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Catchment topography and wetland geomorphology drive macroinvertebrate community structure and juvenile salmonid distributions in south-central Alaska headwater streams

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Abstract. Conservation and management of headwater streams amid rapid global change require an understanding of the spatial and environmental factors that drive species distributions and associated ecosystem processes. We used a hierarchical analytical framework to model effects of catchment-scale topography and wetland geomorphic classes on stream physical habitat, chemistry, and macroinvertebrate and fish communities in 30 headwater streams across the Kenai Lowlands, southcentral Alaska, USA. We identified 135 macroinvertebrate taxa, 122 of which were aquatic insects, of which 79 were dipterans. We collected only 6 species of fish, but juvenile coho salmon and Dolly Varden were collected in 17 and 25 of the 30 streams and reached densities >500 and 1300/km, respectively. Flow-weighted slope, an indicator of water residence time and gradient, was the best catchment-scale correlate of macroinvertebrate and fish community structure, and its effect was mediated by wetland geomorphic classes and numerous water chemistry, substrate composition, and channel geomorphology variables measured at the reach scale. Many macroinvertebrate taxa showed high fidelity to different levels of the topographic gradient, resulting in high β diversity but relatively similar levels of α diversity across the gradient. Juvenile salmonids were segregated among streams by both species and age classes. Coho salmon fry and parr (<10 cm total length [TL]) had significant unimodal distributions that peaked in streams with intermediate slopes and gravel substrate, whereas presmolts ($\geq$10 cm) were found only in lowest-sloping streams with mostly peat substrate and deep, slow channels. Large Dolly Varden ($\geq$8 cm) were found across the entire gradient but were most abundant in high-sloping catchments, whereas small Dolly Varden (<8 cm) followed a similar distribution but were absent from the lowest-gradient sites with low flow velocity, dissolved O_2, and gravel substrate. Predictive modeling indicated that all of the 547 km of headwater streams in the study area might serve as potential habitat for $\geq$1 species and age class of salmonids. Our study should assist in development of catchment management tools for identifying and prioritizing conservation efforts in the region and may serve as a framework for other studies concerning biodiversity and focal species conservation in headwater streams.

Key words: Salmonidae, topographic wetness, peatlands, land cover, wetland classification, landscape indicators.

Headwater streams contribute substantially to local and regional biodiversity (Meyer et al. 2007, Clarke et al. 2008), organic matter processing and nutrient cycling (Wallace and Webster 1996, Gomi et al. 2002), storage of surface water and sediment (Newson and Newson 2000), export of resources to adjacent terrestrial and downstream aquatic ecosystems (Nakano and Murakami 2001, Wipfli and Baxter 2010), and recreational and commercial fisheries (Naiman and Latterell 2005, Wigington et al. 2006). Despite this lengthy list of ecosystem services, many headwater streams have been and continue to be degraded or destroyed by anthropogenic activities, including

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various types of land use (Allan 2004), diversions, blockages, and impoundments (Freeman et al. 2007); burial under urban development; and mountaintop mining waste (Elmore and Kaushal 2008, Palmer et al. 2010); and climate change (Brooks 2009, Heino et al. 2009). Recent legislative decisions have rendered headwater streams even more vulnerable to degradation (Doyle and Bernhardt 2011), leading to a surge of regional studies geared toward understanding the significance of headwater stream ecosystems within the broader context of river networks (Alexander et al. 2007, Clarke et al. 2010).

Conservation and management of headwater streams amid rapid global change requires an understanding of the spatial and environmental factors that drive species distributions and associated ecosystem processes (Schlosser 1995, Sowa et al. 2007). However, cost and logistics limit stream surveys required for conservation prioritization and ecosystem management to a small number of local reaches that may represent only a tiny fraction of headwater stream habitat in a region. One strategy to alleviate this problem has been the use of landscape data derived from satellite imagery to develop models relating physical properties of catchments to stream habitat and species distributions (O'Neill et al. 1997). This approach is now used routinely to inform management and conservation efforts where exhaustive sampling is impractical. However, use of catchment-scale variables as indicators of reach-scale conditions has proven challenging in some instances (Heino et al. 2003, Heino 2005). Thus, landscape data may be of limited value in the absence of strong anthropogenic influences (Heino et al. 2008). Others have found relatively strong relationships between headwater community structure and environmental factors summarized at a variety of spatial scales. These results suggest that the strength of catchment-scale linkages to headwaters is regionally dependent (LeCraw and Mackereth 2010).

The Kenai Lowlands are an ecologically and economically significant subregion of the southern Kenai Peninsula in southcentral Alaska. Rivers in this region support several species of salmon, are used heavily for recreational and subsistence fishing, and support commercial harvests in marine waters. As in much of the world, the region is experiencing human population growth and increased development of natural land. Eighty-nine percent of the streams are on private lands with minimal regulation of development. Moreover, nearly ½ of the land cover in the region consists of a diverse array of wetland classes (Gracz et al. 2008), each with potentially important connections to headwater stream ecosystems. Furthermore, very few 1st-order streams in the region are recognized as directly supporting anadromous fishes, and thus, streams in the region do not receive the same level of protection as streams listed in the state Anadromous Waters Catalog (ADFG 2011). Neither systematic biological surveys nor empirical studies of macroinvertebrate or fish distributions have been conducted in the region. Such studies are fundamental for evaluating landscape linkages to headwater streams and assessing their value for sustaining populations and processes at whole-river network scales.

The objective of our study was to identify catchment-scale linkages to physical, chemical, and biological conditions of headwater streams in support of catchment, wetland, and fisheries management in the Kenai Lowlands. We collected physical, chemical, and biological data from 30 headwater streams across 4 major river basins in this region (Anchor River, Stariski Creek, Deep Creek, and Ninilchik River). We used digital elevation, wetland, and stream data sets to relate catchment physiographic conditions to stream physical habitat, chemistry, macroinvertebrate communities, and the distributions of individual fish species. Previously, we found that topographic metrics related to water residence time and gradient were strongly related to wetland and, ultimately, stream chemistry (Walker et al. 2012). We used this previous work to evaluate whether the relatively strong linkages among catchment topography, wetland cover, and in-stream chemistry could be expanded to include physical habitat and macroinvertebrate and fish community structure, and if so, to identify the strongest abiotic pathways between catchment-scale topography and biological communities.

Our goals were to: 1) describe patterns of macroinvertebrate and fish biodiversity, 2) further our ecological understanding of catchment- and reach-scale controls on headwater stream ecosystems, 3) identify ≥ 1 catchment-scale indicators for classifying streams likely to support salmonids, 4) use catchment-scale indicators to predict potential habitat for age classes of salmonids across the Kenai Lowlands, and 5) provide regional managers with empirical evidence of juvenile salmonid use of headwater streams.

Methods

Study area

The Kenai Lowlands cover ~ 9400 km^2 on the eastern side of Cook Inlet in southcentral Alaska (Fig. 1). This area occupies a low-lying physiographic province between Cook Inlet to the west and the

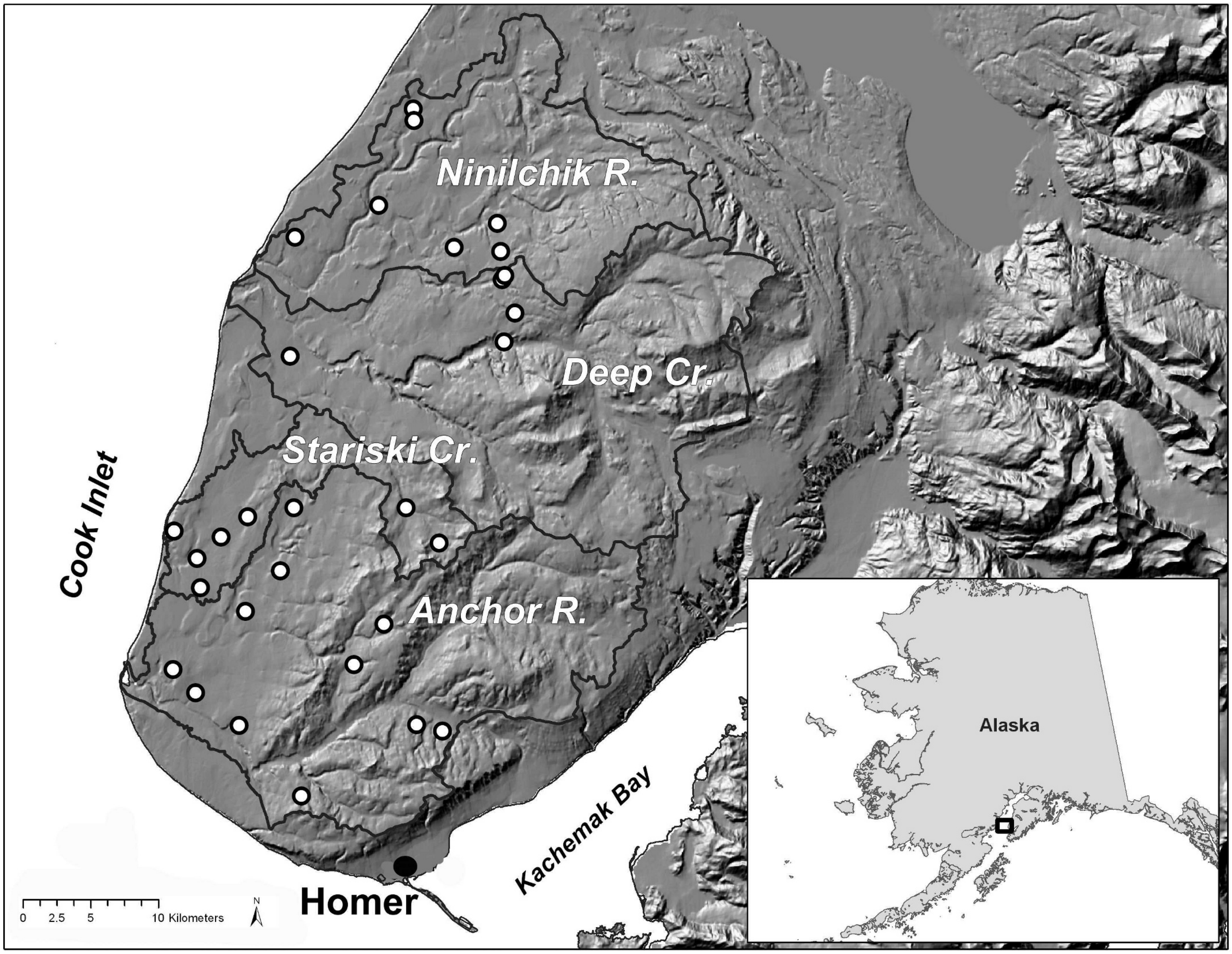

FIG. 1. Location and topography of the lower Kenai Peninsula, Alaska. Boundaries of the 4 major basins are outlined in black. Outlets of the 30 headwater-stream catchments are marked by white points. R = river, Cr = creek.

Kenai Mountains to the southeast. The area is underlain by glacial drift above tertiary sediments. Wetlands occupy 43% of the landscape and are associated with complex geomorphology resulting from the glacial history of the area. These wetlands have been mapped and classified into several major geomorphic settings (Gracz et al. 2008).

Climate in the study area is transitional between maritime and continental. Homer, at the southern end of the Peninsula, has a mean winter (January) temperature of −5.2°C and a mean summer (July) temperature of 11.9°C. The mean annual precipitation in Homer is 61.7 cm, and most precipitation occurs in autumn (September–November). Snowmelt and ice breakup contribute to high stream flows in spring (April–May). Rivers in our study area support populations of several species of anadromous salmonids, primarily Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), steelhead trout (*Oncorhynchus mykiss*), and Dolly Varden char (*Salvelinus malma*) (KBRR and NOAA/CSC 2001).

Study design

We used a stratified probabilistic sampling design to select 1st-order streams following methods published by Lazorchak et al. (1998) and described in detail in Walker et al. (2012). Briefly, we partitioned all 1st-order stream lines resolved from 1:63,360 US Geological Survey (USGS) Digital Line Graphs into 250-m segments. We delineated catchment boundaries with a 60-m digital elevation model (DEM), the finest resolution available at the time. We modified the DEM by decreasing the elevation values of mapped stream channels by normalized excavation (Baker et al. 2006) to ensure flow-lines matched existing stream maps and to improve automated catchment delineation. We assessed each catchment visually for accuracy by overlaying boundaries on digital topographic maps (USGS Digital Raster Graphics) to ensure that stream corridors were completely enclosed within digitized catchments.

We randomly selected 10 stream reaches from 4 strata defined by the amount and type of wetland cover in the catchment with the goal of sampling ≥30 streams from the 40 selected (Walker et al. 2012). We used the strata only to ensure that we selected a representative range of topographic and wetland conditions in the region. We selected more sites than our target of 30 because we anticipated difficulty in accessing some sites, but this difficulty would be unknown until a site visit was attempted. We limited sampling to a target of 30 streams primarily because of temporal and logistical constraints. This number was deemed sufficient to model strong patterns in species distributions if they existed.

Sampling and sample processing

We began field sampling at the end of snowmelt runoff in mid-May and ended in mid-July. We used sampling methods published by Lazorchak et al. (1998) with few modifications. We navigated to the catchment outlet point on the stream map using a global positioning system (GPS). We delineated stream reaches as 250-m-long segments starting from the outlet point and terminating 250 m upstream. We marked reaches with 11 equidistant cross-sections (transects perpendicular to the stream channel) spaced 25 m apart. These transects served as the sampling framework for all physical, chemical, and biological measurements. We sampled sites in random order, starting on 23 May 2006, until we attained our target of 30 streams on 18 July 2006.

We measured specific conductance, dissolved O_2 (DO), temperature, and pH in situ with a YSI 556 multiprobe or YSI 660 Sonde (Yellow Springs Instruments, Yellow Springs, Ohio). We collected water-chemistry samples at the upstream end of the stream reach (250-m marker) and analyzed total and orthophosphate-P, total N, NH_4-N, NO_3-N, and dissolved organic C with methods described in Walker et al. (2012). After collecting the chemistry samples, we estimated stream discharge at that location with a Marsh–McBirney electromagnetic flow meter (Marsh–McBirney, Frederick, Maryland).

We measured stream channel morphology, substrate composition, and other physical habitat metrics at each of the 11 transects. These measurements were either averaged (e.g., mean velocity) or computed as a percentage (e.g., % cobble substrate) to achieve a value for each variable representative of the entire 250-m reach (Appendix 1).

We used the multihabitat composite method described in Lazorchak et al. (1998) with minor modifications to sample macroinvertebrates. We collected macroinvertebrates in 2 subreaches within each reach: 50–100 and 150–200 m. We did not electrofish in these subreaches to avoid disruption of macroinvertebrate habitat, and we did not conduct macroinvertebrate sampling in the areas of the reach allocated for electrofishing. At each of the 6 transects within these subreaches (50, 75, 100, 150, 175, and 200 m), we collected 2 samples from each of the 2 predominant habitats at that location (gravel/cobble riffle, undercut bank, rootwad, leafpack, woody debris, and sand/silt). We used a 350-μm D-frame net to collect organisms dislodged during vigorous disruption of a 0.1-m^2 area of each respective habitat for 30 s. We sampled a total of 24 habitat patches and composited the organisms into a single 2.4-m^2 reach-scale sample of the macroinvertebrate community. We processed samples with a 2-phase subsampling procedure that involved complete removal of organisms retained in a 2-mm sieve and a 300-count subsample of individuals from the remaining fraction (King and Richardson 2002). We identified taxa to the lowest practical taxonomic unit, usually genus but sometimes to species (Appendix 2). Nonchironomid taxa were identified by personnel at the BugLab (Utah State University; http://www.usu.edu/buglab/), whereas chironomids were identified by RSK using keys published by Wiederholm (1983). We standardized taxon abundances to densities (no./m^2) based on enumerations in each separate fraction and the total area represented by that fraction (King and Richardson 2002).

We collected fish for estimating juvenile fish species composition and density with a DC-pulsed backpack electrofishing unit (Smith–Root, Inc., Vancouver, Washington). Lazorchak et al. (1998) recommended using a minimum reach length of 150 m, or 40× mean stream width for larger streams, when characterizing stream fish communities. All of the study streams averaged <4 m in width, so we sampled 150 m of the 250-m stream reach by 2-pass electrofishing three 50-m subreaches. Subreaches corresponded to transect markers 0–50, 100–150, and 200–250 m. We blocked upstream and downstream ends of subreaches with a 5-mm-mesh nylon net to retain stunned fish that were incidentally missed during netting and to prevent movement of fish that had already been counted in a different section of the reach. We checked block nets for trapped fish at the end of each of the 2 passes. We measured (total length [TL], mm), weighed, identified to species, and released all fish.

We expressed fish-count data as uncorrected observed densities. We did not use depletion models to extrapolate observed counts to total fish abundance because these models can be biased and unreliable (Rosenberger and Dunham 2005). We contend that our estimates of abundance were defensible for comparing relative abundance among streams, but we do not recommend their use for comparing population sizes among study areas because a mark–recapture validation study would be required (Rosenberger and Dunham 2005).

Catchment topography, wetland cover, and stream-network variables

We computed several metrics of catchment topography because we expected topographic setting and gradient to be important factors controlling the distribution and type of wetlands, and that % wetland cover would affect stream physical, chemical, and biological condition (Walker et al. 2012). Wetland cover was not limited to flat areas. Thus, wetland parcels of the same class but different slopes would differ in surface-water residence time and potential for biogeochemical interactions between surface water and wetlands. Moreover, wetland classes nominally distinguish land cover as either wetland or upland, whereas slope weights the effective wetness of land cover continuously.

We considered 3 different metrics of catchment gradient because each was identified as a strong predictor of water chemistry in these streams (Walker et al. 2012). We estimated catchment slope (WSlope) by computing the slope of each 60-m pixel in the DEM and averaging by catchment. We computed mean topographic wetness (Wetx) using both upstream contributing area (A) and local (pixel-by-pixel) slope (β) with the equation: $\ln(A/\tan\beta)$ (Sorenson et al. 2006, Shaftel et al. 2012). We computed a similar metric, flow-weighted slope (FWSlope), as the sum of the product of the slope and flow accumulation value for each pixel in the catchment divided by the sum of the flow accumulation of all pixels in the catchment. FWSlope was similar to Wetx in that it incorporated measures of both upstream contributing area and slope. These metrics should be comparable predictors, but FWSlope is easier to interpret because it is scaled in standard units of slope (%). Moreover, Wetx is dependent upon catchment size, whereas FWSlope is not. Last, FWSlope was deemed the best overall predictor of water chemistry in these streams (Walker et al. 2012).

We estimated cover of each of the 5 dominant wetland geomorphic classes (cover >1%) as percentage of total catchment area in each class: discharge slope (DS), relict glacial drainageway (DW), kettle (KT), relict glacial lakebed (LB), and riparian (RP). Total wetland cover was computed as the sum of % cover values of all wetland classes. Many of the 30 catchments contained multiple wetland classes and certain classes tended to covary, so we ordinated catchments by wetland cover classes to identify a gradient in composition among catchments for use as a correlate in community analyses. We used nonmetric multidimensional scaling (NMDS) to ordinate catchments based on 5 cover types as variables with Bray–Curtis dissimilarity (%) as a distance metric (McCune and Grace 2002). We rotated the solution so that axis 1 explained the maximum variance in the distance matrix (67%). After rotation, axis 1 represented a gradient of catchments with greater proportions of LB, KT, and DW class to catchments with greater proportions of RP wetlands. Axis 2 did not represent an interpretable gradient in wetland composition, so we retained only NMDS 1 as the predictor (Wet.mds1).

We computed additional catchment variables as potential predictors or modulators of species–environment relationships: elevation (Elev), catchment area (Area), downstream link (D-link; Osborne and Wiley 1992), flow-length distance to salt water (Salt.m), and flow-length distance to mainstem river channel (Main.m). We computed Area because of its influence on topographic and land-cover relationships to biota and because stream size controls species distributions (Allan 2004). Elev increased with increasing distance inland and was expected to be correlated with topographic and wetland variables, but the range in Elev among catchments was relatively small (Appendix 1). D-link was a metric of downstream tributary size, and we measured it because it is an important indicator of stream-network position, a factor that could influence site accessibility for both spawning adult salmon and upstream-migrating juveniles. Distance from mainstem (Main.m) and distance from Cook Inlet (Salt.m) also were potential factors limiting salmonid distributions.

Data analysis

Our analysis followed a framework described by King et al. (2005) for linking catchment characteristics to streams. First, we used NMDS to ordinate streams into a reduced-dimensional space separately for macroinvertebrate and fish abundance data (McCune and Grace 2002) to identify the primary gradients in macroinvertebrate and fish community composition. Second, we used rotational vector fitting (Faith and Norris 1989) to estimate the direction and magnitude of correlations between catchment and reach-scale variables and macroinvertebrate and fish community ordinations and to identify potential abiotic drivers of community organization. Next, we accounted for spatial autocorrelation and synthesized results among catchment topography, wetland geomorphic classes, in-stream abiotic variables, and community structure using partial Mantel tests in conjunction with path diagrams (Leduc et al. 1992). Last, we regressed individual species responses against the strongest catchment-scale correlate(s) of community structure identified by NMDS vector fitting and validated by Mantel tests.

Community-level analyses

We ran NMDS ordinations of community composition with the *metaMDS* function in the *vegan* package in R (version 2.9.2; R Core Development Team, Vienna, Austria). We analyzed abundances of macroinvertebrate and fish taxa separately. We removed macroinvertebrate or fish taxa that occurred <3 times prior to analysis because their inclusion increased NMDS stress values and degraded the ordination (McCune and Grace 2002). We further partitioned abundances of the 2 most common fish species, coho salmon and Dolly Varden, into size classes based on size-frequency distributions: coho <10 cm and ≥ 10 cm and Dolly Varden <8 cm and ≥ 8 cm. We did not determine the age of each individual fish. However, we used these size classes in the analysis because these length thresholds corresponded to gaps in the size-frequency distribution among individuals within streams and were associated with distinct changes in body shape and color that clearly distinguished coho fry and parr from smolts. Coho <10 cm probably were age 0+ (fry) or 1+ (parr), whereas coho ≥ 10 cm probably were 2+ (smolt) fish preparing to outmigrate. Larger (≥ 8 cm) parr of Dolly Varden were of unknown age but often were found in streams that were outside the range of smaller individuals and, thus, were presumed to be migrating from areas where they were reared to use different habitat. Steelhead (*Oncorhynchus mykiss*) was the only other species that occurred in ≥ 3 streams and, thus, was included in the analysis of fish community structure.

We log(x)-transformed densities of individual taxa prior to analysis to give greater weight to species with numerically small abundance values but potentially strong associations with catchment- and reach-scale gradients (McCune and Grace 2002). We used Bray–Curtis distance as the dissimilarity metric. Following inspection of stability and stress values, we deemed a 2-dimensional solution appropriate for both the macroinvertebrate and fish ordinations (stress = 0.13 and 0.11, respectively).

We related catchment and reach-scale variables to the ordinations using the *envfit* function in the *vegan* package in R 2.9.2. The *envfit* function implemented rotational vector fitting as described by Faith and Norris (1989). Vector fitting determined the direction and magnitude of the maximum correlation between predictor variables and the configuration sample units in the 2-dimensional ordination space. The probability of obtaining an equal or larger correlation from random data (p) was estimated from 1000 random permutations. We deemed correlations with $p < 0.05$ different from random.

We assessed the effect of spatial autocorrelation on apparent linkages between catchment- and reach-scale variables and community structure with the partial Mantel test, a multivariate extension of partial correlation that uses distance matrices as variables. Partial Mantel tests estimate the strength of the correlation (Mantel r) between 2 distance matrices after the effect of ≥ 1 matrices has been eliminated. Mantel r coefficients typically are much smaller than conventional correlation coefficients. Coefficients that are >0.1 are often highly significant statistically, and coefficients that are ~ 0.5 indicate a very strong relationship (Legendre and Fortin 1989). Significance of Mantel r coefficients was evaluated using random permutations of observations in the distance matrices (e.g., 1000 permutations; Manly 1997).

We extended the partial Mantel test into a path-analytical framework (e.g., Leduc et al. 1992, King et al. 2004) to relate catchment-scale topography and wetland cover to stream biota via abiotic pathways. We arranged catchment- and reach-scale abiotic variables in a hierarchical manner so that variation explained by confounding variables was factored out and the remaining variation in the response variable could be evaluated using the predictor variable of interest. For this analysis, we selected variables that were most strongly correlated with macroinvertebrate and fish community composition (NMDS) and organized these variables into 5 sets of matrices: catchment topography (FWSlope, Wetx, WSlope, Elev), wetland geomorphic classes (DS, DW, LB, KT, RP), water chemistry (pH, DO.mgl, Temp, DOC, DIN), substrate composition (Peat, Fines, Sand, Grav.sm, Grav.lg, Cobble, LWD.ct), and channel morphology and gradient (Thalweg, Depth.xs, Bk.ht, BA, Ucut, Canopy%, Velocity, RSlope) (see Appendix 1 for an explanation of variable codes). We converted these groups of variables into distance matrices based on Euclidean distance. Individual variables in multivariable distance matrices were first standardized to *z*-scores (Legendre and Legendre 1998) so that each variable was weighted equally in the matrix.

We arranged distance matrices based on our interpretation of their hierarchical structure and causal order. This procedure resulted in 4 levels of organization: catchment topography, wetland geomorphic classes (dependent upon topography), 3 reach-scale abiotic matrices (each directly dependent upon topography and wetlands via indirect effect of topography), and macroinvertebrate and fish community matrices (directly dependent upon abiotic matrices and indirectly dependent upon topography and wetland matrices). We used this framework to specify appropriate covariates for each partial Mantel test. For all tests, we removed the variance explained by separation distances among sites to account for broad-scale spatial autocorrelation. Furthermore, we accounted for variation explained by other matrices in the same level of the hierarchy and examined the residual effect of each individual matrix on each matrix in the level immediately below it. These pathways represented pure-partial direct effects. However, we also tested for residual effects between indirect predictors and community composition by factoring out variation explained by matrices on the same level and all levels below them (e.g., a significant effect of wetland geomorphic classes on macroinvertebrate community structure after accounting for abiotic intermediaries). Mantel tests were done with the *mantel* function in the *ecodist* library in R 2.9.2.

Individual species responses

We regressed weighted averages and abundance maxima of each of the macroinvertebrate and fish taxa used in the NMDS analysis on FWSlope (Birks et al. 1990). We deemed FWSlope to be the strongest correlate of both macroinvertebrate and fish community structure (see Results). Abundance maxima were the values of FWSlope that corresponded to the largest density of each species. These values also were bootstrapped to determine the range of FWSlope that was most likely to correspond to the optimal zone for each taxon (Bressler et al. 2006). We used abundance maxima in addition to weighted averages because they are not biased toward the middle of the gradient and they provide a complementary measure of environmental niche breadth (Yuan 2005). Bootstrapped weighted averages and abundance maxima were computed with the custom functions *wa.boot* and *sppmax.boot* (written by RSK) in R 2.9.2.

We used generalized additive modeling (GAM) to characterize further the response curves of coho salmon and Dolly Varden densities by size class to FWSlope and to fit models to make predictions of fish distributions across the study area. We avoided fitting species responses to different single- or multiple-predictor models and comparing them with model-selection approaches (e.g., Akaike Information Criterion; Anderson et al. 2000) because the data set was small. Our use of FWSlope was not causal but, rather, an indicator of similar responses to many other catchment- and reach-scale variables that strongly covaried with this predictor.

We fit GAMs with the *mgcv* library in R 2.9.2 (Wood 2008). We specified a negative binomial family and used untransformed abundances of each species size class as response variables because the data were counts and their distribution was approximately negative binomial (O'Hara and Kotze 2010). A negative binomial model is based on the assumption that data are counts, so we compared raw counts (no./150 m of reach sampled) and extrapolated densities (no./km) to determine whether standardizing abundances to km influenced results. The results were virtually identical for each response, so we used density as the response variable because it was more easily compared to density units reported in other studies.

We used significant GAMs to map the predicted mean densities of each juvenile salmonid size class for all 1st-order streams in the study area using FWSlope values extracted from 9119 60-m stream segments totaling 547 km. FWSlope values were supplied to each fitted model in R 2.9.2 to obtain the predicted mean value for each segment. Predictions were exported to ArcGIS (version 9.3; Environmental Systems Research Institute, Redlands, California), linked to segments, and mapped to provide an estimate of relative differences in the spatial distribution of potentially suitable habitat for species by size class across the study area.

Results

We identified 135 macroinvertebrate taxa from the 30 headwater streams (Appendix 2). Density ranged from 870 to 26,297 individuals (ind.)/m^2. Mean and median densities among streams were 10,229 and

TABLE 1. Frequency of occurrence and mean densities of fish species identified from the 30 headwater streams in the Kenai Lowlands, Alaska (USA).

		Density (no./km)		
Species	Freq	Median	Mean	Maximum
Coho salmon (*Oncorhynchus kisutch*)	17	13	86	576
<10 cm	12	0	80	576
≥10 cm	11	0	6	40
Dolly Varden (*Salvelinus malma*)	25	143	258	1313
<8 cm	17	30	90	679
≥8 cm	23	14	169	967
Rainbow/steelhead trout (*Oncorhynchus mykiss*)	4	0	38	1093
Chinook salmon (*Oncorhynchus tshawytscha*)	1	0	1	27
Nine-spine stickleback (*Pungitius pungitius*)	1	0	1	20
Three-spine stickleback (*Gasterosteus aculeatus*)	2	0	38	640

9224 ind./m^2, respectively. Taxon richness ranged from 21 to 45, and mean and median richness were 33.6 and 34, respectively. Richness was dominated by aquatic insects (122) but included a few representatives from several noninsect groups (oligochaetes, hirudineans, gastropods, bivalves, crustaceans, hydracarinans). Diptera was the richest insect order with 79 taxa. Most of the dipterans belonged to the family Chironomidae (50), followed by Tipulidae (8), Simuliidae (5), Empididae (4), and few other families. Diversity among the remaining insect orders was led by Trichoptera (13) and followed by Ephemeroptera (9), Plecoptera (8), Coleoptera (8), Heteroptera (3), and Odonata (1).

Juvenile coho salmon and Dolly Varden were the most abundant fish species (Table 1). These 2 species were collected at >50% and >80% of the sites and reached maximum densities >500 and 1300 ind./km, respectively. Juvenile Chinook salmon and steelhead were collected in only a few locations. Two species of stickleback were the only other fish species collected. Coho salmon, Dolly Varden, and steelhead were the only species with >3 occurrences.

NMDS ordination revealed a single prominent gradient in both macroinvertebrate and fish community composition (Figs 2A, B, 3A, B). NMDS Axis 1 explained 71% and 62% of the variance in the macroinvertebrate and fish dissimilarity matrices, respectively. Several catchment-scale variables were significantly correlated with macroinvertebrate and fish NMDS ordinations and were clearly associated with Axis 1 (Figs 2A, 3A, Table 2). The strongest catchment correlates of both communities were topographic variables related to wetness and water residence time (FWSlope, WSlope, Wetx). FWSlope was the strongest correlate of both communities, but WSlope and Wetx were only marginally weaker. Communities situated in high-WSlope and low-Wetx catchments were clearly clustered at one end of NMDS Axis 1 whereas low-WSlope, high-Wetx sites were at the opposite end of NMDS Axis 1. Elev was a significant but weaker correlate of community structure. Higher-WSlope catchments tended to be at higher Elev, but some high-Elev catchments were relatively flat. These communities resembled those from low-WSlope, low-Elev catchments. RP was the only individual wetland geomorphic class that was correlated to either community and showed a significant but relatively weak correspondence to macroinvertebrate communities on the high-WSlope end of NMDS Axis 1. However, Wet.mds1 was significantly correlated with both macroinvertebrate and fish communities. Catchments with low Wet.mds1 scores consistently had a mixture of LB, KT, and DW wetland types and were associated with macroinvertebrate and fish communities at the low-WSlope, high-Wetx end of NMDS Axis 1. Total wetland cover (Wet) was not related to either community.

Numerous reach-scale variables were strongly related to macroinvertebrate and fish community structure (Figs 2B, 3B). Water chemistry (pH, DO.mgl, DO%, Temp, DIN, DOC), substrate composition (Fines, Peat, Grav.sm, Grav.lg, Embed, LWD.ct), and channel morphology and gradient metrics (Thalweg, Depth.xs, BA, Ucut, Canopy, Velocity, RSlope) all were significantly related to both macroinvertebrate and fish community ordinations. Higher pH, DO.mgl, and DIN were associated with communities in high-WSlope catchments, whereas warmer stream temperatures and higher DOC were associated with communities in low-WSlope, wetter catchments. High-WSlope communities also were associated with larger substrate particle sizes, more large woody debris, low

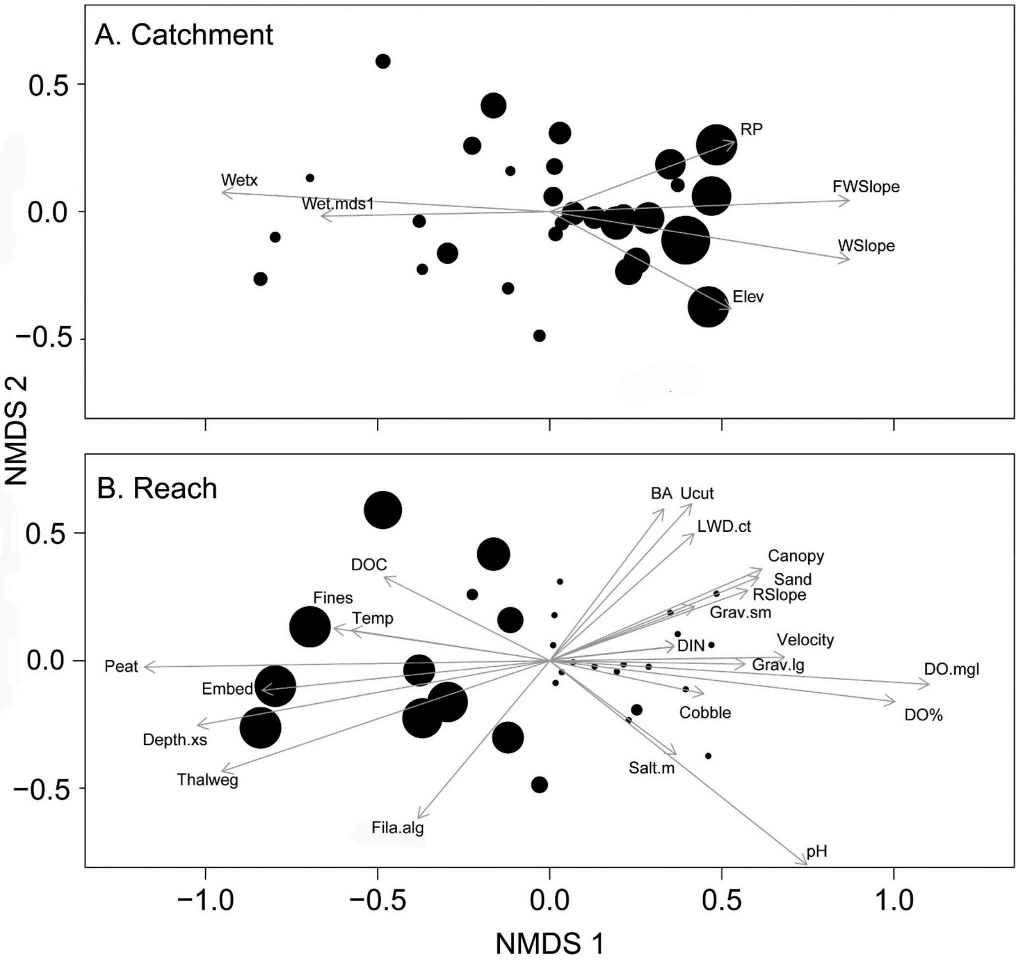

FIG. 2. Nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition from the 30 headwater streams. Arrows correspond to landscape (A) and stream-reach (B) variables significantly related to community composition (see Appendix 1 for variable codes). Arrow length is proportional to the magnitude of the correlation (*r*). Direction of greatest correlation is indicated by the location of the arrow head. Symbols are sized in proportion to FWSlope (A) and % peat substrate (B). NMDS stress = 0.13.

substrate embeddedness, absence of peat substrate, low cover of fine sediment, shallower stream channels with sharper bank angles and undercut banks, and steeper channel slopes with faster stream velocities.

Three substrate variables were correlated with macroinvertebrate communities but not fish (Fila.alg, Cobble, Sand), whereas 1 variable was associated with fish but not macroinvertebrates (Bk.ht). One additional variable, distance from saltwater (Salt.m), was related to macroinvertebrate composition but this correlation probably was an indication that higher-WSlope catchments tended to be farther inland. No stream-network variable was related to fish community structure. All significant reach-scale variables were strongly associated with the topographic and wetland gradient (NMDS Axis 1).

Partial Mantel tests supported the ordination and vector-fitting results and revealed that topography was an important correlate of wetland geomorphic class regardless of spatial autocorrelation (Fig. 4). Wetland geomorphic classes, primarily driven by their dependence upon topography, were significantly related to all 3 sets of reach-scale environmental matrices (water chemistry, substrate composition, channel morphology and gradient), with the strongest correlation to water chemistry. Catchment topography also was a significant correlate of water chemistry and substrate composition independently of wetland geomorphic classes (i.e., it explained variance that was not explained by wetland classes). All 3 reach-scale environmental matrices explained unique variance in macroinvertebrate and fish community structure. Partial Mantel *r*-values were higher for reach–macroinvertebrate linkages than reach–fish linkages. Last, macroinvertebrate community structure was significantly correlated with fish community

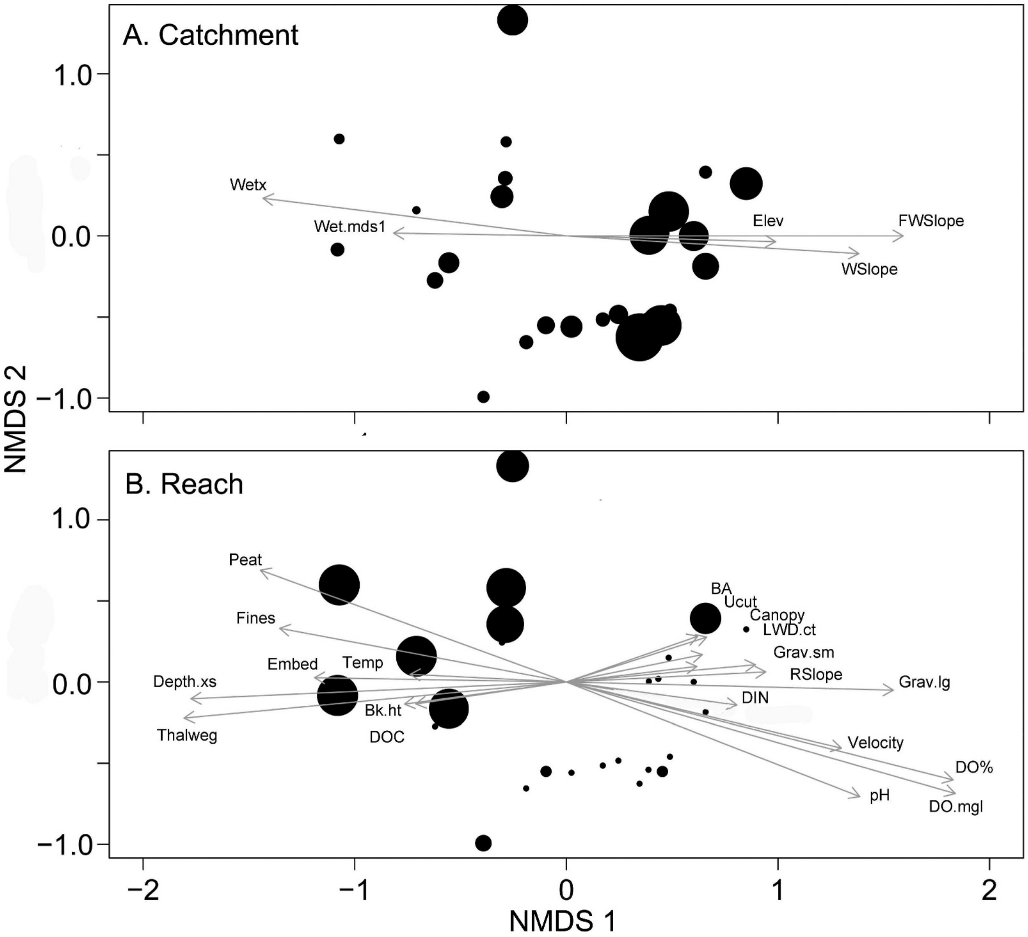

FIG. 3. Nonmetric multidimensional scaling (NMDS) ordination of fish species composition by age class from the 30 headwater streams. Arrows correspond to landscape (A) and stream-reach (B) variables significantly related to composition (see Appendix 1 for codes). Arrow length is proportional to the magnitude of the correlation (*r*). Direction of greatest correlation is indicated by the location of the arrow head. Symbols are sized in proportion to FWSlope (A) and % peat substrate (B). NMDS stress = 0.11.

structure. Macroinvertebrate composition explained variance in fish community structure that could not be explained by any other variable in the path diagram.

Individual species responses

Weighted averages and abundance maxima of individual taxa revealed distinct patterns in the distribution of macroinvertebrates along the topographic gradient. Macroinvertebrates frequently associated with lentic habitats were found primarily in streams with FWSlope values <4% (Fig. 5A). These taxa included genera spanning several families of dipterans (culicids, ceratopogonids, chironomids, chaoborids), hydrophilid coleopterans, cyclopoid copepods, ostracods, and sphaeriid bivalves (Fig. 5A, Appendix 2). Taxa more typically associated with lotic ecosystems began to show strong associations with streams in catchments with FWSlope > 4%, but most obligate lotic taxa reached peak abundances between 6 and 12%. Streams with intermediate-to-high slopes were dominated by large-bodied limnephilid and rhyacophilid trichopterans; numerous orthocladiine, diamesine, and tanytarsine chironomids; empidid, tipulid, and simuliid dipterans; baetid, ephemerellid, and heptageniid ephemeropterans; and perlodid, chloroperlid, capniid, and nemourid plecopterans. Taxa with abundance maxima 95% confidence intervals (CIs) that spanned the highest slopes (>10%) tended to span a broader range of slopes than those that had fidelity to low or intermediate slopes.

Salmonid species and age classes within species showed distinct distributional patterns along the topographic gradient. Large (≥10 cm) coho salmon were associated with low-slope catchments, with abundance maxima that ranged from 2 to 6% slope (Fig. 5B). GAM fitting revealed a strongly nonlinear

TABLE 2. Catchment- and reach-scale variables significantly ($p < 0.05$) related to macroinvertebrate or fish community composition in nonmetric multidimensional scaling (NMDS) ordinations of 30 headwater streams (Figs 2A, B, 3A, B). The magnitude of the correlations (r) corresponds to the relative length of arrows in the ordination diagrams. See Appendix 1 for variable codes. ns = not significant.

		Macroinvertebrates		Fish	
Scale	Variable	r	p	r	p
Catchment	Elev	0.57	0.007	0.50	0.018
	FWSlope	0.71	0.001	0.63	0.002
	RP	0.55	0.007	ns	ns
	Wet.mds1	0.58	0.002	0.45	0.043
	Wetx	0.69	0.001	0.60	0.003
	Wslope	0.68	0.001	0.59	0.003
Reach	BA	0.67	0.001	0.49	0.028
	Bk.ht	ns	ns	0.51	0.018
	Canopy	0.68	0.001	0.47	0.036
	Cobble	0.56	0.007	ns	ns
	DIN	0.55	0.011	0.52	0.015
	Depth.xs	0.84	0.001	0.77	0.001
	DOC	0.62	0.003	0.49	0.023
	DO.mgl	0.86	0.001	0.80	0.001
	DO%	0.82	0.001	0.81	0.001
	Embed	0.75	0.001	0.63	0.002
	Fila.alg	0.70	0.002	ns	ns
	Fines	0.65	0.001	0.68	0.002
	Grav.lg	0.62	0.002	0.72	0.001
	Grav.sm	0.56	0.004	0.55	0.008
	LWD.ct	0.66	0.001	0.46	0.033
	Peat	0.89	0.001	0.73	0.001
	pH	0.85	0.001	0.72	0.001
	RSlope	0.65	0.002	0.56	0.007
	Salt.m	0.59	0.003	ns	ns
	Sand	0.69	0.001	ns	ns
	Temp	0.63	0.002	0.50	0.024
	Thalweg	0.84	0.001	0.78	0.001
	Ucut	0.70	0.001	0.48	0.029
	Velocity	0.67	0.001	0.67	0.001

declining response in the density of coho salmon ≥10 cm with increasing FWSlope (GAM smoother $p < 0.0001$, effective degrees of freedom [EDF] = 2.8, $r^2 = 0.33$; Fig. 6A). Coho salmon ≥10 cm were most abundant in streams with deep, slow channels, warmer water, lower DO.mgl, and soft, unconsolidated peat substrate (Figs 5B, 6A) and were absent from high-WSlope catchments.

Coho salmon <10 cm typically were found in streams in catchments with intermediate slopes (Figs 5B, 6B). Coho salmon <10 cm were absent from catchments with FWSlope <3% and ≥10% and showed a distinct peak in densities at WSlopes between 6 and 8% (GAM smoother $p < 0.0001$, EDF = 2, $r^2 = 0.30$; Fig. 6B).

Dolly Varden also showed distinct patterns in the distribution of size classes along the topographic gradient (Figs 5B, 6C, D). Dolly Varden ≥8 cm were collected across the entire range of FWSlope, but increased sharply and peaked between 6 and 10% (GAM smoother $p < 0.0001$, EDF = 3, r^2 =0.41; Fig 6C). Dolly Varden <8 cm were absent from catchments with FWSlope <3% and sharply increased in density until peaking near 12% (GAM smoother $p < 0.0001$, EDF = 2, $r^2 = 0.48$; Fig. 6D). Steelhead ($n = 4$) were not sufficiently frequent to model using GAMs but were found only in streams with intermediate FWSlope (Fig. 5B).

Predictions of mean densities of salmonids across 9119 reaches revealed distinct spatial patterns in the distribution of size classes of coho salmon and Dolly Varden as a function of FWSlope. Mean abundance of coho salmon was predicted to be significantly >0 (95% CI) across 320 (≥10 cm) and 507 (<10 cm) of 547 km of 1st-order streams, whereas 187 (≥10 cm) and 260 (<10 cm) of 547 km were predicted to support densities above the overall mean density of each coho size class (Fig. 7A, B). Dolly Varden mean abundance was predicted to be significantly >0 in 504 (≥8 cm) and 482 km (<8 cm) of streams, whereas

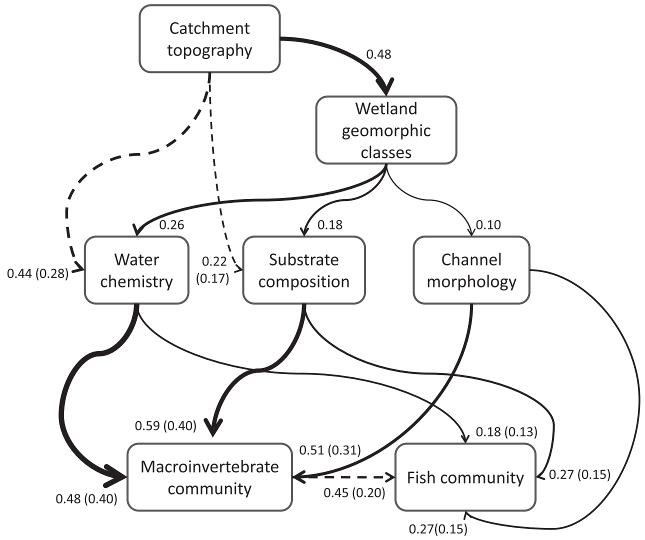

FIG. 4. Partial Mantel path diagram illustrating significant ($p < 0.05$) correlations among catchment- and reach-scale matrices. Solid lines represent direct effects, whereas dashed lines represent residual indirect effects not accounted for by intermediate pathways in the model. Mantel *r*-values are shown adjacent to each significant pathway. Values in parentheses are pure-partial coefficients that account for other covariates, whereas other values account only for spatial autocorrelation.

densities were predicted to exceed the mean in 273 (≥8 cm) and 271 (<8 cm) km of 547 total km of streams (Fig. 7C, D). All 547 km of stream length were predicted to support at least 1 size class of the 2 species.

Discussion

Catchment topography was a strong driver of physical, chemical, and biological condition in Kenai Peninsula headwater streams. This result is consistent with the extensive body of literature about the importance of stream slope, particularly along longitudinal gradients from headwaters to higher-order streams, in governing species distributions and ecosystem processes (Vannote et al. 1980). The physical template of these catchments controlled not only stream velocity and channel morphology, factors viewed as 2 of the most important in governing distributions of macroinvertebrates (Ward 1998) and juvenile salmonids (Quinn 2005), but also the type and amount of wetlands. Catchment metrics of topographic wetness explained the same variance in the physical, chemical, and biological condition of these streams as did wetlands and explained additional variance not explained by wetlands. Thus, the unit effect of wetlands appears to have been mediated by topography, where flatter flow paths near streams probably retained water for longer periods of time. Increased residence time of water in wetlands probably resulted in greater interactions with hydric soils, leading to increased dissolved organic matter, increased respiration and lower dissolved O_2 (DO), higher temperatures, and greater inputs of particulate organic matter contributing to peat substrates (Anderson and Nyberg 2007, 2008). Collectively, these differences in stream gradient, channel morphology, substrate composition, and water chemistry all appeared to contribute to distinct macroinvertebrate communities and distributions of juvenile salmonids. Wetlands were important drivers of stream condition, but their effect was modulated by slope along lateral flow paths.

An important result of our study was that the vast majority of 1^{st}-order streams, regardless of topographic or geomorphic setting, supported relatively high numbers of macroinvertebrate taxa and at least 1 life-history stage of salmonids. We expected low diversity of both macroinvertebrates and fish because the landscape was relatively recently deglaciated and is not old enough to expect extensive adaptive radiation and endemism characteristic of headwater streams elsewhere (e.g., southeastern USA; Meyer et al. 2007). Fish diversity was low because of heavy dependence upon recolonization from marine environments. In contrast, most streams supported high phylogenetic diversity of macroinvertebrates, spanning several noninsect groups through most of the major aquatic insect orders. Number of taxa/site (α diversity) ranged from 21 to 45 with a median of 34. This value falls near the middle of the ranges reported from other headwater stream studies (reviewed by Meyer et al. 2007, Clarke et al. 2008), with the highest values reported from older landscapes (up to 93 taxa/stream and 171 total taxa, eastern USA; Feminella 1996) and lowest values from headwater streams in the Pacific Northwest (as few as 3.5/stream and only 35 total taxa; Haggerty et al. 2002). The latter streams more closely match the landscape history and climate of our streams.

Factors contributing to diversity and community structure in headwater streams vary widely among ecosystems. Clarke et al. (2008) suggested that headwaters do not necessarily support high α (site-level) diversity, but rather contribute heavily to regional (γ) diversity because each site supports many different species not found in many other locations (β diversity). This suggestion was true across 235 headwater streams in boreal regions of northern Europe, where Heino (2003) reported very weak environmental or geographical correlates of macroinvertebrate communities. Differences in taxonomic

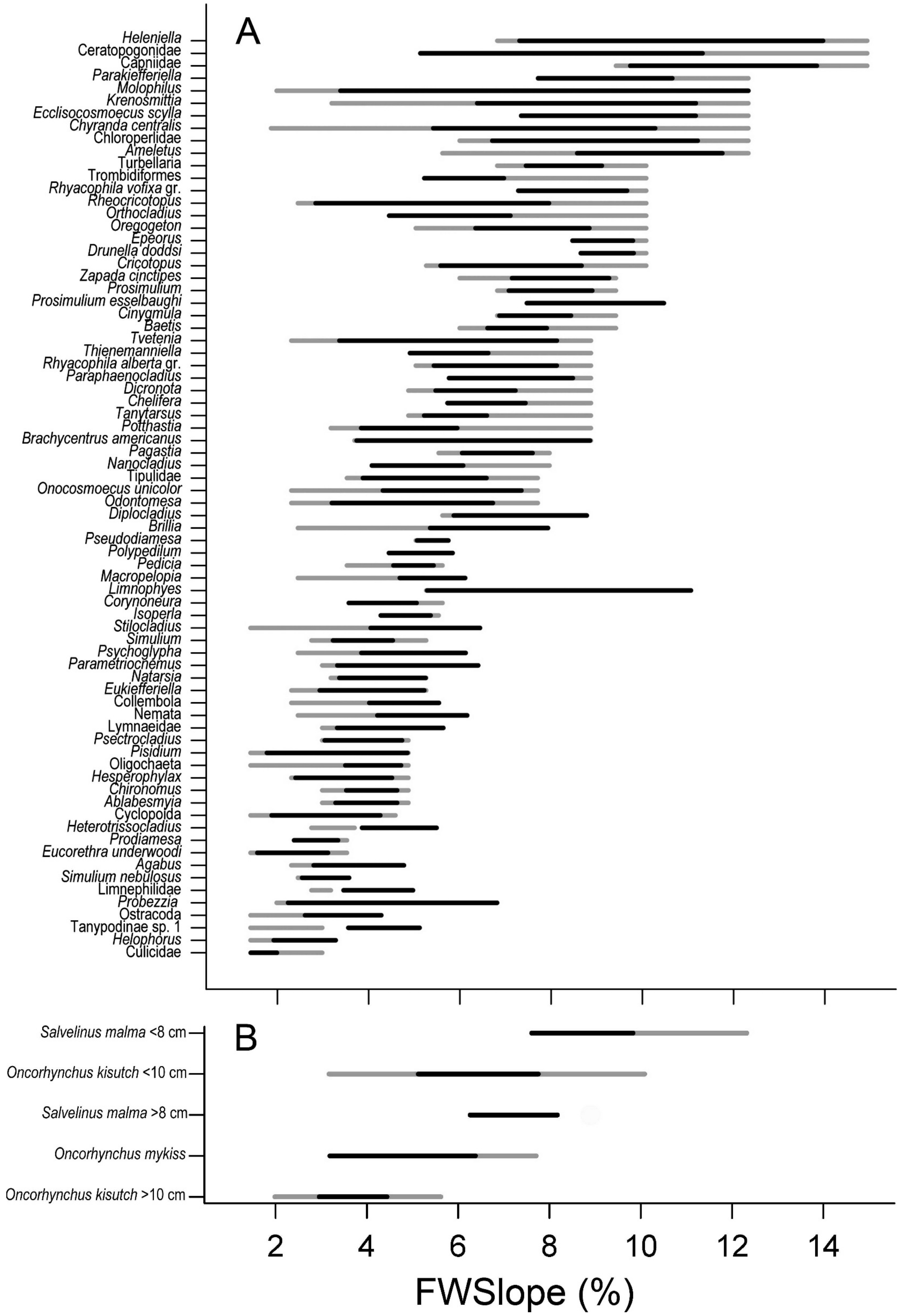

FIG. 5. Distribution of macroinvertebrate taxon (A) and fish species (B) abundances with increasing flow-weighted slope (FWSlope). Black horizontal lines are empirical confidence intervals (CIs; 5th–95th percentile) of weighted-average abundance among 1000 bootstraps, whereas gray lines span the 5th–95th bootstrap percentiles of the maximum abundance observed among sample units. Taxa are plotted in rank order of the upper CI (95th percentile) of maximum abundance. Only taxa that were collected in ≥3 streams are shown.

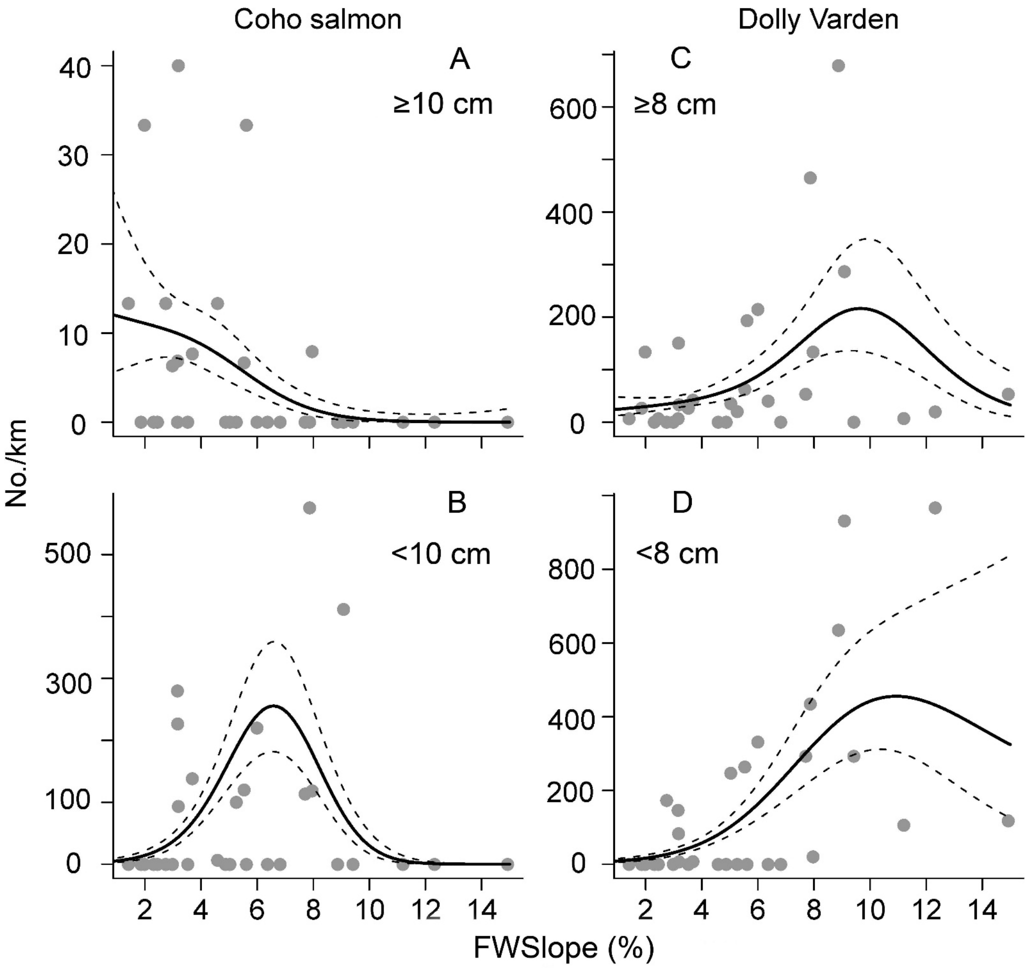

FIG. 6. Negative binomial generalized additive models (GAMs) of juvenile coho salmon ≥10 cm (A) and <10 cm (B), and Dolly Varden ≥8 cm (C) and <8 cm (D) densities in response to flow-weighted slope (FWSlope) (%). Solid line is the fitted mean, whereas the dotted lines are 95% confidence limits.

composition among streams were high (i.e., high β diversity), but streams with similar physical and chemical conditions or in close proximity did not necessarily support similar assemblages. They surmised that high disturbance frequency among boreal headwaters caused high rates of local extinction such that communities were in a constant state of recolonization, resulting in poorly organized assemblages. Heino et al. (2008) suggested that catchment-scale variables might have only limited value in explaining biodiversity indices in headwater streams in the absence of strong gradients in human land use. In contrast, we found very predictable community structure that was strongly tied to catchment topography and its abiotic intermediaries. Most of the variance in the community was explained by NMDS Axis 1, and the continuum of sites along this axis corresponded to physical and chemical conditions tied to topography and wetness. The relatively high degree of overlap in taxa among streams in similar topographic settings implies that these communities are predictable and that the environment, rather than stochastic events, plays the predominant role in organizing species in these systems.

Most macroinvertebrate diversity and numerical abundance consisted of Diptera. Roughly 60% of the total taxa identified were dipterans, and >60% of these taxa were Chironomidae. Of the 19 taxa that had densities $>1000/m^2$ in any stream, 14 were dipterans, and of these, 12 were chironomids. These numbers are similar to those reported for other low-order streams where chironomids were identified to genus or species. For example, 91 of 145 taxa identified from just 3 headwater streams in North Carolina were dipterans, and most of those were chironomids (Meyer et al. 2007). Milner et al. (2008) reported that chironomids were the first taxa to colonize a newly formed glacial stream, and chiron-

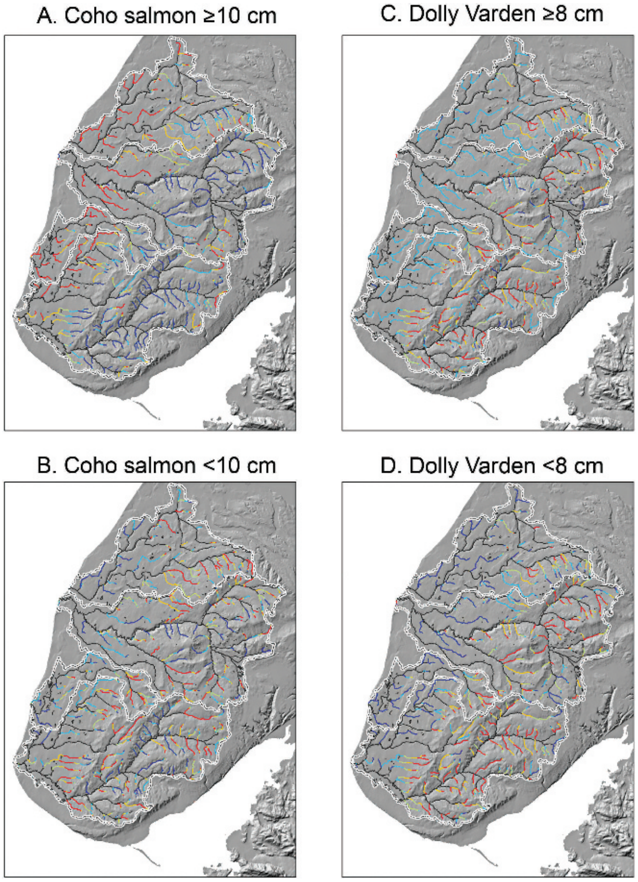

FIG. 7. Mapped generalized additive models (GAMs) predictions of juvenile coho salmon ≥10 cm (A) and <10 cm (B) and Dolly Varden ≥8 cm (C) and <8 cm (D) mean densities, a function of flow-weighted slope (FWSlope) across 547 km of headwater streams. Color ramp is linearly scaled to fish density, ranging from low (dark blue) to high (red).

omids continued to colonize over the next 28 y of succession. High densities and diversity of dipterans in headwaters and intermittently inundated habitats, such as peatlands and marshes, often have been attributed to potentially shorter, less predictable developmental periods associated with stream drying or freezing and the tendency for many dipterans, particularly chironomids, to be small bodied with rapid development (Williams 1996). Kenai Peninsula headwater streams have a relatively short ice-free period (April–October), which would favor smaller, faster developing taxa, such as chironomids (Milner et al. 2001). Shaftel et al. (2011) reported high densities of chironomids and simuliids on bluejoint grass litter from 6 headwater streams in this region. Dekar et al. (2012) further showed that consumers of grass litter, many of which were dipterans, were the dominant energy source supporting juvenile salmonids in Kenai Lowland headwater streams. The abundance and diversity of dipterans across the topographic gradient suggest their importance in community dynamics, secondary production, and consequently, as food for juvenile salmon in these systems, and these results support the work of others who have recommended identification of chironomids to genus or species in studies of headwater streams (e.g., Raunio et al. 2011).

Salmonids were widely distributed across the gradient of catchment topography. All types of catchments appeared to serve at least one life-history stage of salmonids, a finding that further demonstrated the importance of headwater streams as juvenile salmonid rearing habitat. Elsewhere, headwaters have been deemed fishless but important sources of invertebrate food for fish occupying larger, downstream habitats (reviewed by Wipfli and Baxter 2010). Here, we documented juvenile coho salmon in 13 streams not previously entered into the Anadromous Waters Catalog used by the Alaska Department of Fish and Game for special protection of salmon habitat (ADFG 2011). Extrapolating our GAM model results to headwater segments that have not been sampled, but are excluded from the catalog, indicates >50% of the headwaters not catalogued probably are supporting juvenile coho salmon. Dolly Varden are included in the Anadromous Waters Catalog only when the population has been verified to be anadromous. This status has yet to be confirmed in these streams but is certainly likely because anadromous Dolly Varden are abundant in all 4 basins. If these Dolly Varden were deemed anadromous, virtually all of the stream segments on the Kenai Peninsula would have to be included in the Anadromous Waters Catalog.

One of the most interesting patterns revealed by our results was the differential habitat use by species and size classes of juvenile salmonids, particularly the size-specific segregation of coho salmon between low and intermediate-sloping catchments. Coho above and below 10 cm were rarely collected from the same site, and all coho ≥10 cm were collected from streams with deep slow channels, soft peaty bottoms, and warmer temperatures (Fig. 8A, B). The absence of fry or parr at these sites suggests that the drivers of this pattern, at least in part, were absence of spawning gravel, flow, and benthic O_2. Streams in low-slope catchments were all soft-bottomed and had negligible flow velocities. Water-column DO also was well below saturation (40–60%) at these sites, a characteristic suggesting that mid-summer conditions may not have been suitable for fry or parr to use these sites. Conversely, presmolts may have been migrating into

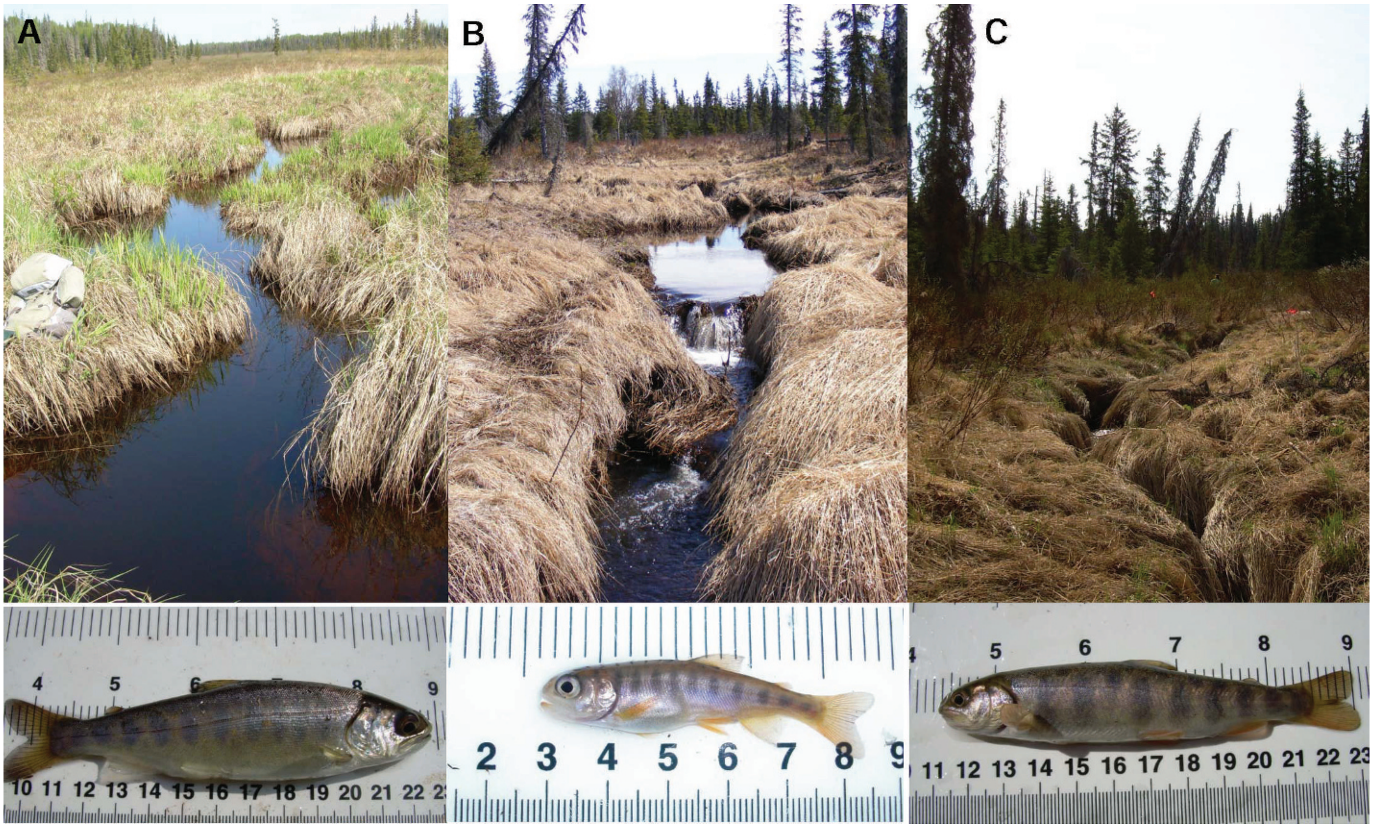

FIG. 8. Photographs of stream reaches situated in catchments with low (A), intermediate (B), and high (C) flow-weighted slopes. Large (≥10 cm) juvenile coho salmon were most abundant in stream type A, small coho (<10 cm) in type B, and Dolly Varden in type C.

these habitats from downstream, higher-gradient waters during autumn to overwinter because we collected fish ≥10 cm in these types of streams from mid-May during recession of snowmelt through mid-summer (Brown and Hartmann 1988, Wigington et al. 2006).

We observed similar but less exclusive size-specific segregation in Dolly Varden. Dolly Varden ≥8 cm were found in every topographic setting but were significantly more abundant in catchments with slopes between 6 and 10% (Fig. 8C; also see Bryant et al. 2004). Similar to the fry and parr of coho salmon, Dolly Varden <8 cm were absent from streams with catchments with <3% slope that lacked gravel, flow, and DO, whereas larger fish reared at higher gradients appeared to be migrating into low-gradient, low-velocity habitats also occupied by smolting coho. Migration into otherwise unused habitats in the lowest-gradient streams by older juveniles of Dolly Varden and coho salmon may indicate ecological release from competition and enhanced bioenergetic conditions (Hearn 1987, Power et al. 2005). Older juveniles also are more tolerant of episodic depression of DO and elevated temperatures, factors that may prevent use of these habitats by fry and parr (Quinn 2005, Dunham et al. 2008).

We failed to detect salmonids at a few of our study streams. Absence of coho fry and parr from sites with optimal catchment topography and instream habitat may be attributed to unknown downstream blockages or lack of spawners in those particular tributaries in the previous 2 y. The latter possibility could be a particularly important element of biocomplexity in these populations because small tributaries absorb surplus spawning pairs during years with above average adult returns elsewhere (Isaak and Thurow 2006). We sampled after an above average escapement year for coho salmon on the Anchor River (>19,000 in 2005 vs 5000–10,000 escapement goal; www.adfg.alaska.gov). How does run size affect the magnitude and spatial extent of headwater use by spawning adults and their young? The importance of headwaters for subsidizing spawning habitat during strong adult return years is a fruitful area for future research in this region.

We avoided using an information-theoretic approach (e.g., Anderson et al. 2000) to fit GAM models with multiple predictors or contrasting single-predictor models because the predominant correlates of both macroinvertebrate and fish community structure were necessarily correlated with catchment topography and the sample size precluded strong inference about multiple predictors. Instead, we used FWSlope as an indicator of the numerous physical and chemical changes that directly influenced biota in these streams. Thus, our use of this catchment-scale metric as a predictor was deliberately integrative. Feist et al. (2010) used predictors spanning multiple spatial scales to compare models of salmonid habitat directly and concluded that endangered salmon habitat was best predicted by landscape data summarized at a catchment scale. We showed that catchment-scale topography was tied to numerous local-scale abiotic conditions and that these abiotic conditions were the pathway linking catchment to biota. We suggest starting with a catchment-scale perspective but developing a strong conceptual model of linkages between catchment and local conditions rather than a dichotomous local vs catchment analytical framework (King et al. 2005).

We recognize that numerous secondary factors that we did not characterize control species distributions in these systems. Moreover, our data set was small, and catchment topographic metrics were derived with coarse DEMs. Analyses using finer-scale elevation data (e.g., LIDAR) and more sample units collected among years differing in adult returns and weather are needed to identify secondary correlates that explain absence of fish from streams that appeared suitable based on measured physical and chemical conditions (see Ebersole et al. 2009). The maps of predicted density of fish by size classes resulting from our GAM models need to be refined and validated and should be used to make inferences only about locations likely to support salmonids by species and age. Furthermore, we acknowledge that many other catchment-scale metrics of slope and gradient exist and could explain similar amounts of variance when compared to the catchment topographic metrics used in our study (e.g., Hjerdt et al. 2004). Nevertheless, we suggest that our study lays a foundation for focused hypotheses about linkages among catchments, abiotic conditions, and biota in this region. For example, what are the implications of climate change (Brooks 2009, Heino et al. 2009) and expanding human population growth (King et al. 2011) in this region for environmental conditions in these streams? Our study should assist in development of catchment management tools for identifying and prioritizing conservation efforts in the region and may serve as a framework for other studies concerning biodiversity and conservation of focal species in headwater streams.

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Appendix 1. Catchment- and stream-reach characteristics among the 30 headwater streams. NMDS = nonmetric multidimensional scaling, DS = discharge slope, DW = relict glacial drainageway, KT = kettle, LB = relict glacial lakebed, RP = riparian.

Scale	Variable	Description	Minimum	Median	Mean	Maximum
Catchment	Northing	Northing (m)	0	20,042	23,950	50,278
	Easting	Easting (m)	0	14,516	13,290	25,612
	Area	Catchment area (km^2)	0.16	2.80	3.80	26.70
	Elev	Elevation (m)	47	130	169	410
	WSlope	Slope (%), catchment mean	1.49	4.79	5.14	12.38
	FWSlope	Flow-weighted slope (%), catchment mean	1.41	5.15	5.80	14.93
	Wetx	Topographic wetness index, catchment mean	6.92	8.12	8.10	9.09
	Wet	Total wetland cover (%)	9.3	41.3	44.3	93.9
	DS	Discharge slope wetland cover (%)	0.0	6.0	12.0	47.1
	DW	Drainageway wetland cover (%)	0.0	1.0	5.6	28.6
	LB	Lakebed wetland cover (%)	0.0	0.7	13.1	50.0
	KT	Kettle wetland cover (%)	0.0	0.1	2.8	30.9
	RP	Riparian wetland cover (%)	0.0	6.6	6.7	16.0
	Wet.mds1	NMDS axis 1; ordination of catchments by % cover of DS, DW, LB, KT, and RP wetland classes	−0.85	−0.027	0	0.85
Reach	Temp	Temperature (°C)	2.5	5.4	5.6	8.3
	Cond	Specific conductance (μS/cm)	37.0	58.0	59.1	96.0
	DO.mgl	Dissolved O$_2$ (mg/L)	4.9	12.6	11.7	14.4
	DO%	Dissolved O$_2$ (%)	42.4	101.5	94.7	116.0
	pH	pH	6.11	7.17	7.13	7.95
	PO4.P	Orthophosphate-P (μg/L)	1.0	10.5	13.0	44.2
	NH4.N	NH$_4$-N (μg/L)	5.9	16.4	22.4	69.7
	NOx-N	NO$_3$ + NO$_2$-N (μg/L)	1.0	30.2	128.1	738.4
	DIN	Dissolved inorganic N (μg/L)	14.3	63.4	150.5	772.6
	TP	Total P (μg/L)	15.6	41.8	49.5	159.8
	TN	Total N (μg/L)	153.4	469.0	524.5	1290.7
	DOC	Dissolved organic C (mg/L)	2.7	10.5	10.5	24.3
	Q.cms	Discharge (m^3/s)	0.007	0.029	0.056	0.512
	Velocity	Flow velocity (m/s)	0.02	0.25	0.26	0.48
	Sinuous	Sinuosity, straight line length of reach (m)	96	175	175	232
	Rslope	Stream slope (%), reach	0.15	2.62	2.82	7.60
	BA	Bank angle (degrees)	53	137	126	163
	Ucut	Undercut bank distance (cm)	0	19	18	38
	Wetwdth	Wetted width (m)	0.72	1.48	1.62	3.16
	Bk.wdth	Bank width (m)	0.78	1.49	1.74	3.99
	Bk.ht	Bank height (m)	0.44	0.72	0.78	1.24
	Incs.ht	Incised bank height (m)	0.57	0.94	0.92	1.53
	Thalweg	Thalweg depth (cm)	12	27	35	116
	Depth.xs	Channel cross-section depth (cm)	7	17	23	93
	Canopy%	Canopy cover (%)	0	42	41	88
	LWD.ct	Large woody debris (no.)	0.0	2.0	4.1	20.0
	LWD.m3	Large woody debris (m^3)	0.0	0.4	2.4	17.2
	Fila.alg	Filamentous algae, cover class (0–4)	0.0	0.0	0.6	4.0
	Peri	Periphyton, cover class (0–4)	0.0	0.5	0.9	4.0
	Macrphy	Macrophyte, cover class (0–4)	0.0	1.0	1.1	3.1
	Root	Instream woody rootwads, cover class (0–4)	0.0	0.0	0.0	0.3
	Overveg	Overhanging vegetation, cover class (0–4)	0.9	3.4	3.0	4.0
	Leafpack	Leaf packs, cover class (0–4)	0.0	0.0	0.1	0.6
	Peat	Peat substrate (%)	0.0	0.0	20.9	100.0
	Silt	Silt substrate (%)	0.0	6.2	11.4	68.6
	Sand	Sand substrate (%)	0.0	18.0	18.5	64.8
	Grav.sm	Gravel substrate, small (%)	0.0	6.2	7.6	29.5
	Grav.lg	Gravel substrate, large (%)	0.0	8.6	14.9	63.0
	Cobble	Cobble substrate (%)	0.0	6.3	13.8	65.0
	Bould.sm	Boulder substrate, small (%)	0.0	3.4	10.3	41.0
	Bould.lg	Boulder substrate, large (%)	0.0	0.0	0.7	6.7
	Wood	Wood substrate (%)	0.0	0.0	1.8	18.1
	Fines	Fine substrate (% peat + silt)	4.8	48.6	50.8	100.0
	Embed	Substrate embeddedness (%)	43	72	73	100

APPENDIX 1. Continued.

Scale	Variable	Description	Minimum	Median	Mean	Maximum
	Dlink	Downstream link number (stream network)	2	4	12.73	70
	Salt.m	Flow-length distance (m) from ocean	4657	30,322	26,774	46,725
	Main.m	Flow-length distance (m) from main river channel	221	1613	2143	6052

APPENDIX 2. Macroinvertebrate taxa identified from the 30 headwater streams listed in approximate phylogenetic sequence by higher taxa. Frequency (Freq) is the number of occurrences among the 30 streams. Mean density was calculated only from streams in which taxa occurred (max. = maximum density observed). Nonmetric multidimensional scaling (NMDS) 1 and 2 are the weighted-average axis scores corresponding to the NMDS ordination (Fig. 2). Increasingly positive NMDS 1 scores correspond to sites with high catchment and reach slopes, lower wetness index scores, lack of deep peat-bottomed channels, higher dissolved O_2 and pH, and lower temperatures. Increasingly positive NMDS 2 scores correspond to lower filamentous algal cover and higher bank angles and undercut banks. Taxa with frequencies <3 were not used in the NMDS analysis and do not have scores.

				No./m^2			
Class/Order	Family	Taxon	Freq	Mean	Max.	NMDS 1	NMDS 2
Turbellaria		Turbellaria	18	393.3	1387.5	0.25	−0.03
Nemata		Nemata	24	141.0	666.0	−0.04	−0.02
Oligochaeta		Oligochaeta	30	528.1	1803.8	−0.04	0.00
Arynchobdellida	Erpobdellidae	Erpobdellidae	2	0.8	1.1		
Arynchobdellida	Hirudinidae	*Haemopis marmorata*	1	0.5	0.5		
Bivalvia	Pisidiidae	*Pisidium*	8	198.4	684.5	−0.45	0.03
Gastropoda	Lymnaeidae	Lymnaeidae	3	42.2	61.7	−0.19	−0.05
Gastropoda	Planorbidae	*Gyraulus deflectus*	1	61.7	61.7		
Ostracoda		Ostracoda	11	2122.5	8510.0	−0.25	−0.05
Cladocera		Cladocera	1	925.0	925.0		
Cyclopoida		Cyclopoida	4	277.4	422.9	−0.69	−0.05
Amphipoda	Gammaridae	*Gammarus*	1	18.4	18.4		
Trombidiformes		Trombidiformes	29	216.3	1040.6	−0.02	−0.03
Collembola		Collembola	17	87.5	317.6	0.02	−0.01
Ephemeroptera	Ameletidae	*Ameletus*	5	5.2	20.6	0.29	0.12
Ephemeroptera	Baetidae	*Baetis*	24	880.5	7307.5	0.19	−0.04
Ephemeroptera	Baetidae	*Callibaetis fluctuans*	2	120.4	194.6		
Ephemeroptera	Ephemerellidae	*Drunella doddsi*	7	4.6	13.5	0.33	−0.20
Ephemeroptera	Ephemerellidae	*Ephemerella aurivillii*	2	6.2	11.9		
Ephemeroptera	Heptageniidae	*Cinygma*	1	2.7	2.7		
Ephemeroptera	Heptageniidae	*Cinygmula*	20	227.8	799.2	0.22	−0.06
Ephemeroptera	Heptageniidae	*Epeorus*	10	87.0	416.3	0.29	−0.15
Ephemeroptera	Heptageniidae	Heptageniidae sp. 1	2	501.0	863.3		
Odonata	Aeschnidae	Aeschnidae	1	0.5	0.5		
Plecoptera	Capniidae	Capniidae sp.1	4	69.8	118.4	0.36	−0.04
Plecoptera	Chloroperlidae	*Alaskaperla oribaris*	1	15.4	15.4		
Plecoptera	Chloroperlidae	*Alloperla*	2	0.5	0.5		
Plecoptera	Chloroperlidae	Chloroperlidae sp.1	6	153.0	508.8	0.32	−0.12
Plecoptera	Chloroperlidae	*Suwallia*	1	6.5	6.5		
Plecoptera	Chloroperlidae	*Swelsta*	1	0.5	0.5		
Plecoptera	Nemouridae	*Zapada cinctipes*	23	675.2	1953.6	0.22	−0.02
Plecoptera	Perlodidae	*Isoperla*	14	28.5	158.8	0.08	−0.03
Heteroptera	Corixidae	*Callicorixa*	1	1.1	1.1		
Heteroptera	Corixidae	*Sigara*	1	61.7	61.7		
Heteroptera	Gerridae	*Gerris*	1	0.5	0.5		
Coleoptera	Dytiscidae	*Agabus seriatus* gr.	16	0.5	0.5	−0.23	−0.05
Coleoptera	Dytiscidae	*Colymbetes dahuricus*	1	0.5	0.5		
Coleoptera	Dytiscidae	Dytiscidae	2	1.1	1.6		
Coleoptera	Dytiscidae	*Hydroporus*	1	14.2	14.2		
Coleoptera	Dytiscidae	*Neoscutopterus hornii*	1	0.5	0.5		

APPENDIX 2. Continued.

				No./m^2			
Class/Order	Family	Taxon	Freq	Mean	Max.	NMDS 1	NMDS 2
Coleoptera	Dytiscidae	*Sanfillipodytes*	2	19.1	20.6		
Coleoptera	Helophoridae	*Helophorus*	4	37.0	61.7	−0.45	0.11
Coleoptera	Staphylinidae	Staphylinidae	1	30.8	30.8		
Trichoptera	Brachycentridae	*Brachycentrus americanus*	3	160.7	370.0	0.03	−0.07
Trichoptera	Glossomatidae	*Glossosoma*	1	1.6	1.6		
Trichoptera	Lepidostomatidae	*Lepidostoma*	1	15.4	15.4		
Trichoptera	Limnephilidae	*Chyranda centralis*	8	1.6	3.8	0.20	0.02
Trichoptera	Limnephilidae	*Ecclisocosmoecus scylla*	9	2.6	10.3	0.32	0.05
Trichoptera	Limnephilidae	*Hesperophylax*	17	31.9	440.5	−0.11	−0.01
Trichoptera	Limnephilidae	Limnephilidae sp.1	20	177.4	397.0	−0.03	−0.12
Trichoptera	Limnephilidae	*Limnephilus*	2	158.7	616.7		
Trichoptera	Limnephilidae	*Onocosmoecus unicolor*	21	7.4	44.0	0.16	−0.08
Trichoptera	Limnephilidae	*Psychoglypha*	15	67.4	555.8	−0.06	−0.11
Trichoptera	Philopotamidae	*Dolophilodes*	2	1.6	2.2		
Trichoptera	Rhyacophilidae	*Rhyacophila alberta* gr.	8	25.5	92.5	0.15	−0.06
Trichoptera	Rhyacophilidae	*Rhyacophila vofixa* gr.	17	264.2	878.8	0.24	−0.01
Diptera	Ceratopogonidae	*Bezzia*	1	74.0	74.0		
Diptera	Ceratopogonidae	Ceratopogonidae sp.1	5	27.3	79.4	0.10	−0.03
Diptera	Ceratopogonidae	*Probezzia*	4	24.7	44.0	0.13	0.02
Diptera	Chaoboridae	*Eucorethra underwoodi*	3	0.5	0.5	−0.43	0.29
Diptera	Chironomidae	*Ablabesmyia*	3	12.6	35.2	−0.79	−0.22
Diptera	Chironomidae	*Brillia*	25	86.1	444.0	0.12	0.04
Diptera	Chironomidae	*Chironomus*	3	12.5	35.8	−0.78	−0.23
Diptera	Chironomidae	*Corynoneura*	14	141.0	422.9	−0.15	−0.03
Diptera	Chironomidae	*Cricotopus*	15	476.0	2254.7	0.00	−0.18
Diptera	Chironomidae	*Diamesa*	1	92.5	92.5		
Diptera	Chironomidae	*Diplocladius*	3	54.1	105.7	0.12	−0.05
Diptera	Chironomidae	*Eukiefferiella*	21	695.8	5329.8	−0.03	−0.08
Diptera	Chironomidae	*Glyptotendipes*	1	0.5	0.5		
Diptera	Chironomidae	*Gymnometriocnemus*	2	25.1	43.5		
Diptera	Chironomidae	*Heleniella*	4	16.5	41.1	0.39	0.07
Diptera	Chironomidae	*Heterotrissocladius*	20	154.4	801.7	0.03	0.07
Diptera	Chironomidae	*Krenopelopia*	2	23.4	46.3		
Diptera	Chironomidae	*Krenosmittia*	5	26.7	46.3	0.33	−0.03
Diptera	Chironomidae	*Lasiodiamesa*	1	6.6	6.6		
Diptera	Chironomidae	*Limnophyes*	3	709.2	1356.7	0.03	−0.23
Diptera	Chironomidae	*Macropelopia*	25	192.9	1004.3	−0.02	0.01
Diptera	Chironomidae	*Metriocnemus*	2	35.2	35.2		
Diptera	Chironomidae	*Micropsectra*	2	213.9	397.0		
Diptera	Chironomidae	*Nanocladius*	8	117.5	397.0	−0.01	−0.03
Diptera	Chironomidae	*Natarsia*	6	118.6	635.2	−0.10	−0.12
Diptera	Chironomidae	*Odontomesa*	5	27.8	46.8	0.20	−0.08
Diptera	Chironomidae	*Orthocladius*	21	331.9	1985.0	−0.10	−0.10
Diptera	Chironomidae	*Orthocladius (Symposiocladius)*	2	269.4	538.2		
Diptera	Chironomidae	*Pagastia*	17	60.1	215.8	0.21	0.01
Diptera	Chironomidae	*Parachironomus*	1	1.6	1.6		
Diptera	Chironomidae	*Paracladopelma*	1	714.6	714.6		
Diptera	Chironomidae	*Parakiefferiella*	7	91.6	216.9	0.29	0.08
Diptera	Chironomidae	*Paramerina*	2	40.0	79.4		
Diptera	Chironomidae	*Parametriocnemus*	12	320.9	2343.3	−0.20	−0.07
Diptera	Chironomidae	*Paraphaenocladius*	11	68.1	231.3	0.16	−0.02
Diptera	Chironomidae	*Paratanytarsus*	2	255.5	458.1		
Diptera	Chironomidae	*Parorthocladius*	1	601.3	601.3		
Diptera	Chironomidae	*Polypedilum*	13	79.7	555.8	−0.09	−0.11
Diptera	Chironomidae	*Potthastia*	6	96.1	476.4	0.06	−0.26
Diptera	Chironomidae	*Procladius*	1	123.3	123.3		
Diptera	Chironomidae	*Prodiamesa*	5	1.4	3.3	−0.31	0.13

Appendix 2. Continued.

				No./m^2			
Class/Order	Family	Taxon	Freq	Mean	Max.	NMDS 1	NMDS 2
Diptera	Chironomidae	*Protanypus*	1	20.6	20.6		
Diptera	Chironomidae	*Psectrocladius*	3	343.6	616.7	−0.71	−0.17
Diptera	Chironomidae	*Pseudodiamesa*	3	20.7	35.2	−0.06	−0.10
Diptera	Chironomidae	*Psilometriocnemus*	1	8.4	8.4		
Diptera	Chironomidae	*Rheocricotopus*	16	672.6	6734.0	0.09	−0.11
Diptera	Chironomidae	*Rheotanytarsus*	1	794.0	794.0		
Diptera	Chironomidae	*Smittia*	1	28.5	28.5		
Diptera	Chironomidae	*Stempellinella*	2	647.5	1248.8		
Diptera	Chironomidae	*Stilocladius*	11	175.6	794.0	0.12	−0.01
Diptera	Chironomidae	Tanypodinae sp.1	30	329.0	1973.3	−0.05	−0.03
Diptera	Chironomidae	*Tanytarsus*	29	893.2	4292.0	−0.01	0.00
Diptera	Chironomidae	*Thienemanniella*	17	592.2	2568.2	0.10	−0.10
Diptera	Chironomidae	*Tvetenia*	13	255.6	1329.7	0.10	−0.10
Diptera	Culicidae	*Aedes*	2	0.8	1.1		
Diptera	Culicidae	Culicidae sp.1	3	72.1	185.0	−0.46	0.13
Diptera	Dixidae	*Dixella*	1	46.3	46.3		
Diptera	Dixidae	Dixidae sp.1	2	54.0	61.7		
Diptera	Empididae	*Chelifera*	17	58.1	174.1	0.20	−0.03
Diptera	Empididae	Empididae sp. 1	1	0.5	0.5		
Diptera	Empididae	*Oreogeton*	12	41.4	123.3	0.29	−0.01
Diptera	Empididae	*Tricoclinocera*	1	1.6	1.6		
Diptera	Ephydridae	Ephydridae	1	0.5	0.5		
Diptera	Psychodidae	*Pericoma*	2	44.9	46.3		
Diptera	Sciomyzidae	Sciomyzidae	1	61.7	61.7		
Diptera	Simuliidae	*Prosimulium esselbaughi*	4	425.3	2261.1	0.20	0.19
Diptera	Simuliidae	*Prosimulium* sp.1	20	34.8	77.1	0.22	0.02
Diptera	Simuliidae	*Simulium nebulosum*	12	127.9	540.8	−0.27	−0.01
Diptera	Simuliidae	*Simulium* sp.1	26	1933.3	12,518.3	0.00	0.00
Diptera	Simuliidae	*Simulium transiens*	1	169.6	169.6		
Diptera	Stratiomyiidae	Stratiomyiidae	1	46.3	46.3		
Diptera	Tipulidae	*Antocha*	1	20.6	20.6		
Diptera	Tipulidae	*Dicranota*	23	51.8	129.5	0.13	0.00
Diptera	Tipulidae	*Hesperoconopa*	2	8.2	15.4		
Diptera	Tipulidae	*Hexatoma*	2	0.8	1.1		
Diptera	Tipulidae	*Molophilus*	3	26.2	46.3	0.23	0.22
Diptera	Tipulidae	*Pedicia*	6	19.6	79.4	−0.19	−0.11
Diptera	Tipulidae	*Tipula*	2	2.7	4.9		
Diptera	Tipulidae	Tipulidae sp.1	11	18.7	46.3	0.09	0.18