North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 22 Nov 2013.

To cite this article: James E. McKenna Jr., Michael T. Slattery & Kean M. Clifford (2013) Broad-Scale Patterns of Brook Trout Responses to Introduced Brown Trout in New York, North American Journal of Fisheries Management, 33:6, 1221-1235

To link to this article: http://dx.doi.org/10.1080/02755947.2013.830998

North American Journal of Fisheries Management 33:1221–1235, 2013

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2013.830998

ARTICLE

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Abstract
Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* are valuable sport fish that coexist in many parts of the world due to stocking introductions. Causes for the decline of Brook Trout within their native range are not clear but include competition with Brown Trout, habitat alteration, and repetitive stocking practices. New York State contains a large portion of the Brook Trout's native range, where both species are maintained by stocking and other management actions. We used artificial neural network models, regression, principal components analysis, and simulation to evaluate the effects of Brown Trout, environmental conditions, and stocking on the distribution of Brook Trout in the center of their native range. We found evidence for the decline of Brook Trout in the presence of Brown Trout across many watersheds; 22% of sampled reaches where both species were expected to occur contained only Brown Trout. However, a model of the direct relationship between Brook Trout and Brown Trout abundance explained less than 1% of data variation. Ordination showed extensive overlap of Brook Trout and Brown Trout habitat conditions, with only small components of the hypervolume (multidimensional space) being distinctive. Subsequent analysis indicated higher abundances of Brook Trout in highly forested areas, while Brown Trout were more abundant in areas with relatively high proportions of agriculture. Simulation results indicated that direct interactions and habitat conditions were relatively minor factors compared with the effects of repeated stocking of Brown Trout into Brook Trout habitat. Intensive annual stocking of Brown Trout could eliminate resident Brook Trout in less than a decade. Ecological differences, harvest behavior, and other habitat changes can exacerbate Brook Trout losses. Custom stocking scenarios with Brown Trout introductions at relatively low proportions of resident Brook Trout populations may be able to sustain healthy populations of both species within their present range.

Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* are valuable sport fish that have similar habitat requirements. These species now coexist in many parts of the world due to Brown Trout (native of Europe) introductions, including within the Brook Trout's native range in eastern North America. Brown Trout flourish in eastern North American streams due to their ability to tolerate warmer water than native trout. Brown Trout grow faster and generally larger than Brook Trout, and these wary fish present a greater challenge to experienced fisherman than do Brook Trout (NYSDEC 2013). The Brook Trout is the native stream salmonid throughout most of eastern North America, and Brook Trout are generally smaller and easier to catch than Brown Trout. Managers have an interest in maintaining fisheries for both of these species in eastern North American streams. However, many Brook Trout populations have been lost due to habitat degradation and the introduction of competing species (e.g., Brown Trout).

The effects of successful invasion by exotic species (often due to illegal or accidental introductions) on native species are diverse and can be ecologically and economically damaging

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Received December 5, 2012; accepted July 24, 2013

(Vitule et al. 2009). Numerous field and laboratory investigations indicate that the Brown Trout is the superior competitor (Fausch and White 1981; Blanchet et al. 2007; Öhlund et al. 2008; Korsu et al. 2009) and has displaced the Brook Trout in parts of its native range (Hudy et al. 2008). However, some studies provide conflicting results, and several other factors have been cited in the decline of Brook Trout within the species' native range (Gard and Flittner 1974; Fausch and White 1986; Fausch 1988; Öhlund et al. 2008), including predation by Brown Trout and other carnivores (Alexander 1977, 1979), limited availability of appropriate habitat and habitat alteration (Taniguchi et al. 1998; Korsu et al. 2010), and differential harvest susceptibility (Cooper 1952; NYSDEC 2013). In addition, repeated fish stocking is known to have a strong influence on resident populations and may affect the abundance and persistence of Brook Trout within their native habitat (Hindar et al. 1991; Philipp and Claussen 1995; McKenna 2000).

A better understanding of factors affecting the relationship between Brook Trout and Brown Trout would help to elucidate the response of native species to exotic species invasion and would assist managers with their goals for these two species. If Brown Trout have a negative effect on Brook Trout, either as a superior competitor or as a predator, we would expect an inverse relationship in their abundances. If environmental conditions affect the suitability of habitat for each species, we would expect the two species to be dominant within different habitat domains. Many habitats have been altered by numerous environmental disturbances, which may enhance the habitat effect and the segregation of habitat domains.

Work by the Eastern Brook Trout Joint Venture has clarified the status of Brook Trout throughout the species' native range and identified areas where more information is needed (Hudy et al. 2008). However, most of the previous experiments and field examinations have been local in nature, and the mechanisms of Brook Trout decline have rarely been evaluated across multiple watersheds of a large region (Kocovsky and Carline 2006; Hudy et al. 2008; Öhlund et al. 2008). New York is ideal for such an examination because it is located in the center of the Brook Trout's native range; contains the headwaters of watersheds draining to the lower Great Lakes, the St. Lawrence River, Mid-Atlantic estuaries, and the Ohio River system; and has the full range of habitat conditions experienced by Brook Trout. Extensive databases and new predictive models of trout distributions throughout New York (and most of the Great Lakes basin) allow us to better assess the mechanisms of Brook Trout population dynamics over broad areas (McKenna et al. 2006; McKenna and Johnson 2011).

We used the New York State Department of Environmental Conservation's (NYSDEC) extensive Statewide Fisheries Database (SWFD) and new predictive models of Brook Trout and Brown Trout distribution and abundance (McKenna et al. 2006; McKenna and Johnson 2011) to examine the effects of Brown Trout introductions, habitat condition, and stocking on Brook Trout abundance and distribution. Our objectives were to (1) identify the extent and locations of habitats within New York watersheds that have conditions expected to support both Brook Trout and Brown Trout; (2) assess evidence for direct effects of Brown Trout on sympatric Brook Trout; (3) evaluate the contribution of broad-scale, enduring landscape conditions and habitat degrading factors on Brook Trout distribution where habitat is appropriate for both species; and (4) examine the likely effects of repeated Brown Trout stocking into streams that support Brook Trout.

METHODS

Field observation data and models of sympatry.—Models of the Brook Trout abundance that each stream in New York watersheds is expected to support were developed by McKenna and Johnson (2011). In the present study, we developed models of potential Brown Trout abundance for each New York stream reach (confluence-to-confluence segment on the 1:100,000-scale National Hydrography Database) by using similar methods and data. Standardized Brown Trout abundance, classified into broad CPUE categories of 0, 1–10, 11–100, and over 100 fish/$\sim$100 m^2 to smooth the high data variability, was calculated for each stream reach in which fish were captured by active fishing methods (i.e., electrofishing or seining) between 1978 and 2002 (SWFD version 14). Samples collected on the same stream reach at different times were averaged (McKenna et al. 2006). Values of broad-scale, enduring environmental landscape variables (with highly correlated variables removed first) were matched to the stream reaches from which fish were collected and were used in model development (Brenden et al. 2006; McKenna and Johnson 2011). These landscape attributes included stream network geometry (e.g., Strahler stream order and landscape slope), geology (e.g., bedrock and soil permeability), climate (e.g., growing degree-days and precipitation), estimated water temperature (model predicted; McKenna et al. 2010), and basic land use variables (e.g., percent forest cover). Values were available at the channel, local riparian buffer zone (60 m), local watershed, entire upstream riparian buffer zone, and upstream watershed area (Table 1). Georeferenced habitat disturbance variables were also matched to each stream reach for subsequent analysis (NFHB 2010). Short-term anthropogenic factors (e.g., nutrient loadings, anoxia, and impervious surfaces) were excluded from model development to provide predictions of each stream's potential to support trout (McKenna and Johnson 2011). New York State was divided into four modeling units (based on drainage basin and geological history; Figure 1), and a separate Brown Trout model was developed for each unit to provide regional specificity (McKenna and Johnson 2011). A more extensive field collection data set from 1978 to 2012 (SWFD version 40) was used to evaluate the distribution of stream reaches that supported Brook Trout, Brown Trout, or both species. All of these collections targeted complete fish communities, game fish, or all trout species.

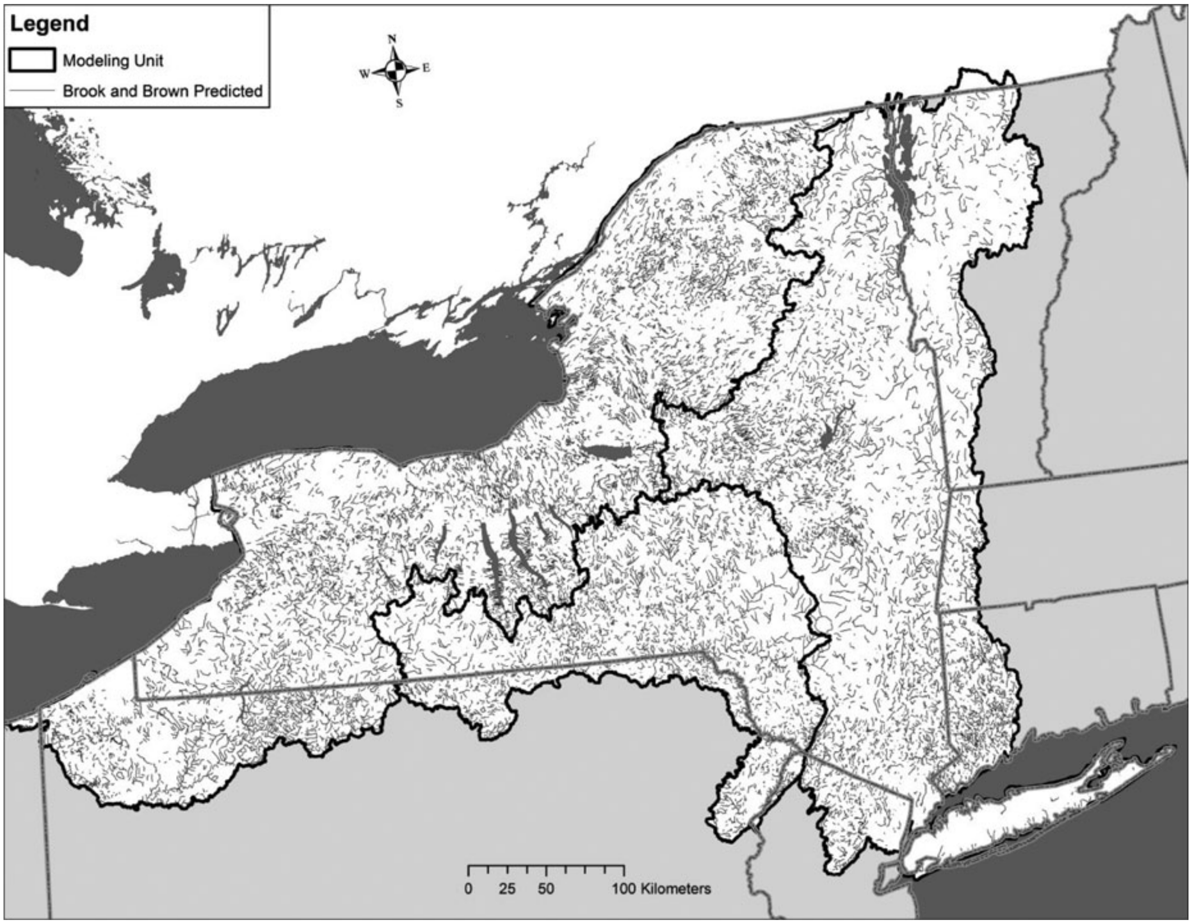

FIGURE 1. Map of New York streams (by modeling unit) that were expected to support both Brook Trout and Brown Trout. Modeling units are bounded by coasts and heavy black lines.

We used artificial neural networks (NNs) to develop each Brown Trout model (and each Brook Trout model; McKenna and Johnson 2011) because they typically produce more effective predictive models than many classical modeling techniques—particularly when relationships are multivariate and nonlinear—as they are not dependent upon assumptions about the underlying response model (typically linear) and specified error structure (Rumelhart et al. 1988; Hertz et al. 1991; Olden and Jackson 2001; McKenna et al. 2006). We trained a simple back-propagation NN model with one hidden layer, applying a logistic activation function (NeuroShell version 2.0; Wards Systems Group, Inc., Frederick, Maryland) to predict classified Brown Trout abundance from associated enduring environmental variables. The number of neurons in the hidden layer was determined by

$$N_H = (1/2)(N_I + N_O) + \sqrt{D_T}, \qquad (1)$$

where N_H is the number of neurons in the hidden layer, N_I and N_O are the number of input (I) and output (O) neurons, and D_T is the number of observations in the training data set (McKenna 2005). Neural network training is an iterative process of adjusting input variable weights at stages through the network and retesting the fit of the input pattern to the abundance prediction. Twenty percent of the data was held out as a validation data set, which provides the models with a greater ability to extrapolate beyond the training data and prevents overfitting (Ripley 1996; Olden and Jackson 2002). Leaning (0.1) and inertia (0.1) rates were implemented to ensure global, rather than local, convergence during training. The 10–16 most influential habitat variables retained throughout the reduction process (described by McKenna et al. 2006) were used in NN model development (Table 1). Each model was deemed acceptable if 80% or more of classified Brown Trout abundance variability (adjusted R^2 [R^2_{adj}]) was accounted for while minimizing mean square error (MSE). Model performance was evaluated using several measures, including R^2_{adj}, MSE, error prediction rates, and Cohen's kappa (κ). Model predictions and field collection samples were entered into a GIS and were mapped with ArcMap version 9.3 (ESRI, Inc., Redlands, California).

Combining the species-specific predictions of the Brook Trout models (McKenna and Johnson 2011) and Brown Trout

TABLE 1. Habitat variables used in the Brook Trout (BROK) and Brown Trout (BTRT) neural network models and other influential variables identified by principal components analysis. The BROK and BTRT model columns indicate the model(s) in which the habitat variable was used (by modeling unit: GL = Great Lakes; HC = Hudson–Champlain; MA = Mid-Atlantic; LI = Long Island). The spatial scale of each variable and the sign of the effect in the neural network model are provided in parentheses after each modeling unit where the variable was used (C = local channel; R = local riparian buffer; RT = total upstream riparian buffer; W = local watershed; WT = total upstream watershed). Areal variable values were proportions of spatial area (LU within a variable name represents land use; LU11 = commercial/industrial urban; LU12 = residential urban; LU13 = other urban; LU21 = non-row crop agriculture; LU22 = row crop agriculture; LU23 = orchards, vineyards, and other agriculture; LU41 = deciduous forest; LU42 = evergreen forest; LU43 = mixed forest).

Variable class	Habitat variable	Code	BROK model (effect scale)	BTRT model (effect scale)	Source
Climate	Growing degree-days	GDD	GL (+W, −WT); HC (−WT)	GL (+W, −WT)	Computed from local watershed mean annual air temperature (base 50°F)[a]
	July precipitation (cm)	JPRECIP	GL (+W)	GL (−W, −WT)	U.S. average July precipitation (1971–2000)[b]
	Mean annual air temperature	MAAT		GL (−WT)	U.S. average mean annual air temperature (1971–2000)[a]
	Mean July air temperature	JL_T	GL (+W)	GL(−W)	U.S. average July air temperature (1971–2000)[a]
Geology	Bedrock, carbonate	BR3		GL (+W)	Statewide bedrock geology[c]
	Bedrock, shale	BR2	MA (+W)	MA (+W)	Statewide bedrock geology[c]
	Soil permeability	PERM	HC (+W)		Soils data from the conterminous USA[b]
Land use/cover	Agriculture, composite	C_AG	GL (−RT); MA (+C)	GL (+RT); MA (+C)	Computed from NLCD 1992[d] (combination of LU21, LU22, and LU23)
	Agriculture, non-row crop	LU21	GL (−R); MA (−WT)	GL (+RT); MA (+WT)	NLCD 1992[d]
	Forest cover, composite	FOR	GL (−W, −WT); HC (+R, +W, +WT); LI (+C); MA (+C)	GL (−W); HC (−R, −W); LI (−C); MA (+C)	Computed from NLCD 1992[d] (combination of LU41, LU42, and LU43)
	Forest, deciduous	WT_LU41		GL (+WT)	NLCD 1992[d]
	Forest, mixed	LU43	LI (−C)	LI (−C)	NLCD 1992[d]
	Open water	LU50	LI (−C); MA (−W)	LI (−C); HC (−W); MA (+W)	NLCD 1992[d]
	Urban, composite	Urban	LI (+R)	LI (−R)	Computed from NLCD 1992[d] (combination of LU11, LU12, and LU13)
	Urban, residential	LU12	LI (−C)	LI (−C)	NLCD 1992[d]
Stream/landscape geometry	Distance upstream from drain point (km)	DownLength	−GL, +LI, +HC	+GL, −LI	Computed from NHD[e]
	Elevation midrange (m)	Elevation	+GL, −HC, −MA	−GL, +HC, +MA	Computed from NED 2002[f]
	Landscape slope	Slope	GL (+W, +WT); HC (+RT, +W, +WT); LI (−W); MA (−R, −RT, −W, −WT)	GL(+W); HC (−RT, −W, +WT); LI (+W); MA (+R, +RT, −W, +WT)	Computed from DEM[f]

TABLE 1. Continued.

Variable class	Habitat variable	Code	BROK model (effect scale)	BTRT model (effect scale)	Source
	Shreve number	Shreve	−HC	−HC	Computed from NHD[e]
	Shreve number of next downstream reach	DLink	−LI	−LI	Computed from NHD[e]
	Strahler number	Order	−HC, +LI	−HC, −LI	Computed from NHD[e]
	Strahler number of next downstream reach	DownOrder	+HC, −LI	+GL, +HC, +LI	Computed from NHD[e]
Stream water temperature	Predicted water temperature category	Temp_Cat	+GL, −HC, −LI, −MA	+GL, −HC, −LI, −MA	Model predicted (McKenna et al. 2010)
Disturbance	Urban, low density	URB_L (W, WT)			NFHB 2010
	Urban, medium density	URB_M (W, WT)			NFHB 2010
	Urban, high density	URB_H (W, WT)			NFHB 2010
	Human population density	POP (W, WT)			NFHB 2010
	Road crossings	RoadX (WT)			NFHB 2010
	Road length	RoadL (WT)			NFHB 2010
	Dams	Dams (WT)			NFHB 2010
	Mines	Mines (WT)			NFHB 2010
	National Pollution Discharge Elimination System sites	NPDS (W, WT)			NFHB 2010
	Toxic Release Inventory sites	TRIC (W, WT)			NFHB 2010
	Superfund sites	CERC (W, WT)			NFHB 2010

[a]PRISM Group 2002.
[b]Schwarz and Alexander 1995.
[c]NYSGS 1999.
[d]National Land Cover Dataset (NLCD 1992).
[e]U.S. Geological Survey, National Hydrography Database (USGS 2013).
[f] Digital elevation model (DEM), which was derived from the National Elevation Dataset (NED 2002).

models provided an indication of the streams that are expected to have habitat conditions appropriate to support either or both species. We focused on habitats that were most likely to support both species, so that there was some chance for competition and/or predation.

Direct interspecific effects.—The effect of Brown Trout on Brook Trout abundance and occurrence was evaluated with several regression models relating observed CPUE values of each species on matching stream reaches. Among the linear, logarithmic, polynomial, and exponential models, the best fit was specified by the exponential model:

$$\mathrm{BROK} = \alpha \cdot e^{(\beta \cdot \mathrm{BTRT})}, \quad (2)$$

where BROK is Brook Trout CPUE, BTRT is Brown Trout CPUE, and α and β are fitted parameters. Only observations from streams that were predicted to support both species and where Brown Trout were present were used for the regression.

Habitat influence.—Principal components analyses (PCAs) of habitat variables associated with each observation of Brook Trout, Brown Trout, or both among the streams predicted to support both species were used to identify influential habitat and disturbance variables that might distinguish Brook Trout habitat from Brown Trout habitat (ter Braak 1995; Johnson et al. 2011). Data were centered and standardized by habitat variables to remove effects of different units and value ranges. Separate PCAs were conducted on landscape variables and disturbance variables to examine the influence of each type of effect. Points were classified as sites supporting (1) both species, (2) only Brook Trout, or (3) only Brown Trout, and the overlap of these habitat domains was examined. Most of the habitat and disturbance data did not meet normality and variability assumptions for parametric ANOVA. Therefore, we used nonparametric Kruskal–Wallis (K–W) rank-sum tests in combination with Wilcoxon comparison tests (using a Bonferroni significance adjustment) to determine the significance of differences in values of the most heavily weighted habitat and disturbance variables among the three classes of points.

Stocking effect.—Records of fish stocking by the NYSDEC for 6 years (2005, 2006, and 2008–2011) were available and indicated the species and number of fish released at each stocked location. Spatial overlay of these records with model predictions and field collections allowed us to (1) determine which streams were exposed to stocked fish during the period of record and (2) assess which of those streams continued to support Brook Trout. However, field collections were not frequent enough to reveal any response of Brook Trout to repeated stocking of Brown Trout into the same stream. In addition, Brown Trout have been stocked into New York streams for over 100 years; thus, without earlier stocking and collection records, we could not be certain what the initial Brook Trout population might have been (although the Brook Trout model was designed to provide a benchmark estimate of that number). Therefore, we applied the FITPOP population dynamics simulation model (McKenna 2000) to illustrate the likely response of a resident Brook Trout population to repeated Brown Trout stocking; this was done by using estimates of mean Brook Trout densities in streams that were not exposed to Brown Trout stocking and mean estimates of Brown Trout density that was added to streams by stocking during the period of record. The simulation assumed that the Brook Trout population was near carrying capacity before Brown Trout introduction and that the Brown Trout were added by a single stocking event each year. All other aspects of the two species' populations (e.g., intrinsic growth, mortality, carrying capacity, etc.) were assumed to be equivalent. An additional simulation was conducted with the same settings, except with Brook Trout mortality set to three times that of Brown Trout to represent the effect of differential fishing harvest (Cooper 1952).

RESULTS

Brown Trout models explained 82% of the variation in classified Brown Trout abundance in the Mid-Atlantic modeling unit and over 87% of the variation in the other modeling units; omission error rates were generally low (<10% except for the Mid-Atlantic modeling unit; Table 2). Brook Trout model performance was reported by McKenna and Johnson (2011) for each modeling unit; each model explained over 90% of the variation in classified Brook Trout abundance. The combined Brook Trout and Brown Trout model correctly predicted 92% of the streams that were observed to support both Brook Trout and Brown Trout. The combined model projected that 19,639 stream reaches (39% of the stream network) would have conditions appropriate for both Brook Trout and Brown Trout. Those stream reaches were distributed throughout the state but tended to be smaller order reaches with higher slope and elevation than other streams (Figure 1). Of those reaches, 2,202 (11%) were sampled between 1978 and 2012 (see Supplementary Figure 1 in the online version of this article). Among that subset of stream reaches, 362 reaches (16%) had Brook Trout but no Brown Trout, 488 reaches (22%) had Brown Trout but no Brook Trout, and 538 reaches (24%) had both Brook Trout and Brown Trout. Multiple samples may have been taken within any given stream reach over the sampling period, and the above numbers are based on the

TABLE 2. Summary of the performance of Brook Trout and Brown Trout neural network models by modeling unit in New York State (N = total number of samples used for training and validation; R^2_{adj} = adjusted coefficient of multiple determination; MSE = mean square error). Omission is the percentage of instances (number of streams, in parentheses) in which trout were present but the model predicted their absence. Commission is the percentage of instances (number of streams, in parentheses) in which trout were absent but the model predicted their presence. Cohen's kappa (κ) is a measure of chance prediction that combines omission and commission.

Modeling unit	N	R^2_{adj}	MSE	Cohen's κ	Correct absences	Correct presences	Omission (%)	Commission (%)
Brook Trout								
Great Lakes	3,777	0.95	13.8	0.31	1,364	933	1 (50)	36 (1,377)
Hudson–Champlain	1,689	0.91	6.1	0.52	452	826	<1 (8)	23 (395)
Long Island	553	0.92	0.4	0.16	18	497	1 (1)	49 (37)
Mid-Atlantic	1,749	0.99	31.2	0.47	354	926	2 (39)	21 (380)
Brown Trout								
Great Lakes	3,805	0.91	6.67	0.36	953	1,622	6 (225)	26 (1,005)
Hudson–Champlain	1,689	0.87	7.7	0.29	255	957	10 (168)	18 (309)
Long Island	548	0.99	<0.1	0.65	75	412	0 (0)	11 (61)
Mid-Atlantic	1,749	0.82	42.2	0.27	282	906	15 (263)	17 (298)

average abundance of each species within each stream reach. It is possible that Brook Trout and Brown Trout could have occurred in the same stream reach but at different times and thus would not have been sympatric. However, based on collection event records, the vast majority (515) of such stream reaches included at least one event where both species were present in the same catch. Available stocking records showed that among stream reaches that had been sampled and were expected to support both Brook Trout and Brown Trout, 384 reaches (17%) were exposed to stocked Brown Trout. Field collections from those streams showed that 146 reaches (38%) sustained both species, 233 reaches (61%) had Brown Trout but no Brook Trout, and only 5 reaches (1%) had Brook Trout but no Brown Trout.

Direct Interference and Habitat Conditions

Inspection of the pattern of Brook Trout CPUE values as a function of Brown Trout CPUE showed an exponential decrease, and the exponential model had a significant fit to the data ($\alpha = 0.02$, $\beta = 1.80$, $R^2 = 0.003$, $P < 0.03$; Figure 2). However, the model explained less than 1% of the variability in the data, indicating that factors other than direct competition with or predation by Brown Trout were responsible for most of the Brook Trout response to the presence of Brown Trout or associated conditions.

Neither habitat conditions nor environmental disturbances explained the majority of variation in Brook Trout dominance. The first three axes of the PCA of landscape variables explained 41.2% of the variability in the data. The most heavily weighted variables of the first axis were forest cover, broad-scale agriculture, and watershed slope; the second axis emphasized surficial geology, elevation, agriculture in the riparian zone, climate, and soil permeability (Figure 3). However, the distributions of samples representing each of the three groups (Brook Trout only, Brown Trout only, or both species) occupied nearly the same hypervolume. A tiny fringe of space (occupied by 1.9% of samples) with only stream reaches that had Brook Trout but no Brown Trout suggested weak dominance of Brook Trout in habitats with the highest proportion of forest cover within a watershed. Similarly, a small area (occupied by 1.4% of samples) containing only stream reaches that had Brown Trout but no Brook Trout suggested weak dominance of Brown Trout in habitats with the highest proportion of agricultural cover within a watershed. The K–W ANOVA results showed that agricultural cover variables

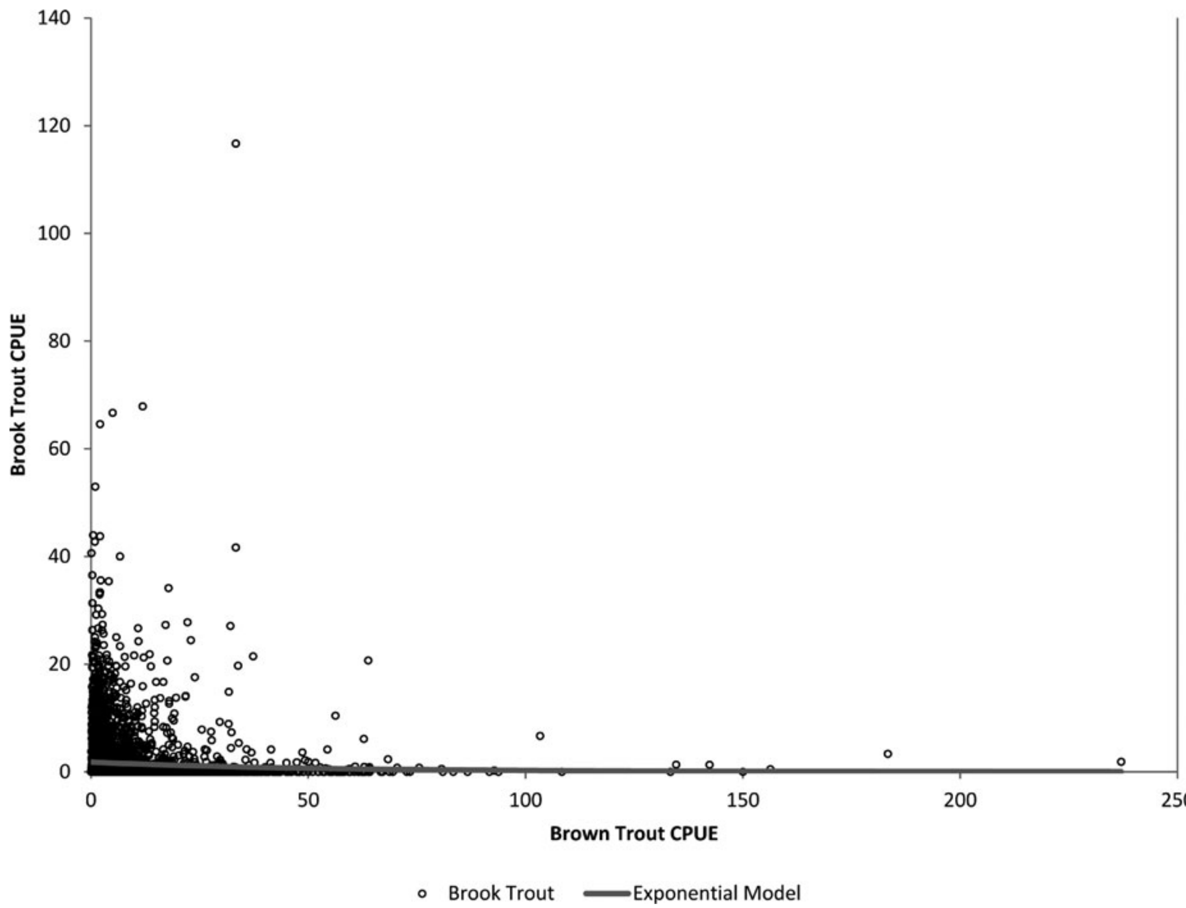

FIGURE 2. Plot of Brook Trout CPUE (fish/∼100 m^2) versus Brown Trout CPUE, with a curve for the fitted exponential model (gray line; $N = 5{,}472$). Circles indicate observed Brook Trout abundances.

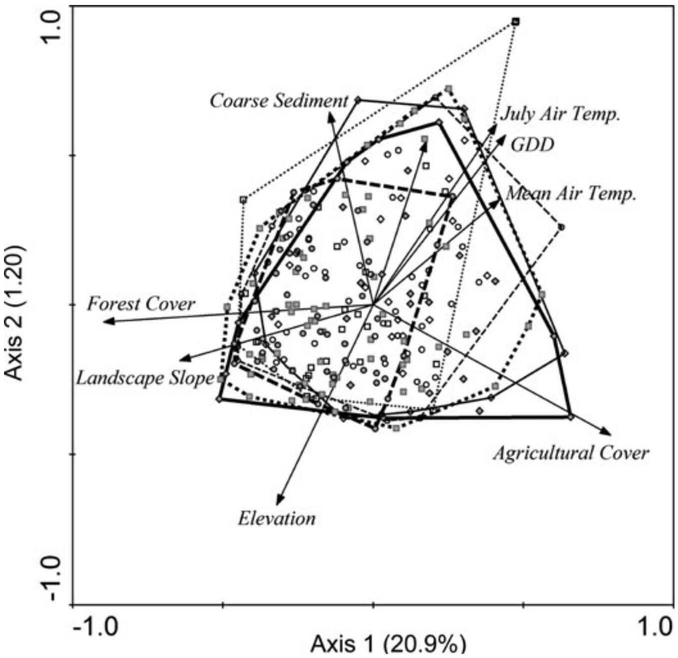

FIGURE 3. First two ordination axes from principal components analysis of enduring landscape habitat variables, with eigenvalues provided after each axis label ($N = 687$). The dotted polygons enclose the areas occupied by samples with only Brook Trout (open squares = abundance class 1–10 fish/~100 m^2; solid squares = abundance class > 10 fish/~100 m^2); the solid lines enclose the areas occupied by samples with only Brown Trout (open circles = abundance class 1–10 fish/~100 m^2; solid circles = abundance class > 10 fish/~100 m^2); and the dashed lines enclose the areas occupied by samples with both species (open diamonds = Brook Trout abundance class 1–10 fish/~100 m^2; solid diamonds = Brook Trout abundance class > 10 fish/~100 m^2). Not all data points are represented within each polygon. Vectors indicate the direction of each habitat gradient, pointing in the direction of increasing values; only the most influential vectors are shown. A single vector is used to indicate the general direction and magnitude of influences from geology, agricultural cover (non-row crop, pasture, and orchards), forest cover (evergreen, deciduous, and mixed forest within the watershed and riparian zones), and landscape slope (at the riparian and watershed scales) variables (GDD = growing degree-days).

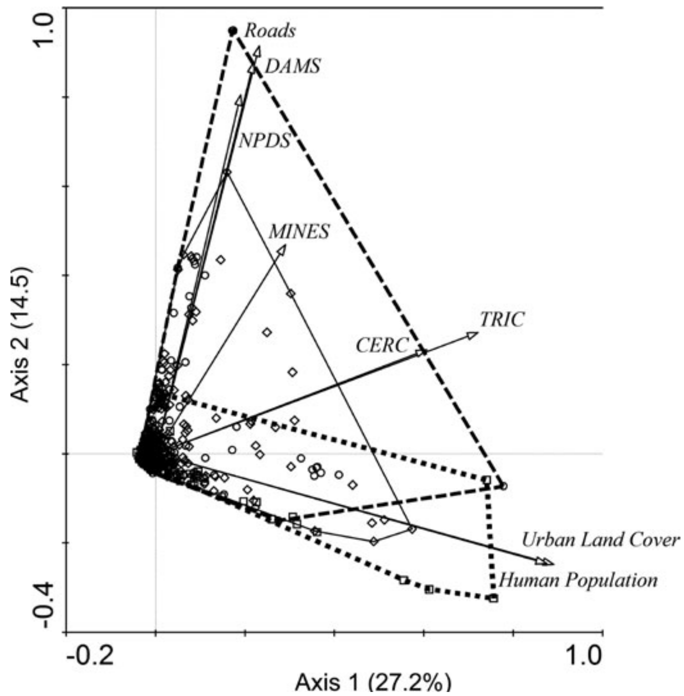

FIGURE 4. First two ordination axes from principal components analysis of habitat disturbance variables, with eigenvalues provided after each axis label ($N = 501$). The dotted polygon encloses the area occupied by samples with only Brook Trout (squares), the solid line encloses the area occupied by samples with only Brown Trout (circles), and the dashed line encloses the area occupied by samples with both species (diamonds). Vectors indicate the direction of each habitat disturbance gradient, pointing in the direction of increasing values; only the most influential vectors are shown. Disturbance variable codes apply to the upstream watershed (CERC = Superfund sites; DAMS = number of dams; MINES = number of mines; NPDS = National Pollution Discharge Elimination System sites; TRIC = Toxic Release Inventory sites). A single vector is used to indicate the general direction and magnitude of influences from roads (road crossings and road length within the local and total watersheds), urban land cover (low-, medium-, and high-density development within the local and total watersheds), and human population variables (population density within the local and total watersheds).

associated with streams that had only Brown Trout were significantly higher than those for streams with only Brook Trout (Appendix Table A.1). Conversely, forest cover variables associated with streams that had only Brook Trout were significantly higher than those for streams with only Brown Trout.

The first three axes from the PCA of environmental disturbance conditions explained 51.7% of the variability in the data. The most heavily weighted variables composing the first axis were measures of habitat fragmentation, urban development, and human population density; the second axis emphasized measures of habitat fragmentation (road crossings, dams, and mines; Figure 4). As with landscape conditions, most samples representing each of the three groups occupied nearly the same hypervolume. The envelope containing sites with both species occupied the largest volume, but two extreme points were responsible for greatly extending the area. If those two points are excluded as outliers, then the sites supporting both species encompass a smaller volume than that occupied by Brown Trout-only samples. A few samples extended the volume occupied by Brook Trout-only samples along the high urbanization and human population gradients, but all were from a few stream reaches on Long Island (a densely populated urban area). The volume of space occupied by stream reaches that had Brown Trout but not Brook Trout was associated with high values for road crossings, road length, dams, mines, and pollutant discharge. The K–W results indicated elevated values of these variables for Brown Trout-only sites (Table A.1).

Stocking Effects

The NYSDEC stocks Brook Trout and Brown Trout (as well as Rainbow Trout *Oncorhynchus mykiss* and other species) in various streams throughout the state. However, the available records show that Brook Trout and Brown Trout were rarely stocked together at the same time and place (Supplementary

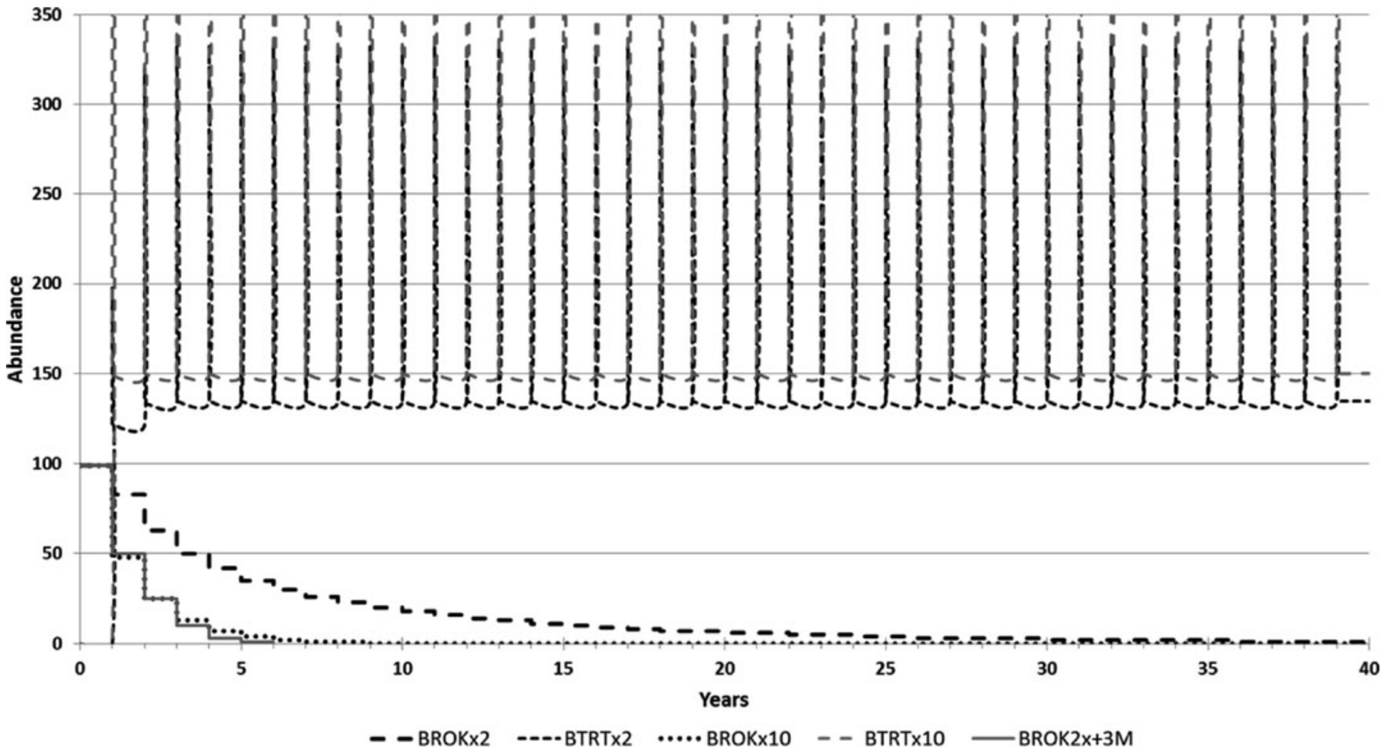

FIGURE 5. Simulated effects of annual Brown Trout (BTRT) stocking (2 × times and 10 × times the number of Brook Trout [BROK] initially present) into a stream with a resident population of ecologically similar Brook Trout near carrying capacity (set to 100). Brook Trout harvest mortality at three times the Brown Trout harvest mortality was also simulated in combination with the 2 × stocking scenario (i.e., BROK2x+3M). The maximum Brown Trout abundance value of 1,140 fish/∼100 m^2 is not shown; the ordinate is truncated at 350.

Figure 2). In fact, most Brook Trout were stocked in streams of the Adirondack region, while most Brown Trout were stocked elsewhere in the state. Nearly all of the streams ($n = 357$) that were observed to contain Brook Trout but not Brown Trout had not been stocked with Brown Trout during the 6 years of available stocking records (only five streams were exceptions). However, over 60% of streams that were stocked with Brown Trout did not also support Brook Trout. In a few rare cases, Brown Trout occupied streams with no record of stocking, and those were all downstream of stocked stream reaches, often without barriers to fish movement.

Simulation of Brook Trout and Brown Trout in sympatry showed the great potential for stocking to dramatically affect the population dynamics of resident Brook Trout. Under the scenario of a Brook Trout population near the carrying capacity of a stream reach, repeated annual stocking of Brown Trout at twice the density of the resident Brook Trout population (mean CPUE = 6.2 fish/∼100 m^2; estimated stocked Brown Trout densities ranged from less than 0.1 to over 80 times the mean Brook Trout population), and assumed ecological equivalence, Brook Trout will be eliminated from that stream in 36 years (dark dashed line in Figure 5). If stocked Brown Trout densities are 10 times that of the resident Brook Trout population, Brook Trout will be eliminated from the stream in less than 10 years (dotted line in Figure 5). When differential fishing harvest mortality (Brook Trout mortality 3 times that of Brown Trout; based on Cooper 1952) was included in the simulation with Brown Trout stocking at twice the Brook Trout population, the native Brook Trout population was eliminated in 5.7 years.

DISCUSSION

Our examination of the effects of Brown Trout on Brook Trout within New York watersheds showed only weak evidence of Brook Trout suppression or elimination in the presence of Brown Trout. Although the model fit was weak, the shape of the direct relationship indicated a decline in Brook Trout abundance as Brown Trout abundance increased, and many streams that were stocked with Brown Trout did not contain Brook Trout. However, the data also indicated many conditions of coexistence and a weak direct influence of Brown Trout on Brook Trout abundance or occurrence. The results suggest that the two species may persist in the same habitat conditions and can generally tolerate similar environmental disturbances (Figures 3, 4) although Brook Trout appear to perform better where forest cover is most extensive and Brown Trout may be better able to persist where much of the landscape is fragmented and used for agriculture (Table A.1). The potential effects of repeated Brown Trout stocking into Brook Trout habitat were vividly illustrated by the simulation, showing how quickly Brook Trout could be eliminated by continuous supplementation of the Brown Trout population.

Several studies have concluded that Brown Trout are superior competitors to sympatric Brook Trout (Fausch and White 1981; Blanchet et al. 2007; Korsu et al. 2009), but other research shows that Brook Trout can be the superior competitors (Fausch and White 1986; Magoulick and Wilzbach 1998; Strange and Habera 1998; Buys et al. 2009). Another direct effect of Brown Trout is predation (Alexander 1977) by large adult Brown Trout on juvenile Brook Trout. The poor fit of our exponential model to the species abundance data indicates that these direct effects have little to do with the distribution of Brook Trout across the range of habitat conditions in New York, where both species may be sympatric. Competition seems equivocal and can only occur where a shared resource is limiting (Larson and Moore 1985; Rose 1986; Fausch 1988; Lohr and West 1992). Predation by large Brook Trout on juvenile Brown Trout seems as likely as the inverse. The importance of competition and predation is also likely to change with Brook Trout life stage (Browne and Rasmussen 2009; Johnson et al. 2009, 2010).

Habitat condition and alteration have been shown to affect Brook Trout distribution, and interspecific microhabitat partitioning is evident in some systems (Kocovsky and Carline 2006; Johnson 2008; Johnson et al. 2011). However, most of these environmental studies focus on water temperature or altitude and typically fine-scale habitat conditions (Gard and Flittner 1974; Taniguchi et al. 1998; Wehrly et al. 2007; Stranko et al. 2008). Such results can be confounded by the fit of species-specific adaptations to habitat conditions in the study areas (Öhlund et al. 2008; Korsu et al. 2010). Our examination of habitat and disturbance conditions indicates the general congruence of Brook Trout and Brown Trout over the range of conditions where they are likely to coexist but supports the common observation that Brook Trout may dominate in some habitats (i.e., higher quality habitats), whereas Brown Trout dominate in others (more disturbed habitats; Werner 2004). Loss and degradation of habitat are certainly major reasons for the decline of Brook Trout but are independent of Brown Trout occurrence (Hudy et al. 2008).

As indicated by the high proportion of stocked streams where only Brown Trout were found in field collections and by the results of our simulations, there is a strong likelihood that the loss of Brook Trout from many of the streams containing Brown Trout can be caused by stocking practices. The genetic and population effects of adding cultured fish to streams with native populations are varied and sometimes subtle but can exert impacts on the sustainability of those populations (e.g., Taggart and Ferguson 1986; Hindar et al. 1991; Philipp and Claussen 1995; McKenna 1996, 2000). Regular supplementation of cultured fish can force resident populations into competition for limited resources, especially if the resident population is already near the carrying capacity. The high proportion of stocked streams with coexisting populations of Brook Trout and Brown Trout suggests the possibility of stocking scenarios that can sustain populations of both species (e.g., annual introductions of half as many Brown Trout as the resident number of Brook Trout).

Caveats and Limitations

The Brook Trout is the native stream-resident salmonid in eastern North America, and for this study we have assumed that Brook Trout were present in any suitable stream habitat before Brown Trout were introduced (e.g., Greeley and Bishop 1933). It is possible that Brook Trout were absent from areas where Brown Trout were introduced, thereby producing the illusion that Brook Trout were excluded by Brown Trout. However, historic records support our assumption, and it seems highly unlikely that there are many cases of persistent Brown Trout populations in habitats that were historically devoid of Brook Trout. Because Brown Trout are native to Europe, we have also assumed that wherever Brown Trout were present, they had been stocked or introduced nearby—Brown Trout have been stocked in New York State for more than 100 years. Even the limited stocking data available to us support this assumption; rarely were Brown Trout present in stream reaches for which no record of stocking existed. Rainbow Trout and several species of Pacific salmonids have also been introduced into New York watersheds and could also influence Brook Trout distributions. However, the areas affected by these introductions are limited, and they are unlikely to have an influence as strong as that of Brown Trout.

Our NN models generally performed well, and Table 2 provides a variety of performance measures. However, model construction and the data must be considered when interpreting the model performance measures, particularly commission error and Cohen's κ. For example, the κ for Brook Trout in the Long Island modeling unit was quite low (0.16) even though there was only a single omission error. Our models assume that habitat conditions are of high quality (aside from any general effect conveyed by basic land use); acute anthropogenic influences have been excluded. Thus, in a highly urbanized area like Long Island, there are likely to be stream habitats that would be good for Brook Trout if not for the effects of high impervious surface percentages, elevated plant nutrient concentrations, anoxia or hypoxia, etc. Commission errors help us to identify streams that may benefit from restoration efforts, assuming that on-the-ground examination identifies anthropogenic issues that can be addressed. Furthermore, the commission error rate is high in some cases because Brown Trout have not been stocked in many upstate New York streams. Therefore, the models indicate streams that could support Brown Trout if they were released there.

The model of habitats suitable for both species was based on separate, species-specific model predictions; no interspecific interactions were considered by those models. As a result, the predicted set of streams may be somewhat liberal. However, it provides a picture of the basic abiotic conditions that are suitable to support either of the two species and thus the locations where one might expect long-term coexistence or the proper conditions for competition.

Our habitat analyses included a suite of 35 landscape variables and 26 disturbance variables, 16 of which had the strongest influence on Brook Trout and Brown Trout distributions (see also McKenna et al. 2006; McKenna and Johnson 2011). There are certainly other abiotic factors and disturbance variables that we did not consider but that could affect trout distributions. Other studies have cited several habitat variables (most of which were included here) that contribute to Brook Trout distribution and abundance as well as the Brook Trout's persistence in sympatry with Brown Trout, but it is likely that a combination of habitat condition factors (in association with biotic influences) is responsible rather than any single variable (Fausch and White 1981). Although we detected some environments that were better suited to Brook Trout or Brown Trout, the extensive overlap of suitable conditions for Brook Trout and Brown Trout was clear. Other studies have shown microhabitat and diet partitioning among these species (Johnson 1981, 2008; Korsu et al. 2010; Johnson et al. 2011), and the broad scale of this analysis prevents detection of those relationships. The stream reach was the spatial unit of our analysis, and many reaches are quite long. It is likely that suitable microhabitats exist for each species in different places within these reaches, which may promote coexistence at the reach scale.

Predation and differential harvest are other factors that have been cited as contributing to the decline in Brook Trout. Several species of fish, birds, and mammals are known to prey on Brook Trout and Brown Trout (Alexander 1977, 1979; Fausch and White 1981; Fausch 1988; Öhlund et al. 2008); therefore, if Brown Trout are better able to avoid or escape predation than Brook Trout, population declines may be enhanced. It is also known that Brook Trout catchability is higher than Brown Trout catchability (Cooper 1952), and fishing harvest may accelerate Brook Trout loss relative to Brown Trout, as highlighted by the simulation that included this effect.

The available stocking records represent a short but recent period of New York fish stocking history and span more than the typical life span of most fish in the wild. However, there could have been streams where Brown Trout had been stocked prior to the period represented by our stocking records but where Brook Trout were present and Brown Trout were absent by the time of the surveys. Such cases would indicate the possible recovery of Brook Trout to their native habitat after suspension of Brown Trout stocking. Future investigations of the historic stocking records would help to identify where such streams may exist. Our simple, deterministic simulation experiment illustrates the population dynamics of two ecologically similar species and may be used to explore questions of native species recovery or sustainable multispecies fisheries. However, this simulation is an oversimplification of the true system. A more accurate simulation would account for any fitness advantage of the native species (if such an advantage exists), any competitive advantage of the exotic species, and any population growth rate or mortality advantage of the exotic species in fragmented, agricultural habitats. Variability of these factors and various stocking scenarios can have a strong effect on the dynamics of either species (McKenna 2000). Additional information on the ecological differences between Brook Trout and Brown Trout is needed for more thorough evaluations (Philipp and Claussen 1995).

Fish culture is expensive, but the economics of a fishery may well justify hatchery operations. Ecological costs (e.g., loss or decline of native species and strains) should also be considered. We found that direct interactions and even habitat conditions were relatively minor factors (at least within streams that were expected to have suitable habitat for each species) in comparison with the effects of the repeated stocking of Brown Trout into Brook Trout habitat. Although these species are ecologically similar and have similar habitat requirements, any advantage of Brown Trout over Brook Trout will be magnified by Brown Trout population supplementation. For example, if fishermen (aware of the stocking schedule) descend on Brown Trout stocking sites and more effectively remove Brook Trout than Brown Trout, then the displacement of Brook Trout will occur faster. The displacement effect will be further accelerated if forest cover is reduced in favor of agriculture and if Brown Trout are better than Brook Trout at avoiding predators in those environments. Experimentation with different stocking scenarios may help to identify strategies that sustain healthy populations of both of these valuable game fish species within their present range.

ACKNOWLEDGMENTS

We are grateful to the NYSDEC, C. Festa, and J. Daley for sharing the SWFD and fish stocking information and for assistance with data management. We are indebted to all NYSDEC agents involved with field collections and data recording. We thank D. Infante and the National Fish Habitat Action Plan for sharing habitat disturbance data with us. We also appreciate the time and effort applied by those that have reviewed this paper. This article is Contribution 1662 of the U.S. Geological Survey Great Lakes Science Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Appendix: Results of Kruskal–Wallis ANOVA

TABLE A.1. Results of Kruskal–Wallis ANOVA and Wilcoxon comparison test (χ^2: df = 2). See Table 1 for definitions of variables (BROK = Brook Trout; BTRT = Brown Trout). Medians of significantly distinct groups are indicated by different letters. Asterisks indicate values that were based on sparse counts and that are reported here as means.

Variable (scale)	χ^2	*P*	Data subset	Median	Group(s)
Agriculture, composite (C)	12.61	0.002	BROK only	0.090	z
			BROK + BTRT	0.074	z
			BTRT only	0.122	y
Agriculture, non-row crop (C)	15.34	<0.001	BROK only	0.067	z
			BROK + BTRT	0.050	z
			BTRT only	0.082	y
Forest, deciduous (C)	1.76	0.41	BROK only	0.390	z
			BROK + BTRT	0.377	z
			BTRT only	0.406	z
Forest, mixed (C)	75.71	<0.001	BROK only	0.025	z
			BROK + BTRT	0.029	z
			BTRT only	0.000	y
Forest, composite (R)	56.68	<0.001	BROK only	0.774	z
			BROK + BTRT	0.766	z
			BTRT only	0.646	y
Agriculture, non-row crop (R)	32.03	<0.001	BROK only	0.092	z
			BROK + BTRT	0.092	z
			BTRT only	0.138	y
Forest, deciduous (R)	1.85	0.40	BROK only	0.378	z
			BROK + BTRT	0.379	z
			BTRT only	0.364	z
Forest, evergreen (R)	91.63	<0.001	BROK only	0.036	z
			BROK + BTRT	0.034	z
			BTRT only	0.008	y
Agriculture, composite (RT)	74.24	<0.001	BROK only	0.106	z
			BROK + BTRT	0.115	z
			BTRT only	0.215	y
Agriculture, non-row crop (RT)	76.14	<0.001	BROK only	0.082	z
			BROK + BTRT	0.092	z
			BTRT only	0.183	y
Agriculture, composite (W)	74.75	<0.001	BROK only	0.101	z
			BROK + BTRT	0.118	z
			BTRT only	0.235	y
Forest, deciduous (W)	50.43	<0.001	BROK only	0.445	z
			BROK + BTRT	0.432	z
			BTRT only	0.355	y
Forest, evergreen (W)	72.02	<0.001	BROK only	0.033	z
			BROK + BTRT	0.032	z
			BTRT only	0.039	y
Human population density (W)	103.79	<0.001	BROK only	4.721	zy
			BROK + BTRT	5.198	y
			BTRT only	10.397	z
Urban, low density (W)	103.50	<0.001	BROK only	2.800	z
			BROK + BTRT	3.500	z
			BTRT only	5.150	y

TABLE A.1. Continued.

Variable (scale)	χ^2	P	Data subset	Median	Group(s)
Agriculture, composite (WT)	113.71	<0.001	BROK only	0.088	z
			BROK + BTRT	0.096	z
			BTRT only	0.248	y
Agriculture, non-row crop (WT)	113.65	<0.001	BROK only	0.071	z
			BROK + BTRT	0.067	z
			BTRT only	0.207	y
Forest, evergreen (WT)	47.05	<0.001	BROK only	0.042	z
			BROK + BTRT	0.036	z
			BTRT only	0.021	y
National Pollution Discharge Elimination System sites (WT)	20.488	<0.001	BROK only	0.003*	zy
			BROK + BTRT	0.063*	y
			BTRT only	0.080*	z
Human population density (WT)	122.35	<0.001	BROK only	4.828	zy
			BROK + BTRT	5.406	y
			BTRT only	9.731	z
Road crossings (WT)	278.43	<0.001	BROK only	4.000	z
			BROK + BTRT	9.000	z
			BTRT only	21.50	y
Road length (WT)	278.56	<0.001	BROK only	10,624.62	z
			BROK + BTRT	33,107.67	z
			BTRT only	74,231.41	y
Dams (WT)	115.06	<0.001	BROK only	0.287*	z
			BROK + BTRT	1.874*	z
			BTRT only	2.242*	y
Mines (WT)	53.95	<0.001	BROK only	0.0276*	z
			BROK + BTRT	0.0967*	z
			BTRT only	0.248*	y
Urban, low density (WT)	104.56	<0.001	BROK only	2.426	z
			BROK + BTRT	2.707	z
			BTRT only	3.734	y
Urban, medium density (WT)	135.62	<0.001	BROK only	0.000	zy
			BROK + BTRT	0.000	y
			BTRT only	0.038	z