freshw. Res. **32**: 307–322.

Leopold, L.B., Wolman, M.G., and Miller, J.P. 1964. Fluvial processes in geomorphology. Dover, New York.

Lobón-Cerviá, J., and Rincón, P.A. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout, *Salmo trutta*. Oikos, **105**: 641–646.

Lobón-Cerviá, J., and Utrilla, C.G. 1993. A simple model to determine stream trout (*Salmo trutta* L.) densities based on one removal with electrofishing. Fish. Res. **15**: 369–378.

McLaughlin, R.L., and Noakes, D.L.G. 1998. Going against the flow: an examination of the propulsive movements made by young brook trout in streams. Can. J. Fish. Aquat. Sci. **55**: 853–860.

McMahon, T.E., and Hartman, G.F. 1989. Influence of cover and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **46**: 1551–1557.

Milner, N.J., Wyatt, R.J., Barnard, S., and Scott, M.D. 1995. Variance structuring in stream salmonid populations, effects of geographical scale and implications for habitat models. Bull. Fr. Pêche Piscic. **339**: 387–398.

Poizat, G., and Pont, D. 1996. Multi-scale approach to species–habitat relationships: juvenile fish in a large river section. Freshw. Biol. **36**: 611–622.

Rabeni, C.F., and Sowa, S.P. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. Can. J. Fish. Aquat. Sci. **53**: 252–259.

Rasbash, J., Steele, F., Browne, W., and Prosser, B. 2004. A user's guide to MLwiN. Version 2.0. Institute of Education, London, UK.

Rodríguez, M.A. 1995. Habitat specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. Evol. Ecol. **9**: 169–184.

Roghair, C.N., Dolloff, C.A., and Underwood, M.K. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Trans. Am. Fish. Soc. **131**: 718–730.

Schneider, D.C. 2001. The rise of the concept of scale in ecology. Bioscience, **51**: 545–553.

Snijders, T.A.B., and Bosker, R.J. 1999. Multilevel analysis: an introduction to basic and advanced multilevel modeling. SAGE Publications Inc., Thousand Oaks, California.

Watson, G., and Hillman, T.W. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. N. Am. J. Fish. Manag. **17**: 237–252.

Wing, M.G., and Skaugset, A. 2002. Relationships of channel characteristics, land ownership, and land use patterns to large woody debris in western Oregon streams. Can. J. Fish. Aquat. Sci. **59**: 796–807.

Yang, M., Rasbash, J., Goldstein, H., and Barbosa, M. 2001. MLwiN macros for advanced multilevel modelling. Institute of Education, London, UK.