# Distribution, Status, and Land Use Characteristics of Subwatersheds within the Native Range of Brook Trout in the Eastern United States 

Mark Hudy* and Teresa M. Thieling<br>U.S. Forest Service, Fish and Aquatic Ecology Unit, James Madison University, Mail Stop Code 7801, Harrisonburg, Virginia 22807, USA<br>Nathaniel Gillespie<br>Trout Unlimited, Arlington, Virginia 22209-3801, USA

Eric P. Smith<br>Department of Statistics, Virginia Polytechnic Institute, Blacksburg, Virginia 24061, USA


#### Abstract

We examined and summarized existing knowledge regarding the distribution and status of selfsustaining populations of brook trout Salvelinus fontinalis at the subwatershed scale (mean subwatershed area $=8,972 \mathrm{ha}$ ) across their native range in the eastern USA. This region represents approximately $25 \%$ of the species' entire native range and $70 \%$ of the U.S. portion of the native range. This assessment resulted in an updated and detailed range map of historical and current brook trout distribution in the study area. Based on known and predicted brook trout status, each subwatershed was classified according to the percentage of historical brook trout habitat that still maintained self-sustaining populations. We identified 1,660 subwatersheds ( $31 \%$ ) in which over $50 \%$ of brook trout habitat was intact; 1,859 subwatersheds ( $35 \%$ ) in which less than $50 \%$ of brook trout habitat was intact; 1,482 subwatersheds ( $28 \%$ ) from which self-sustaining populations were extirpated; and 278 subwatersheds ( $5 \%$ ) where brook trout were absent but the explanation for the absence was unknown (i.e., either extirpation from or a lack of historical occurrence in those subwatersheds). A classification and regression tree using five core subwatershed metrics (percent total forest, sulfate and nitrate deposition, percent mixed forest in the water corridor, percent agriculture, and road density) was a useful predictor of brook trout distribution and status, producing an overall correct classification rate of $71 \%$. Among the intact subwatersheds, $94 \%$ had forested lands encompassing over $68 \%$ of the land base. Continued habitat loss from land use practices and the presence of naturalized exotic fishes threaten the remaining brook trout populations. The distribution of brook trout subwatershed status and related threshold metrics can be used for risk assessment and prioritization of conservation efforts.


Evaluations of the integrity of watersheds over the native range of brook trout are needed to guide decision makers, managers, and the public in setting priorities for watershed-level conservation, restoration, and monitoring programs. The Eastern Brook Trout Joint Venture (EBTJV), a consortium of 17 state agencies, 6 federal agencies, and numerous conservation organizations (EBTJV 2006), conducted a population status assessment of brook trout Salvelinus fontinalis because of concerns over declining or locally extirpated populations within the species' native range in the eastern USA. Historical and current land use practices (King 1937, 1939; Lennon 1967; Kelly et al. 1980; Nislow and Lowe 2003), changes in water quality (Fiss and Carline 1993; Gagen et al. 1993;

[^0]Clayton et al. 1998; Hudy et al. 2000; Driscoll et al. 2001), elevated water temperatures (Meisner 1990), the spread of exotic and nonnative fishes (Moore et al. 1983, 1986; Larson and Moore 1985; Strange and Habera 1998), fragmentation of habitats by dams and roads (Belford and Gould 1989; Gibson et al. 2005), habitat impairment and destruction (e.g., stream channelization, poor riparian management, and sedimentation; Curry and MacNeill 2004), and natural stochastic events (Roghair et al. 2002) have eliminated or severely reduced brook trout populations at a local or regional scale (Bivens et al. 1985; SAMAB 1996a, 1996b; Galbreath et al. 2001; Habera et al. 2001; McDougal et al. 2001). The last century has been a period of particularly dramatic change (MacCrimmon and Campbell 1969; Jenkins and Burkhead 1993; Marschall and Crowder 1996; Yarnell 1998). Construction of over 75,000 dams (USACE 1998) and more than 1.61 million km of roads (Navtech 2001) and an increase of 90 million residents (U.S. Census

Bureau 2002) have occurred in the study area over the last 100 years. For an average subwatershed (i.e., sixthlevel hydrologic unit watersheds; Seaber et al. 1987; McDougal et al. 2001; USEPA 2002; USGS 2002; NRCS 2005), $30 \%$ of the area is devoted to human land uses (USGS 2004b; Thieling 2006). However, local extirpations due to human activities have occurred both historically and in the present day (Hudy et al. 2006).

The cumulative impacts of historical and current perturbations have not been evaluated at a large scale. Large-scale assessments for many aquatic species have been useful in identifying and quantifying problems, information gaps, restoration priorities, and funding needs (Williams et al. 1993; Davis and Simon 1995; Frissell and Bayles 1996; Warren et al. 1997; Master et al. 1998). Previous landscape-scale studies of bull trout S. confluentus (Rieman et al. 1997) and Pacific salmon (Thurow et al. 1997) have been useful in developing large-scale conservation and restoration efforts and have increased public awareness of and funding for these impaired resources. Our goal was to determine the distribution, status, and perturbations of brook trout in lotic habitats throughout their native range in the eastern USA. Our approach was based on a summary of current knowledge of self-sustaining brook trout populations, as provided by more than 23 state and federal agencies that manage brook trout in this region.

Specific objectives were to (1) classify each subwatershed based on the percentage of habitat that still maintained self-sustaining brook trout populations, (2) develop a model that can be used by land managers and fisheries biologists to predict brook trout status in areas where status is unknown, and (3) determine whether cutoffs exist for subwatershed metrics that identify changes in brook trout status.

## Methods

Study area and assessment scale.-We summarized existing knowledge regarding the distribution and status of self-sustaining brook trout populations across the native range in the eastern USA (from Ohio eastward), a region that represents approximately $25 \%$ of the species' entire native range and $70 \%$ of the U.S. portion of the native range. We created a $50-\mathrm{km}$ buffer zone around a 1969 map of the species' native distribution in the eastern USA (developed from fish collections and personal communications with fisheries experts; MacCrimmon and Campbell 1969) and classified all 11,754 subwatersheds (mean area $=$ 8,927 ha, $\mathrm{SD}=7,589 \mathrm{ha}$ ) that were situated wholly or partially within the map and buffer zone (Figure 1).

We used subwatersheds for this assessment because (1) they are the smallest watershed units that are currently delineated with nationally defined protocols,


Figure 1.-Map indicating the historical range of brook trout in the eastern USA (shaded area; includes a $50-\mathrm{km}$ buffer zone around the range; from MacCrimmon and Campbell 1969), where brook trout population status in subwatersheds was evaluated. The study area includes Maine (ME), New Hampshire (NH), Vermont (VM), Massachusetts (MA), Rhode Island (RI), Connecticut (CT), New York (NY), Ohio (OH), Pennsylvania (PA), New Jersey (NJ), West Virginia (WV), Maryland (MD), Delaware (DE), Virginia (VA), Tennessee (TN), North Carolina (NC), and South Carolina (SC).
(2) they are of great interest for land management (McDougal et al. 2001), and (3) the scale of these units allow for the reasonable development of conservation management plans (Moyle and Yoshiyama 1994; Master et al. 1998). Larger watersheds (fourth-level units) were determined by managers to be of little value in managing and restoring brook trout (D. Beard, U.S. Geological Survey, personal communication), and the stream segment scale was designated as too fine because of the high percentage of segments with little or no data ( $>375,000$ segments in the study area). In cases where subwatersheds were not finalized, we used the latest available drafts from the Natural Resources Conservation Service (U.S. Department of Agriculture). Subwatershed-level delineations were not available for New York State at the time of this assessment, so we used fifth-level watersheds, which averaged approximately twice the average subwatershed size within the remainder of the study area.

TABLE 1.—Definitions of subwatershed classifications based on the current presence of self-sustaining brook trout populations in historical (pre-European settlement) brook trout habitat (Hudy et al. 2006); classifications were used in a dichotomous key for determining brook trout population status in a subwatershed. All categories designated as "predicted" include subwatersheds from the unknown and present-qualitative classifications.

| Classification category | Description |
| :--- | :--- |
| Extirpated | All self-sustaining brook trout populations no longer exist in the subwatershed. |
| Predicted extirpated | All self-sustaining populations are predicted to be extirpated from the subwatershed. |
| Reduced | Of the historical brook trout habitat, $50-99 \%$ no longer supports self-sustaining populations. |
| Predicted reduced | Of the historical habitat, $50-99 \%$ is predicted to no longer support self-sustaining populations. |
| Intact | Of the historical habitat, over $50 \%$ currently supports self-sustaining populations. |
| Predicted intact | Of the historical habitat, over $50 \%$ is predicted to currently support self-sustaining populations. |
| Absent-unknown | Brook trout are currently absent; historical status is unknown. |
| Present-qualitative | No quantitative data exist, or quantitative data are older than 10 years; available qualitative data show |
|  | that self-sustaining populations are present. |
| Unknown | No data are available, or there are not enough data to classify the subwatershed into any other category. |

Classification of subwatersheds.-We used a myriad of agency databases $(N>25)$ with different objectives, methods, completeness, quality, and resolution, which made some questions difficult to answer at the scale of the study area. The lowest common denominator for most subwatersheds was the location and extent of selfsustaining brook trout populations. Consequently, we used a classification system designed to consistently classify subwatersheds throughout the study area based on the percentage of habitat that still maintained selfsustaining brook trout populations. This approach eliminated finer-scale data that were not available for every subwatershed.

We developed a dichotomous key to classify subwatersheds based on brook trout distribution (Hudy et al. 2006; Appendix). Each couplet in the key was designed to be mutually exclusive, and definitions and rules were consistent. The benchmark was selfsustaining brook trout populations under historical (pre-European settlement) conditions, and subwatersheds were categorized based on work by Hudy et al. (2006; Table 1).

We reviewed existing databases but limited the use of qualitative (presence-absence) data or data older than 10 years in establishing historical presence. All subwatershed classifications were initially based strictly on data provided to the authors; later, subwatersheds were classified based on discussions with local experts during site visits. Two authors independently classified each subwatershed after making additional enquiries with local experts. If there was disagreement in the classification, all information was again run through the classification key to determine whether an agreement could be reached. If agreement could not be reached or if data were insufficient to distinguish among classification categories, then the subwatershed was classified as either unknown or present-qualitative (Table 1). The on-site classification process changed the original classifications $3 \%$ of the time on average
(range by state $=0-15 \%$ ). Changes usually were made because additional data became available or because interpretation of the original data was discovered to be incorrect. Authors independently agreed on the initial classification category $93 \%$ of the time; for $90 \%$ of subwatersheds, very little discussion or analysis was required to reach a consensus.

We developed several rules to consistently determine whether self-sustaining populations were supported by or lost from the brook trout habitats within each subwatershed (Appendix):
(1) The presence of self-sustaining, nonnative coldwater fish species in a habitat within the native range of brook trout was considered evidence that brook trout should have occurred in that habitat (the exception was cold tailwater habitats in previously warmwater streams).
(2) Warmwater habitats and transient habitats that never supported spawning or extended rearing and that functioned only as migration corridors, staging habitats, or wintering areas for moving fish were not included in calculations of the percentage of habitat from which self-sustaining brook trout populations were lost.
(3) The documented loss of self-sustaining brook trout populations based on current or historical reference data was used to indicate brook trout habitat loss.
(4) Nonnative coldwater species making up over $90 \%$ of the coldwater fish biomass or density in a given habitat was considered evidence that the selfsustaining brook trout population was lost.
(5) Habitats in which brook trout carrying capacity was reduced by greater than $90 \%$ (based on historical or reference data within the subwatershed) were considered to have lost their selfsustaining populations.
(6) Habitats with documented changes in water
chemistry (due to acid mine drainage, acid rain, etc.) or water temperature (due to habitat alterations from dams, riparian habitat loss, channelization, etc.) were assumed to no longer support self-sustaining populations.
(7) Coldwater lotic habitats that were inundated by reservoirs and converted to warmwater lentic habitats were designated as having lost selfsustaining populations of brook trout.

Candidate metrics, metric screening, metric calcu-lation.-During an on-site visit, fisheries biologists familiar with the area were asked to list all perturbations and potential threats to brook trout populations in each subwatershed where the species was known to have occurred (Hudy et al. 2006). These threats were derived from each individual's professional opinion, so they were not necessarily repeatable or consistent among experts. However, we used this information to identify potential quantifiable subwatershed metrics or surrogates for model development.

We calculated and evaluated 63 candidate metrics (Table 2) that were based on whole subwatersheds and water corridors within subwatersheds, and these metrics were used instead of site-specific variables (Moyle and Randall 1998). Subwatershed-level metrics can provide an indicator of watershed health when many anthropogenic factors potentially contribute to a problem, and such metrics can assist in identification of key limiting factors (Barbour et al. 1999; McCormick et al. 2001). Many candidate metrics were eliminated from consideration because data were not available at a suitable resolution for all subwatersheds.

The candidate metrics were screened in a manner similar to that described by Hughes et al. (1998) and McCormick et al. (2001); screening was used to reduce the number of metrics, remove irrelevant variables, and determine which metrics were most likely to be predictive of brook trout status (Thieling 2006). Candidate metrics underwent four consecutive tests (completeness, range, redundancy, and responsiveness). First, screening for completeness was used to ensure that the measurements would be comparable throughout the study area. Metrics were excluded if appropriate data were not available for the entire study area or if they did not have consistent resolution or definitions. Second, metrics with a small range of values ( $<30$ unique values, and a majority in one or two values) were eliminated because they would not be useful for indicating differences in subwatershed characteristics. Third, when two metrics were highly correlated ( $|r|>0.80$ ), one metric was removed to eliminate redundancy. We used professional judgment to select which metric to retain based on comprehen-
sibility, repeatability, and usefulness to land managers. Fourth, the responsiveness of the metrics to brook trout subwatershed status classifications was measured using rankings of $P$-values from Wald's chi-square test for significance of logistic regression parameters and analysis of variance for significant differences among metric means (Sokal and Rohlf 1995; Hosmer and Lemeshow 2000). The metric screening helped prevent spurious correlations, overanalysis, and interpretation problems. Metrics were obtained or developed in a geographical information system (GIS) to allow for data analysis in a spatial context (Lo and Yeung 2002).

The metric screening reduced the pool of candidates from the original 63 metrics to 5 core metrics (Table 2) that were defined and calculated as follows (see EBTJV [2006] and Thieling [2006] for more details and metadata describing core and noncore metrics):
(1) TOTAL_FOREST is the sum of the percentages of deciduous, evergreen, and mixed forest types in the National Land Cover Dataset (NLCD; USGS 2004b). The NLCD was produced using satellite imagery data acquired in $30-\mathrm{m}$ grid coverage (USGS 2005).
(2) PERCENT_AG is the sum of the percentages of all agricultural land use types from the NLCD.
(3) MIXED_FOREST2 is the percentage of mixed forest (NLCD) within the water corridor of the subwatershed. The water corridor, defined via the National Hydrography Dataset (1:100,000 scale; USGS 2004a), included the area within 100 m of each sides of a stream or within the 100 m surrounding a lake.
(4) ROAD_DN is the road density ( km of road $/ \mathrm{km}^{2}$ of land; hereafter, $\mathrm{km} / \mathrm{km}^{2}$ ) of all roads within the subwatershed and is based on data developed from the improved Topological Integrated Geographic Encoding and Referencing System (Navtech 2001).
(5) DEPOSITION is the sum ( $\mathrm{kg} / \mathrm{ha}$ ) of mean sulfate $\left(\mathrm{SO}_{4}\right)$ and mean nitrate $\left(\mathrm{NO}_{3}\right)$ deposition in the subwatershed, as derived from 2004 wet deposition grid data (National Atmospheric Deposition Program 2005). The deposition grids had a $2.5-\mathrm{km}$ cell resolution and contained spatially interpolated wet deposition.

Modeling approaches and selection.-The relationships between brook trout status classification and subwatershed- or water corridor-level metrics were modeled (CART version 9; Steinberg and Colla 1997) via a trinomial variable describing brook trout status (i.e., extirpated, reduced, or intact; Thieling 2006). The categorical status variable was the dependent variable, and subwatershed or water corridor metrics were the

TABLE 2.-Screening results and descriptions of subwatershed- and water corridor-level candidate metrics used to examine brook trout self-sustaining population status and distribution in the eastern USA. All variables were screened based on four tests (completeness, range, redundancy, and responsiveness). Five core variables met the criteria and were used for further analysis. Excluded variables are those indicated as redundant (highly correlated with another metric; $|r|>0.80$ ), unresponsive to subwatershed status classifications, or having a narrow range of values ( $<30$ unique values).

| Screening result | Subwatershed metric code | Description |
| :---: | :---: | :---: |
| Core | DEPOSITION | Derived from sum of mean $\mathrm{SO}_{4}$ and $\mathrm{NO}_{3}$ deposition (kg/ha) in the subwatershed |
|  | MIXED_FOREST2 | Percentage mixed forested lands in the water corridor |
|  | PERCENT_AG | Derived from subwatershed sum of agricultural uses |
|  | ROAD_DN | Road density ( km of road/ $\mathrm{km}^{2}$ of land) |
|  | TOTAL_FOREST | Derived from subwatershed sum of forested lands |
| Redundant | EVERGREEN | Percentage evergreen forest in the subwatershed |
|  | EVERGREEN2 | Percentage evergreen forest in the water corridor |
|  | MIXED_FOREST | Percentage mixed forested lands in the subwatershed |
|  | LATITUDE | Latitude measured in decimal degrees |
|  | LONGITUDE | Longitude measured in decimal degrees |
|  | NO3_Mean | Mean $\mathrm{NO}_{3}$ deposition (kg/ha) |
|  | PASTURE_HAY | Percentage pasture or hay in the subwatershed |
|  | PASTURE_HAY2 | Percentage pasture or hay in the water corridor |
|  | PERCENT_AG2 | Derived from water corridor sum of agricultural uses |
|  | PRCNT_HUMAN | Derived from subwatershed sum of percentage human uses |
|  | PRCNT_HUMAN2 | Derived from water corridor sum of percentage human uses |
|  | STRM_XINGS | Number of road crossings per kilometer of stream |
|  | TOTAL_FOREST2 | Derived from water corridor sum of forested lands |
| Unresponsive | DAMS_SQKM | Number of dams per square kilometer |
|  | DECIDUOUS | Percentage deciduous forest in the subwatershed |
|  | DECIDUOUS2 | Percentage deciduous forest in the water corridor |
|  | ELEV_MEAN | Mean elevation |
|  | ELEV_MIN | Minimum elevation |
|  | ELEV_MAX | Maximum elevation |
|  | EXOTICS | Weighted number of exotic fish species within the subwatershed |
|  | HERB_WETLNDS | Percentage herbaceous wetlands in the subwatershed |
|  | HERB_WTLNDS2 | Percentage herbaceous wetlands in the water corridor |
|  | HIGH_RES | Percentage high-intensity residential lands in the subwatershed |
|  | HIGH_RES2 | Percentage high-intensity residential lands in the water corridor |
|  | INDUST_TRANS | Percentage commercial, industrial, or transportation in the subwatershed |
|  | INDUST_TRANS2 | Percentage commercial, industrial, or transportation in the water corridor |
|  | LOW_RES | Percentage low-intensity residential in the subwatershed |
|  | LOW_RES2 | Percentage low-intensity residential in the water corridor |
|  | OPEN_WTR | Percentage open water in the subwatershed |
|  | OPEN_WTR2 | Percentage open water in the water corridor |
|  | ORCH_VINEYRD | Percentage orchards, vineyards, or other in the subwatershed |
|  | ORCH_VINYRD2 | Percentage orchards, vineyards, or other in the water corridor |
|  | Pop_Density | Mean human population density (number/ $\mathrm{km}^{2}$ ) |
|  | PRCNT_RES2 | Derived from the sum of high and low residential use in the water corridor |
|  | QRY_MINE_GPIT | Percentage quarries, strip mines, or gravel pits in the subwatershed |
|  | QRY_MINE_GPIT2 | Percentage quarries, strip mines, or gravel pits in the water corridor |
|  | ROW_CROPS | Percentage row crops in the subwatershed |
|  | ROW_CROPS2 | Percentage row crops in the water corridor |
|  | SHRUBLAND | Percentage shrubland in the subwatershed |
|  | SOIL_GRTR5 | Percentage of soils in the water corridor with a $\mathrm{pH} \geq 5.0$ |
|  | SOIL_LESS5 | Percentage of soils in the water corridor with a $\mathrm{pH}<5.0$ |
|  | SHRUBLAND2 | Percentage shrubland in the water corridor |
|  | SMALL_GRAINS | Percentage small grains in the subwatershed |
|  | SMALL_GRAINS2 | Percentage small grains in the water corridor |
|  | TRANSITIONAL | Percentage transitional (areas of sparse vegetation) in the subwatershed |
|  | TRANSITIONAL2 | Percentage transitional in the water corridor |
|  | URBAN_REC | Percentage urban or recreational grasses in the subwatershed |
|  | URBAN_REC2 | Percentage urban or recreational grasses in the water corridor |
|  | WOOD_WETLNDS | Percentage wooded wetlands in the subwatershed |
|  | WOOD_WTLNDS2 | Percentage wooded wetlands in the water corridor |
| Narrow range | BAREROCK | Percentage bare rock in the subwatershed |
|  | BAREROCK2 | Percentage bare rock in the water corridor |
|  | FALLOW | Percentage fallow fields in the watershed |
|  | FALLOW2 | Percentage fallow fields in the water corridor |
|  | GRASSLAND | Percentage natural grasslands or herbaceous lands in the subwatershed |
|  | GRASSLAND2 | Percentage natural grasslands or herbaceous lands in the water corridor |

predictor variables. Numerous models and methods were developed using all candidate metrics, and known status classifications were used as a training set. A detailed evaluation of all methods tested is given by Thieling (2006).

Although many modeling methods showed promise, classification trees were chosen by the EBTJV steering committee as the best method for reporting and analysis because (1) thresholds and interactions are relatively easy to interpret, display, and explain to natural resource managers, (2) a higher overall correct classification rate was provided, (3) correct classification rates were well balanced among categories, and (4) very few assumptions and no data transformations were required. A classification tree is a type of decision tree that uses input variable values to successively split data into more-homogenous groups (Breiman et al. 1984; Clark and Pregibon 1992). Classification trees are similar to taxonomic keys in that they consist of a dichotomous rule set that is produced through recursive partitioning. Data are split into two groups based on a single predictor value (determined from the input variables) that produces the greatest difference in the resulting groups. Each juncture, or node, is considered in isolation without anticipating how the next node will be split (Neville 1999). These groups are then partitioned again based on a different splitting criterion, and the process continues until data can no longer be divided, resulting in a terminal node. In our case, the metrics were the input variables and subwatershed classifications based on brook trout status were the terminal nodes. Classification trees used the given measurements of subwatershed metrics in known classifications to develop splitting criteria for predicting classifications of subwatersheds with unknown brook trout status. Through the development of classification trees, one can also determine the metric values that most prominently influence or predict the terminal nodes or classifications. Resubstitution and 10 -fold cross-validation methods were used to evaluate the prediction errors of the classification trees (Breiman et al. 1984). If the full classification tree was too large to display, we used a "pruned" classification tree in presenting results. Classification trees were pruned by deleting the terminal and lower (near-terminal) nodes with small sample sizes that minimally contributed to overall accuracy (based on the Gini index as an optimization function in CART; Steinberg and Colla 1997).

## Results

Based on our analyses, 1,660 subwatersheds (31\%) within the study area were classified as having intact habitat (known or predicted) that supported self-
sustaining brook trout populations, 1,859 subwatersheds ( $35 \%$ ) were classified as having reduced habitat (known or predicted) for self-sustaining populations, and 1,482 subwatersheds ( $28 \%$ ) were classified as having habitat (known or predicted) from which brook trout were extirpated (Figure 2; Table 3). Brook trout were known to be absent in another 278 subwatersheds ( $5 \%$ ), but the explanation for the absence (i.e., extirpation or a lack of historical occurrence) was unknown. We determined that brook trout were absent from an additional 5,837 subwatersheds within the potential historical range and buffer zone, because these areas historically lacked habitat that would have supported self-sustaining populations. Brook trout occurred in every state; the percentage of subwatersheds with extirpated populations varied from less than $1 \%$ (Maine and New Hampshire) to more than $40 \%$ (Maryland, Tennessee, North Carolina, South Carolina, and Georgia; Table 3). The percentage of subwatersheds with intact habitat that supported self-sustaining populations ranged from a high of $38 \%$ (Virginia) to a low of $3 \%$ (Tennessee, North Carolina, South Carolina, and Georgia; Table 3). Maine ( $68 \%$ ) and New Hampshire ( $70 \%$ ) had the highest percentages of subwatersheds that were described only by qualitative data and required prediction of status classification.

The core metric distributions were examined in relation to all subwatersheds and individual classification categories (Figures 3-7). Of the subwatersheds with intact habitat, $94 \%$ had TOTAL_FOREST values exceeding $68 \%$ (Figure 3), and the majority had ROAD_DN values less than $2.0 \mathrm{~km} / \mathrm{km}^{2}$ (Figure 4). Only $17 \%$ of subwatersheds with intact habitat had PERCENT_AG values greater than $19 \%$, whereas $74 \%$ of the subwatersheds from which self-sustaining populations were extirpated had PERCENT_AG values greater than $12 \%$ (Figure 5). Our classification tree model had overall correct classification rates of $71 \%$ (resubstitution method) and $62 \%$ (cross validation method); within status categories, correct classification rates were $76 \%$ (resubstitution) and $69 \%$ (cross validation) for subwatersheds with extirpated populations, $64 \%$ and $51 \%$ for subwatersheds with reduced brook trout habitat, and $79 \%$ and $72 \%$ for subwatersheds with intact brook trout habitat. In classification tree models, the metrics and splitting criteria that most prominently influence or predict the terminal nodes or classifications are found in the top tier of nodes. In our analysis, the metrics (and associated values) in the top nodes were TOTAL_FOREST ( $68.1 \%$ ) in node 1 , DEPOSITION in nodes $2(27.9 \mathrm{~kg} / \mathrm{ha})$ and $6(18.5 \mathrm{~kg} /$ ha), and PERCENT_AG (27.1\%) in node 3 (Table 4; Figure 8). Among the 1,664 subwatersheds in which brook trout status was categorized as present-qualita-


Figure 2.-Distribution of brook trout status classifications (defined in Table 1; status was predicted or known) in subwatersheds throughout the species' eastern U.S. range and a $50-\mathrm{km}$ buffer zone (see Figure 1).
tive or unknown (predicted), the model predicted that $399(24 \%)$ would be areas of brook trout extirpation, $378(23 \%)$ would have reduced habitat, and $887(53 \%)$ would have intact habitat (see Table 3 and Figure 2 for spatial distribution; the absent-unknown category was not predicted in this analysis).

## Discussion

This assessment resulted in a map of historical and current brook trout distribution in the eastern USA that
is updated and of a finer scale than previous range maps, which have categorized entire river systems as containing brook trout even though the species was limited to only select subwatersheds (e.g., those in higher elevations; MacCrimmon and Campbell 1969). Understanding the current distribution and population status at an appropriate scale is one of the key tools in the conservation of a given species (Williams et al. 1993; Warren et al. 1997). By combining known and predicted brook trout status in subwatersheds within

TABLE 3.-Status classification of eastern U.S. subwatersheds (number of subwatersheds in each category; state abbreviations defined in Figure 1) based on the amount of historical (pre-European settlement) brook trout habitat that currently maintains selfsustaining populations (classifications defined in Table 1).

|  | Status |  |  |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| State | Intact | Predicted <br> intact | Reduced | Predicted <br> reduced | Extirpated | Predicted <br> extirpated | Absent | Never <br> occurred |
| ME | 222 | 611 | 88 | 66 | 5 | 0 | 0 | 12 |
| NH | 34 | 151 | 13 | 80 | 0 | 1 | 0 | 1 |
| VT | 95 | 27 | 85 | 12 | 6 | 4 | 0 | 27 |
| MA | 30 | 19 | 80 | 58 | 20 | 10 | 4 | 19 |
| RI | 0 | 0 | 0 | 10 | 0 | 3 | 18 | 0 |
| CT | 19 | 0 | 127 | 4 | 29 | 4 | 0 | 0 |
| NY | 87 | 61 | 148 | 66 | 115 | 62 | 0 | 36 |
| NJ | 3 | 0 | 24 | 7 | 31 | 19 | 0 | 667 |
| PA | 134 | 9 | 507 | 43 | 444 | 168 | 0 | 72 |
| OH | 0 | 0 | 3 | 0 | 1 | 0 | 7 | 71 |
| MD | 8 | 2 | 42 | 6 | 82 | 4 | 0 | 175 |
| WV | 20 | 2 | 130 | 7 | 24 | 3 | 248 | 283 |
| VA | 115 | 5 | 56 | 10 | 148 | 57 | 0 | 836 |
| NC | 3 | 0 | 116 | 5 | 95 | 17 | 0 | 1,301 |
| SC | 0 | 0 | 7 | 0 | 12 | 8 | 0 | 943 |
| TN | 3 | 0 | 33 | 4 | 18 | 23 | 0 | 985 |
| GA | 0 | 0 | 22 | 0 | 53 | 16 | 0 | 409 |
| Total | 773 | 887 | 1,481 | 378 | 1,083 | 399 | 278 | 5,837 |

the study area, we provide a more-complete picture that can be used by natural resource managers, nongovernment organizations, and the public.

Most of the data used here was provided by state and federal agencies and had not been published or peer
reviewed. Despite the criteria developed for status classification, there remains some element of subjectivity. It was impossible to generate a comprehensive review without such data (Reiman et al. 1997). We attempted to limit errors, reduce subjectivity, and


Classification Groups
Figure 3.-Box plot of the percentage of forested lands (TOTAL_FOREST in Table 2) within eastern U.S. subwatersheds classified based on brook trout population status (defined in Table 1) and for all subwatersheds combined. Dashed line is the mean, solid line is the median, and the box represents $50 \%$ of all values.


Classification Groups
Figure 4.-Box plot of road density ( km of road $/ \mathrm{km}^{2}$ of land; ROAD_DN in Table 2) within eastern U.S. subwatersheds classified based on brook trout population status (defined in Table 1) and for all subwatersheds combined. See Figure 3 for explanation of box plot components.


Figure 5.-Box plot of the percentage of area in agricultural land use (PERCENT_AG in Table 2) within eastern U.S. subwatersheds classified based on brook trout population status (defined in Table 1) and for all subwatersheds combined. See Figure 3 for explanation of box plot components.


## Classification Groups

FIgure 6.-Box plot of the combined sulfate $\left(\mathrm{SO}_{4}\right)$ and nitrate $\left(\mathrm{NO}_{3}\right)$ deposition ( $\mathrm{kg} / \mathrm{ha}$; DEPOSITION in Table 2) within eastern U.S. subwatersheds classified based on brook trout population status (defined in Table 1) and for all subwatersheds combined. See Figure 3 for explanation of box plot components.
provide consistency in data by using consistency rules and data standards (quality and age); developing broad classification categories; and employing standard, validated procedures in consulting experts.

Although the core metrics were effectively used in combination to predict status classification, these metrics are not the only factors influencing brook trout distribution. Exclusion from our final model does not necessarily mean that a specific metric is biologically unimportant in its influence on brook trout. Some metrics may have greater influence on brook trout populations and are better predictors at different scales (Kocovsky and Carline 2006). For example, Rashleigh et al. (2005) were able to predict brook trout presenceabsence in stream segments in the Mid-Atlantic Highlands with a correct classification rate of $79 \%$ by use of depth, temperature, substrate, percent riffles, cover, and riparian vegetation. Global warming is another example of a factor that has not yet been linked to brook trout extirpations but potentially could be important in the future at a different scale of analysis.

Limitations of models in predicting brook trout status can be evaluated by mapping the misclassified subwatersheds; overall, $28 \%$ of the subwatersheds were misclassified (those with extirpated populations: $24 \%$;
those with a reduced amount of habitat that maintained self-sustaining populations: $36 \%$; those with intact habitat: $20 \%$ )). Most of the misclassified subwatersheds contained reduced habitat, which suggests that the models are better at separating the two extremes (extirpation or intact habitat) of status. Misclassifications may also be due to historical factors. The models use current subwatershed characteristics, even though past land use practices may have caused brook trout extirpation from the subwatershed. Even when past land use practices have been remedied, it may take more than 50 years for the stream habitat to recover (Harding et al. 1998). Cases in point are subwatersheds that were predicted to have intact or reduced brook trout habitat but in fact were sites of extirpation. This type of misclassification predominately occurred for subwatersheds in the Southeast, where historical brook trout populations were extirpated through abusive land use practices (King 1937, 1939). Today, many of these subwatersheds are protected (National Forest, National Park, and state lands) and have core metric values that would suggest the presence of intact habitat for brook trout (i.e., high TOTAL_FOREST, low PERCENT_ AG). However, as past land use practices abated and these subwatersheds recovered, rainbow trout Onco-


Figure 7.-Box plot of the percentage of mixed forestlands in the water corridor (MIXED_FOREST2 in Table 2) within eastern U.S. subwatersheds classified based on brook trout population status (defined in Table 1) and for all subwatersheds combined. See Figure 3 for explanation of box plot components.
rhynchus mykiss were stocked and became naturalized (King 1937, 1939; Lennon 1967; Kelly et al. 1980). Naturalized rainbow trout now preclude the restoration of brook trout in these subwatersheds, despite the
recovery of habitat. Subwatersheds that were predicted to be areas of extirpation but were known to have reduced or intact habitat supporting self-sustaining populations had greater geospatial variability. The

Table 4.-Subwatershed numbers (total $n=3,337$ ) and status probability at each terminal node of a classification tree (Figure 8) used to predict brook trout population status within subwatersheds of the eastern USA (status classifications defined in Table 1). Splitting criteria are based on five core metrics (further described in Table 2): total forested land (TF; \%), nitrate and sulfate deposition ( $\mathrm{D} ; \mathrm{kg} / \mathrm{ha}$ ), road density ( $\mathrm{RD} ; \mathrm{km} / \mathrm{km}^{2}$ ), agricultural land use (AG; \%), and mixed forested land in the water corridor (MF; \%). Only subwatersheds with known status (based on quantitative data) are included here.

| Terminal node | Number of subwatersheds | Splitting criteria | Probability of status |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | Extirpated | Reduced | Intact |
| 1 | 19 | TF $<68.1 ; \mathrm{D}<27.9 ; \mathrm{AG}<27.1 ; \mathrm{D}<17.5$ | 0.0 | 27.5 | 72.5 |
| 2 | 183 | $\mathrm{TF}<68.1 ; \mathrm{D}<27.9 ; \mathrm{AG}<27.1 ; \mathrm{D}>17.5$ | 23.4 | 62.9 | 13.7 |
| 3 | 100 | $\mathrm{TF}<68.1 ; \mathrm{D}<27.9 ; \mathrm{AG}>27.1 ; \mathrm{MF}<15.5$ | 56.4 | 14.9 | 28.6 |
| 4 | 40 | $\mathrm{TF}<68.1 ; \mathrm{D}<27.9 ; \mathrm{AG}>27.1 ; \mathrm{MF}>15.5$ | 4.0 | 11.7 | 84.3 |
| 5 | 947 | TF $<68.1$; $\mathrm{D}>27.9$ | 72.9 | 24.2 | 2.9 |
| 6 | 267 | $\mathrm{TF}>68.1 ; \mathrm{D}<18.5$ | 0.9 | 9.1 | 90.0 |
| 7 | 351 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}<1.67 ; \mathrm{D}<28.1 ; \mathrm{TF}<94.5$ | 10.8 | 24.7 | 64.4 |
| 8 | 25 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}<1.67 ; \mathrm{D}<28.1 ; \mathrm{TF}>94.5 ; \mathrm{D}<24.7$ | 10.3 | 17.6 | 72.1 |
| 9 | 103 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}<1.67 ; \mathrm{D}<28.1 ; \mathrm{TF}>94.5 ; \mathrm{D}>24.7$ | 35.8 | 46.0 | 18.2 |
| 10 | 345 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}<1.67 ; \mathrm{D}>28.1 ; \mathrm{TF}<89.9$ | 20.2 | 59.9 | 19.8 |
| 11 | 104 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}<1.67 ; \mathrm{D}>28.1 ; \mathrm{TF}>89.9 ; \mathrm{D}<33.5$ | 23.4 | 49.8 | 26.8 |
| 12 | 237 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}<1.67 ; \mathrm{D}>28.1 ; \mathrm{TF}>89.9 ; \mathrm{D}>33.5$ | 1.2 | 35.8 | 63.0 |
| 13 | 47 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}>1.67 ; \mathrm{D}<22.9$ | 5.4 | 83.2 | 11.4 |
| 14 | 63 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}>1.67 ; \mathrm{D}>22.9 ; \mathrm{D}<25.9 ; \mathrm{AG}<16.8$ | 18.8 | 47.6 | 33.6 |
| 15 | 32 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}>1.67 ; \mathrm{D}>22.9 ; \mathrm{D}<25.9 ; \mathrm{AG}>16.8$ | 30.2 | 12.1 | 57.7 |
| 16 | 39 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}>1.67 ; \mathrm{D}>22.9 ; \mathrm{D}>25.9 ; \mathrm{D}<34.9 ; \mathrm{RD}<1.84$ | 21.8 | 43.8 | 34.4 |
| 17 | 188 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}>1.67 ; \mathrm{D}>22.9 ; \mathrm{D}>25.9 ; \mathrm{D}<34.9 ; \mathrm{RD}>1.84$ | 55.3 | 35.7 | 9.1 |
| 18 | 247 | $\mathrm{TF}>68.1 ; \mathrm{D}>18.5 ; \mathrm{RD}>1.67 ; \mathrm{D}>22.9 ; \mathrm{D}>25.9 ; \mathrm{D}>34.9$ | 26.1 | 55.6 | 18.3 |



Figure 8.-A classification tree for predicting brook trout population status (extirpated, reduced, intact; defined in Table 1) in eastern U.S. subwatersheds; the tree was developed based on only those subwatersheds for which status was known (from quantitative data). At node 1, all subwatersheds are split based on a TOTAL_FOREST (see Table 2) splitting criterion of $68.1 \%$. At each subsequent node, the subwatersheds are split again. Subwatersheds proceed through the splitting criteria until they reach a terminal node (red boxes), where status classification is predicted with a given probability (presented below terminal nodes).
greatest concentration of these subwatersheds was in New York State, probably because the larger watershed sizes caused greater variability in the predicted probability of extirpation.

Although exotic fishes have been identified as being responsible for major past and current perturbations to brook trout populations (EBTJV 2006), a metric that represented such fishes was unresponsive to brook trout status. Our EXOTICS metric (Table 2) was developed from the number of exotic fish species within the subwatershed and from professional opinion. Smaller-scale (stream segment) data for exotic
fishes was highly variable among states, thus preventing development of a quantitative exotic metric. The unresponsiveness of the EXOTICS metric was probably attributable to a complex interaction of natural and manmade barriers, stocking history, and variability among experts in identifying exotics as a threat at the subwatershed level. Exotic fishes may be affecting brook trout at different scales throughout the species' range (e.g., stream segment scale), and subwatershedlevel analysis may not be appropriate to determine these effects.

Extirpation and presence of various brook trout life


Figure 8.-Continued.
history strategies (e.g., anadromous, adfluvial, and fluvial) were anecdotally noted during the many classification interviews with local experts. No attempt was made to distinguish among different life history strategies or to examine possible genetic differences, because these data were unavailable or unknown for over $80 \%$ of the subwatersheds. Although genetic information is important (Krueger and Menzel 1979; Stoneking et al. 1981; Perkins et al. 1993; Kriegler et al. 1995; Hayes et al. 1996; Hall et al. 2002), it was beyond the scope of our study. In addition, because of past stocking practices and the existence of multiple populations in one subwatershed, many of the potential genetic factors cannot be evaluated at the subwatershed level.

## Management Implications

Although not causal, observational data based on an examination of the box plots and splitting criteria for the classification tree may be useful to natural resource managers in setting priorities and conducting risk assessment for conservation work. Because $94 \%$ of subwatersheds with intact habitat had a TOTAL_ FOREST value greater than $68 \%$, we recommend that natural resource managers consider values below 65$70 \%$ as indicating reduced status of a subwatershed. Values of ROAD_DN greater than $1.8-2.0 \mathrm{~km} / \mathrm{km}^{2}$ are another potential threshold for determining subwatershed status. Although $47 \%$ of all subwatersheds had ROAD_DN values of $1.8 \mathrm{~km} / \mathrm{km}^{2}$ or greater, subwatersheds with intact habitat only constituted $8 \%$ of
that group (only $17 \%$ of all subwatersheds with intact status had ROAD_DN values $\geq 1.8 \mathrm{~km} / \mathrm{km}^{2}$ ). Another potential cutoff is a PERCENT_AG value of $12 \%$; only $17 \%$ of subwatersheds with intact habitat had a PERCENT_AG greater than $19 \%$, and $74 \%$ of subwatersheds with extirpated populations had a value greater than $12 \%$. We found that DEPOSITION was also an important variable. Thieling (2006) reported that $33 \mathrm{~kg} / \mathrm{ha}$ was the optimum value of DEPOSITION for producing correct classifications based on singlemetric logistic regression. However, it is possible to include subwatersheds with extirpated populations in the classification and regression tree models based on DEPOSITION values as low as $28 \mathrm{~kg} / \mathrm{ha}$. Natural resource managers should be aware when subwatersheds approach a DEPOSITION value exceeding 24 $\mathrm{kg} / \mathrm{ha}$. However, the aforementioned cutoffs are not absolute. Because of interactions with other metrics, the impact of a metric at its threshold value can either be compounded or mitigated in the classification tree model. For example, some subwatersheds with TOTAL_FOREST values less than $68 \%$ had intact status if DEPOSITION and PERCENT_AG values were low (i.e., terminal node 1; Table 4; Figure 8).

Improved inventory and monitoring are critical for tracking the successes and failures of conservation and restoration efforts and for validating the prediction models. Although this assessment produced a comprehensive, large-scale appraisal of brook trout distribution within the eastern USA, $33 \%$ of subwatersheds within the study area were not described by enough information to indicate the percentage of habitat that supported self-sustaining brook trout populations. Inventory and monitoring efforts in large sections of Maine and New Hampshire are needed.

Many of the subwatersheds classified as having reduced brook trout populations contained only one or two small populations that were restricted to isolated headwater habitats. These subwatersheds lack the redundancy and connectivity required to reestablish populations and are therefore especially prone to becoming sites of brook trout extirpation due to increased human land use impacts or natural stochastic events. Increased monitoring effort is recommended for these subwatersheds.

The future protection, restoration, and enhancement of brook trout will rely on changes in land use, control of exotics, and an improved inventory and monitoring system. Similar to large-scale assessments of salmonids in the western USA (Reiman et al. 1997), we suggest that future changes in brook trout distribution and status in the study area will be driven by changes in land use practices and habitat fragmentation. However, the unchecked spread of exotic fishes can overshadow
even the best land use practices aimed at conserving brook trout. Unfortunately, based on hundreds of interviews with local experts, the rates of many land use changes and the spread of exotic fishes exceed the frequency of monitoring or inventory efforts. Increased sampling will be needed to evaluate and monitor land use changes and the spread of exotic species. Closer monitoring of brook trout status should be a priority for long-term conservation efforts. Because funds for increased monitoring and inventory are often unavailable, reliance on predictive models may still be necessary to determine brook trout status in many areas. Once validated, core metrics should be updated every 5 years, and the models should be populated to monitor changes.

## Acknowledgments

The following biologists contributed to the project: L. Mohn, P. Bugas, and S. Reeser (Virginia); M. Gallagher, P. Johnson, G. Burr, R. Jordan, R. Brokaw, F. Bonney, D. Howatt, J. Pellerin, F. Brautigam, T. Obrey, N. Kramer, and D. Basley (Maine); D. Besler, W. Taylor, W. Humphries, K. Hining, and K. Hodgen (North Carolina); T. Green, J. Detar, J. Frederick, D. Moti, D. Arnold, B. Muomo, R. Lorson, and M. Kaufmann (Pennsylvania); D. Rankin (South Carolina); L. Keefer and T. Litts (Georgia); T. Oldham and M. Shingleton (West Virginia); J. Habera (Tennessee); R. Kirn, B. Pientka, B. Chipman, K. Cox, C. MacKenzie, and S. Roy (Vermont); D. Emerson, D. Miller, J. Viar, S. Perry, D. Grot, S. Decker, and M. Proudt (New Hampshire); N. Hagstrom and M. Humphreys (Connecticut); P. Hamilton and L. Barno (New Jersey); A. Heft, R. Morgan, M. Kline, A. Klotz, J. Mullican, and C. Gougeon (Maryland); T. Richards, A. Madden, and S. Hurley (Massachusetts); A. Burt (Ohio); A. Richardson and A. Liby (Rhode Island); D. Bishop, J. Robins, B. Hammers, F. Angold, W. Pearsall, C. Guthrie, D. Zielinski, F. Linhart, D. Cornwell, W. Elliot, L. Suprenant, R. Angyal, R. Pierce, M. Flaherty, F. Flack, R. Preall, and J. Daley (New York). Reference to trade names does not imply endorsement by the U.S. Government.

## References

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, 2nd edition. U.S. Environmental Protection Agency, Office of Water, Report EPA 841-B-99-002, Washington, D.C.
Belford, D. A., and W. R. Gould. 1989. An evaluation of trout passage through six highway culverts in Montana. North American Journal of Fisheries Management 9:437-445.
Bivens, R. D., R. J. Strange, and D. C. Peterson. 1985. Current
distribution of the native brook trout in the Appalachian region of Tennessee. Journal of the Tennessee Academy of Science 60:101-105.
Breiman, L., J. H. Friedman, R. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth, Belmont, California.
Clark, L. A., and D. Pregibon. 1992. Tree based models. Pages 377-419 in J. M. Chambers and T. J. Hastie, editors. Statistical models. Wadsworth and Brooks/Cole, South Pacific Grove, California.
Clayton, J. L., E. S. Dannaway, R. Menendez, H. W. Rauch, J. J. Renton, S. M. Sherlock, and P. E. Zurbuch. 1998. Application of limestone to restore fish communities in acidified streams. North American Journal of Fisheries Management 18:347-360.
Curry, R. A., and W. S. MacNeill. 2004. Population-level responses to sediment during early life in brook trout. Journal of the North American Benthological Society 23:140-150.
Davis, W. S., and T. P. Simon. 1995. Biological assessment and criteria: tools for watershed resource planning and decision making. Lewis Publishers, Washington, D.C.
Driscoll, C. T., G. B. Lawrence, A. J. Bulgur, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience 51:180-198.
EBTJV (Eastern Brook Trout Joint Venture). 2006. About the Eastern Brook Trout Venture. Available: www. easternbrooktrout.org. (December 2006).
Fiss, F. C., and R. F. Carline. 1993. Survival of brook trout embryos in three episodically acidified streams. Transactions of the American Fisheries Society 122:268-278.
Frissell, C. A., and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. Water Resources Bulletin 32:229240.

Gagen, C. J., W. E. Sharpe, and R. F. Carline. 1993. Mortality of brook trout, mottled sculpins, and slimy sculpins during acidic episodes. Transactions of the American Fisheries Society 122:616-628.
Galbreath, P. F., N. D. Adams, S. Z. Guffey, C. J. Moore, and J. L. West. 2001. Persistence of native southern Appalachian brook trout populations in the Pigeon River system, North Carolina. North American Journal of Fisheries Management 21:927-934.
Gibson, R. J., R. L. Haedrich, and C. M. Wernerheim. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. Fisheries 30(1):10-17.
Habera, J. W., R. J. Strange, and R. D. Bivens. 2001. A revised outlook for Tennessee's brook trout. Journal of the Tennessee Academy of Science 76:68-73.
Hall, M. R., R. P. Morgan, and R. G. Danzmann. 2002. Mitochondrial DNA analysis of mid-Atlantic populations of brook trout: the zone of contact for major historical lineages. Transactions of the American Fisheries Society 131:1140-1151.
Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Sciences of the USA 95:14843-14847.

Hayes, J. P., S. Z. Guffey, F. J. Kriegler, G. F. McCracken, and C. R. Parker. 1996. The genetic diversity of native, stocked, and hybrid populations of brook trout in the southern Appalachians. Conservation Biology 10:14031412.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edition. Wiley, New York.
Hudy, M., D. M. Downey, and D. W. Bowman. 2000. Successful restoration of an acidified native brook trout stream through mitigation with limestone sand. North American Journal of Fisheries Management 20:453-466.
Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2006. Distribution, status, and perturbations to brook trout within the eastern United States. Final report to the Eastern Brook Trout Joint Venture. Available: www. easternbrooktrout.org. (January 2007).
Hughes, R. M., P. R. Kaufmann, A. T. Herlihy, T. M. Kincaid, L. Reynolds, and D. P. Larsen. 1998. A process for developing and evaluating indices of fish assemblage integrity. Canadian Journal of Fisheries and Aquatic Sciences 55:1618-1631.
Jenkins, R. E., and N. M. Burkhead. 1993. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.
Kelly, G. A., J. S. Griffith, and R. D. Jones. 1980. Changes in distribution of trout in Great Smoky Mountains National Park, 1900-1970. U.S. Fish and Wildlife Service Technical Paper 102.
King, W. 1937. Notes on the distribution of native speckled and rainbow trout in the streams of Great Smokey Mountains National Park. Journal of the Tennessee Academy of Science 12:351-361.
King, W. 1939. A program for the management of fish resources in Great Smokey Mountains National Park. Transactions of the American Fisheries Society 68:8695.

Kocovsky, P. M., and R. F. Carline. 2006. Influence of landscape-scale factors in limiting brook trout populations in Pennsylvania streams. Transactions of the American Fisheries Society 135:76-88.
Kriegler, F. J., G. F. McCracken, J. W. Habera, and R. J. Strange. 1995. Genetic characterization of Tennessee's brook trout populations and associated management implications. North American Journal of Fisheries Management 15:804-813.
Krueger, C. C., and B. W. Menzel. 1979. Effects of stocking on genetics of wild brook trout populations. Transactions of the American Fisheries Society 108:277-287.
Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195-203.
Lennon, R. E. 1967. Brook trout of Great Smokey Mountains National Park. U.S. Fish and Wildlife Service Technical Paper 15.
Lo, C. P., and A. K. W. Yeung. 2002. Concepts and techniques of geographic information systems. PrenticeHall, Upper Saddle River, New Jersey.
MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, Salvelinus fontinalis. Journal of the Fisheries Research Board of Canada 26:16991725.

Marschall, E. A., and L. B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with brook trout. Ecological Applications 6:152-167.
Master, L. L., S. R. Flack, and B. A. Stein, editors. 1998. Rivers of life: critical watersheds for protecting freshwater biodiversity. Nature Conservancy, Arlington, Virginia.
McCormick, F. H., R. M. Hughes, P. R. Kaufmann, D. V. Peck, J. L. Stoddard, and A. T. Herlihy. 2001. Development of an index of biotic integrity for the mid-Atlantic Highlands region. Transactions of the American Fisheries Society 130:857-877.
McDougal, L. A., K. M. Russell, and K. N. Leftwich, editors. 2001. A conservation assessment of freshwater fauna and habitat in the southern national forests. U.S. Forest Service, Southern Region, R8-TP 35, Atlanta.
Meisner, J. D. 1990. Effect of climatic warming on the southern margins of the native range of brook trout, Salvelinus fontinalis. Canadian Journal of Fisheries and Aquatic Sciences 47:1065-1070.
Moore, S. E., G. L. Larson, and B. Ridley. 1986. Population control of exotic rainbow trout in streams of a natural area park. Environmental Management 10:215-219.
Moore, S. E., B. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. North American Journal of Fisheries Management 3:72-80.
Moyle, P. B., and P. J. Randall. 1998. Evaluating the biotic integrity of watersheds in the Sierra Nevada, California. Conservation Biology 12:1318-1326.
Moyle, P. B., and R. M. Yoshiyama. 1994. Protection of aquatic biodiversity in California: a five-tiered approach. Fisheries 19(2):6-18.
National Atmospheric Deposition Program. 2005. Isopleth grids. Available: nadp.sws.uiuc.edu. (July 2005).
Navtech. 2001. Navstreets: street data, version 2.5. Available: www.navteq.com. (January 2007).
Neville, P. G. 1999. Decision trees for predictive models. SAS Institute, Cary, North Carolina.
Nislow, K. H., and W. H. Lowe. 2003. Influences of logging history and stream pH on brook trout abundance in firstorder streams in New Hampshire. Transactions of the American Fisheries Society 132:166-171.
NRCS (Natural Resource Conservation Service). 2005. Watershed boundary dataset (WBD). NRCS, Washington, D.C. Available: www.ncgc.nrcs.usda.gov. (November 2005).
Perkins, D. L., C. C. Krueger, and B. May. 1993. Heritage brook trout in the northeastern USA: genetic variability within and among populations. Transactions of the American Fisheries Society 122:515-532.
Rashleigh, B., R. P. Parmar, J. M. Johnston, and M. C. Barber. 2005. Predictive habitat models for the occurrence of stream fishes in the mid-Atlantic Highlands. North American Journal of Fisheries Management 25:13531336.

Reiman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins.

North American Journal of Fisheries Management 17:1111-1125.
Roghair, C. N., C. A. Dolloff, and M. K. Underwood. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Transactions of the American Fisheries Society 131:718-730.
SAMAB (Southern Appalachian Man and the Biosphere). 1996a. The Southern Appalachian Assessment Aquatics Technical Report. Report 2 of 5. U.S. Forest Service, Southern Region, Atlanta.
SAMAB (Southern Appalachian Man and the Biosphere). 1996b. The Southern Appalachian Assessment Atmospheric Technical Report. Report 3 of 5. U.S. Forest Service, Southern Region, Atlanta.
Seaber, P. R., F. P. Kapinos, and G. L. Knapp. 1987. Hydrologic unit maps. U.S. Geological Survey, WaterSupply Paper 2294.
Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd edition. Freeman, New York.
Steinberg, D., and P. Colla. 1997. CART: classification and regression trees. Salford Systems, San Diego, California.
Stoneking, M., D. J. Wagner, and A. C. Hildebrand. 1981. Genetic evidence suggesting subspecific differences between northern and southern populations of brook trout (Salvelinus fontinalis). Copeia 1981:810-819.
Strange, R. J., and J. W. Habera. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. Transactions of the American Fisheries Society 127:434-440.
Thieling, T. M. 2006. Assessment and predictive model for brook trout (Salvelinus fontinalis) population status in the eastern United States. Master's thesis. James Madison University, Harrisonburg, Virginia.
Thurow, R. F., D. C. Lee, and B. E. Reiman. 1997. Distribution and status of seven native salmonids in the interior Columbia River basin and portions of the Klamath River and Great basins. North American Journal of Fisheries Management 17:1094-1110.
USACE (U.S. Army Corps of Engineers). 1998. National inventory of dams data. USACE, Washington, D.C. Available: crunch.tec.army.mil. (November 2004).
U.S. Census Bureau. 2002. Census 2000: summary files. U.S. Census Bureau, Washington, D.C. Available: www. census.gov. (November 2002).
USEPA (U.S. Environmental Protection Agency). 2002. Hydrologic unit boundaries from USGS. USEPA, Washington, D.C. Available: www.epa.gov. (November 2004).

USGS (U.S. Geological Survey). 2002. Water resources of the United States: hydrologic unit maps. USGS, Washington, D.C. Available: water.usgs.gov. (November 2004).

USGS (U.S. Geological Survey). 2004a. National hydrography dataset. USGS, Washington, D.C. Available: nhd. usgs.gov. (June 2004).
USGS (U.S. Geological Survey). 2004b. National land cover dataset 1992. USGS, Washington, D.C. Available: www. mrlc.gov. (June 2004).
USGS (U.S. Geological Survey). 2005. Accuracy assessment of 1992 national land cover data. USGS, Washington, D.C. Available: www.mrlc.gov. (January 2006).

Warren, M. L., Jr., P. L. Angermeier, B. M. Burr, and W. R.

Haag. 1997. Decline of a diverse fish fauna: patterns of imperilment and protection in the southeastern United States. Pages 105-164 in G. W. Benz and D. E. Collins, editors. Aquatic fauna in peril: the southeastern perspective. Southeast Aquatic Research Institute, Lenz Design and Communications, Special Publication 1, Decatur, Georgia.

Williams, J. D., M. L. Warren, Jr., K. S. Cummings, J. L. Harris, and R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18(9):6-22.
Yarnell, S. L. 1998. The southern Appalachians: a history of the landscape. U.S. Forest Service General Technical Report SRS-18.

## Appendix: Brook Trout Status Classification Key (Modified from Hudy et al. 2006)

1a. No quantitative (see definition below) or qualitative databases are available to evaluate presence or absence of historic and/or current naturally reproducing brook trout in the subwatershed; classification = unknown.
1b. Quantitative or qualitative databases exist that document presence or absence of reproducing populations of brook trout; go to question 2.
2a. Quantitative and/or qualitative databases document that there are no reproducing brook trout populations today; it is unknown whether brook trout populations never occurred in the subwatershed or occurred there but were extirpated; classification $=$ absent-unknown.
2b. Historical or current databases document that the subwatershed is within the possible historic range of reproducing brook trout populations; go to question 3.
3a. Quantitative and/or qualitative databases support that naturally reproducing brook trout historically never occupied the habitat or that no lotic habitat exists within the subwatershed; classification $=$ never occurred.
3b. Based on quantitative or qualitative databases, brook trout historically occupied suitable habitat within the subwatershed; go to question 4.
4 a . Based on quantitative or qualitative databases, naturally reproducing brook trout populations or fisheries existed historically but none are currently present within the subwatershed today; classification $=$ extirpated.
$4 b$. Based on quantitative or qualitative databases, brook trout populations (historically naturally reproducing and currently naturally reproducing) exist within the subwatershed; go to question 5.
5a. Brook trout data describe presence-absence only (number per unit area or catch per unit effort is not available), the data are quantitative but over 10 years old, or not enough quantitative data are available to determine the percentage of habitat lost; classification $=$ present-qualitative.
5b. Available data meet the criteria for quality (number of brook trout per unit area or catch per unit effort), resolution (data were collected within the subwatershed and not expanded from data outside the watershed), and age ( $<10$ years old): go to 6 .
6a. Greater than $50 \%$ of historically occupied lotic habitats within the entire subwatershed support naturally reproducing brook trout populations; classification $=$ intact.
6b. Of the historically occupied lotic habitats within the entire subwatershed, $50-99 \%$ no longer support naturally reproducing brook trout populations; classification $=$ reduced.

Quantitative databases are those for which sampling methods (electrofishing, snorkeling, gill nets, creel surveys, trap nets, explosives, etc.) recorded brook trout number per unit area, time, or effort; these data are used directly or in a classification system derived from quantitative data. They do not include modeled, predicted, or expanded brook trout numbers (i.e., the data must describe actual captures or observations).


[^0]:    * Corresponding author: hudymx@csm.jmu.edu

    Received January 30, 2007; accepted November 28, 2007
    Published online August 21, 2008

