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[Article]

Influences on Brown Trout and Brook Trout Population Dynamics in a Michigan River

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Abstract.—Understanding the influences of local and regional processes on the dynamics of self-sustaining trout populations would help fishery biologists better manage trout populations and protect rivers supporting trout. We explored hypotheses behind long-term temporal variation in density, growth, and survival of brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* using data collected over several decades on Michigan's Au Sable River. Regression models developed for these species emphasized the influence of year-class strength on older age-classes, year-class strength being positively related to spawner abundance for both species and negatively related to high spring streamflow conditions for brown trout. Age-class density was also positively associated with high levels of large woody debris (LWD) in streams. Annual growth increments of brown trout and brook trout were often negatively related to increased age-class density and LWD and positively affected by elevated total phosphorus levels, cool summers, and warm winters. Annual survival of trout from age 0 to age 4 was negatively related to intra- and interspecific age-class density, and in three of seven models, positively associated with levels of LWD. Our findings emphasize the importance of year-class strength to trout population dynamics as well as the need to include collection of regional- and local-scale habitat data in studies of trout population dynamics.

Stream fisheries for brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* in Midwestern states such as Michigan are influenced by a combination of natural and anthropogenic regional- and local-scale factors as well as human-induced changes to local habitats, water quality, and trout mortality (i.e., from angling or influences on other, interacting species). Some management actions (e.g., angler regulation changes, habitat enhancement, water quality improvements) have been undertaken without explicit evaluations of their physical or biological effectiveness (Thompson 2006). Where evaluations have occurred, results can be difficult to interpret if substantial stochastic variation in population levels and long-term changes in stream conditions occur. Such is the case in Michigan's Au Sable River, where more than 40 years of data from a trout population index station have provided the backdrop for testing effects of angler regulations and various ecological hypotheses (e.g., Ball et al. 1973; Clark et al. 1981; Merron 1982; Clark 1983). Still, there is considerable interest in understanding past and present influences of these various factors on long-term trout population dynamics and using this knowledge to steer management toward projects that will provide greatest benefits to the resource.

Changes in habitat conditions over time, particularly nutrient levels, habitat complexity, and river hydrology, are considered by many to be the primary factors responsible for the long-term changes in trout populations in the Au Sable River. Phosphorus may limit fish populations in aquatic systems (Johnston et al. 1990; Hoyer and Canfield 1991; Waite and Carpenter 2000). Ball et al. (1973) concluded that phosphorus most likely limited growth of macrophyte beds (used as trout cover) in the main-stem Au Sable River. Levels of phosphorus in the Au Sable River system have undergone substantial changes over time with notable declines during the 1970s and 1980s (Alexander et al. 1979; Merron 1982; Zorn and Sendek 2001). Likewise, large woody debris (LWD) is probably an important component of habitat in the river and one thought to have undergone substantial change. Flow conditions during incubation and at the time of fry emergence have been negatively correlated with year-class strength and density of older age-classes of stream dwelling brown trout (Strange et al. 1992; Nuhfer et al. 1994; Jensen and Johnsen 1999; Spina 2001; Cattanéo et al. 2002; Lobón-Cerviá 2004). Nuhfer et al. (1994) documented negative effects of high flows on year-

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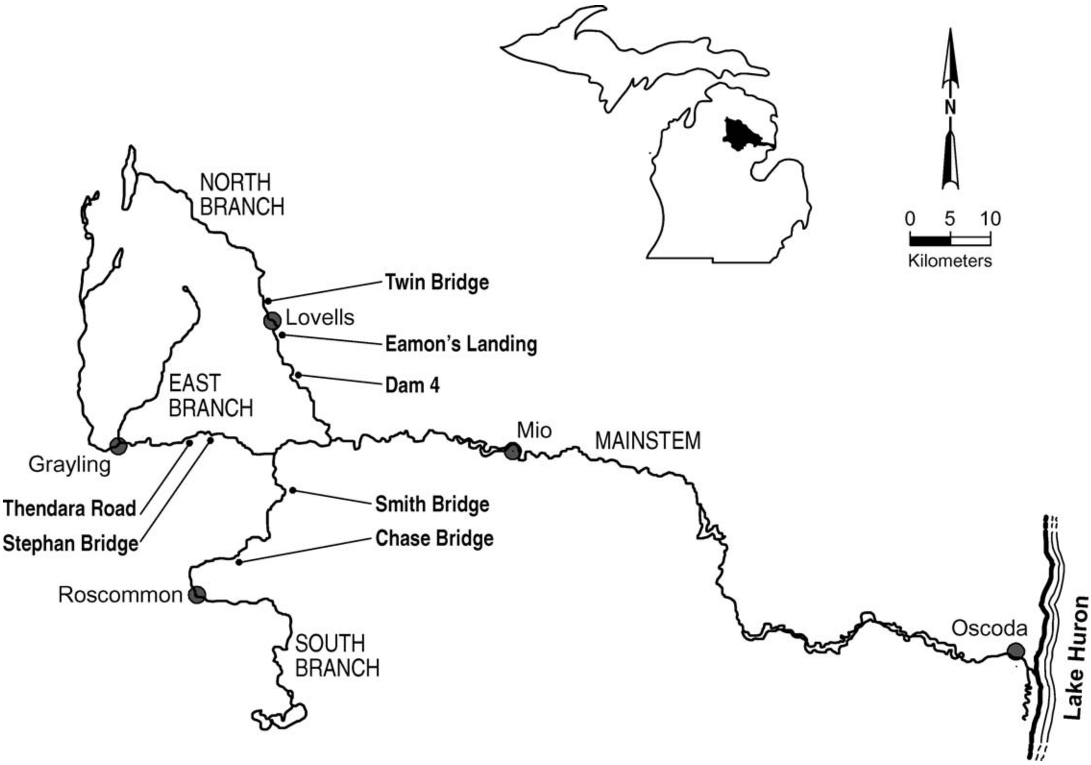

FIGURE 1.—Fish population monitoring stations on the main-stem, North Branch, and South Branch Au Sable River, Michigan.

class strength in the South Branch Au Sable River, but the hydrologic stability and low-gradient (low-velocity) nature of the river's three branches may preclude its general importance as a factor driving fish reproductive success.

The primary objective of this study was to explore potential causes of long-term temporal variation in brown trout and brook trout density, growth, and survival using data collected over several decades on Michigan's Au Sable River. At a coarse scale, we assessed potential effects on trout populations of major and long-term changes in nutrient levels and LWD. Compared with the long-term fish population data for the Au Sable River, information on nutrient levels and LWD was very limited, but we synthesized existing information to assess their potential influences on trout population dynamics and help determine the need for tracking them in future habitat monitoring. In addition, we explored potential influences of other factors on fish populations in the river system.

Methods

Study area.—This study occurred in three branches (the main stem, North Branch, and South Branch) of the Au Sable River, all located in the upper portion of the watershed (Figure 1). Each branch primarily drains glacial outwash and ice-contact outwash deposits of sand and gravel, and is mostly fed by groundwater. Seasonal flow stability is extremely high, with ratios between the 10% and 90% annual exceedance flows ranging from 1.9:1 to 3.1:1 for the three branches (Table 1). Slope or gradient (vertical drop divided by distance) is quite low with all channels having gradient values less than 0.002 (Table 1). Populations of brown trout and brook trout in each branch are sustained entirely by natural reproduction.

Temporal trend data sources and analyses.—Long-term fish population data were obtained for two sites on the main stem of the Au Sable River, two sites on the South Branch, and three sites on the North Branch (Table 1; Figure 1). Fish populations in all sites were assessed in fall (usually September) by two-pass mark–recapture electrofishing using a three-anode, 240-V DC tow barge electrofishing unit. Population estimates were computed for 25-mm length-groups of trout using the Chapman modification of the Petersen mark–recapture method (Ricker 1975). Every year we aged 10 or more trout per 25-mm length-group (if sufficient

TABLE 1.—Physical dimensions, mean July water temperature, and discharge and slope at long-term trout population index stations in the Au Sable River. Mean July temperatures were derived from hourly measurements by electronic thermometers. Flow stability values, expressed as the ratio of the 10% and 90% exceedance flows, are given for rivers for which U.S. Geological Survey gauging station data were available. Slope values were calculated from the 1:100,000-scale National Hydrologic Database as the channel's vertical drop divided by its length for the confluence-to-confluence segment containing the population index station.

Stream and station	Data period	Station length (m)	Station width (m)	Mean July temperature (°C)	Summer discharge (m^3/s)	Flow stability	Slope
Main-stem Au Sable River							
Grayling					2.15	1.92	
Thendara Road	1960–1963 1974–2001	236	29	16.8	6.06		0.0013
Stephan Bridge Road	1960–1963 1974–2003	213	28	16.0	6.54		0.0013
North Branch Au Sable River							
Twin Bridge Road	1957–1967 1973–1996	383	35	17.3	3.54		0.0016
Eamon's Landing	1962–1967 1973–2001	305	33				0.0016
Dam 4 Road	1957–1967 1973–2001	390	32	17.8	5.21		0.0016
South Branch Au Sable River							
Chase Bridge Road	1974–2001	274	19	16.0	2.58		0.0002
Smith Bridge	1974–2003	274	22	16.6	3.99	3.11	0.0017

fish were available) from scales and used the aging results to apportion population estimates by length-groups into estimates by age-group (Table 2). Estimates of egg deposition were made for both species by combining the population estimates by 25-mm group with previous measures of fecundity by 25-mm group for brown and brook trout in the Au Sable River (Alexander 1974) and Wisconsin trout streams (Avery 1985). Growth increments were computed as the change in mean length at age between years for a

TABLE 2.—Variables used in multiple linear regression models for density, growth, and survival of brook trout and brown trout in the Au Sable River.

Variable name	Description
A*x*M*y*QD	Average April *x*–May *y* discharge for a given year divided by the mean April *x*–May *y* discharge for the period of record (includes measured and predicted daily flow values). Periods were 5 April to 5 May, 10 April to 10 May, and 15 April to 15 May.
*x*AVEQD	Average monthly discharge for a given year divided by the mean monthly discharge for the period of record (includes measured and predicted daily flow values). This was calculated for month *x*, with *x* being April or May.
APR*x*DHI	Highest average flow during a period of *x* days in April, *x* being 7 or 14 d.
BKAGE*x*	Number of age-*x* brook trout/ha for ages 0 to 2.
BKEGGYR-1	Estimated brook trout eggs/ha laid the previous fall.
BKAGE*x*P	Age-*x* brook trout/ha in previous fall for ages 0 to 1.
BKLN*x*	Mean length (mm) of age-*x* brook trout for ages 0 to 2.
BKINC*x*	Brook trout growth increment (mm) from previous fall to fall at age-*x* for ages 0 to 2.
BNAGE*x*	Number of age-*x* brown trout/ha for ages 0 to 5.
BRNEGGS	Estimated brown trout eggs/ha laid the previous fall.
BNAGE*x*P	Age-*x* brown trout/ha in the previous fall for ages 0 to 4.
BNLN*x*	Mean length (mm) of age-*x* brown trout for ages 0 to 4.
BNINC*x*	Brown trout growth increment (mm) from previous fall to fall at age-*x* for ages 0 to 4.
BNTSIZE	Minimum brown trout size limit for harvest. The lower end of the slot was used during the period of slot limits; a 510-mm minimum size was used to simulate no-kill regulations.
BKTSIZE	Minimum brook trout size limit for harvest. A 300-mm minimum size was used to simulate no-kill regulations.
PREDATORS	Age-3 and older brown trout/ha.
LWD	Large woody debris quality and quantity rating (scale; 0–10, with 10 being best).
MAYAUGC	Average water temperature (°C) from 1 May to 31 August.
MINUS*x*	Number of days in previous winter having a minimum air temperature less than *x*°C, for *x* values of −10, −15, −20, and −25°C.
MINKHAR	Annual estimated mink harvest based on 2003 Michigan DNR Wildlife Division Report.
GBHERON	Index of abundance of great blue herons from the Breeding Bird Survey trend for 1966–2003.
PERRELEA	Fraction of legal-sized trout that were voluntarily released based on (and extrapolated from) 1976–1990 data in Clark and Alexander (1992).
TOTAL_P	Hypothesized total phosphorus concentration (mg/L).

given year-class. Annual survival was calculated as the proportion of a year-class surviving between fall surveys. We identified annual survival values higher than 150% as outliers (probably related to immigration or small sample sizes for older age-group s of trout) and removed them from the analysis.

Despite a long time series of fisheries data, relatively few local-scale habitat data span the more than 40-year period of trout population estimates for the Au Sable River. Nevertheless, we assembled habitat information on the river from a variety of sources to enable us to evaluate influences of several potentially important habitat parameters (Table 2). Data on spring flow conditions at the expected time of brown trout swim-up (Nuhfer et al. 1994) were obtained from U.S. Geological Survey (USGS) hydrologic records or predicted from nearby USGS-gauged sites when gauge data did not occur for the reach or time period of interest. Because of differences in catchment area (discharge) and years of fish data among sites on each branch, we standardized discharge values for each river branch by dividing the flow from an individual year by the average value for years when fish surveys occurred on the branch.) Since 1990, water temperatures have been measured in the river with electronic recording thermometers during the summer growing season (May through August), and water temperatures in previous years could readily be predicted from air temperatures recorded at a nearby National Weather Service station in Grayling, Michigan (mean R^2 for predictions $=$ 0.91). Data to describe severity of winter temperatures were also available from this station.

We synthesized existing information on nutrient and LWD levels for the Au Sable River to test our hypotheses of their potential influences on trout population dynamics. Data on total phosphorus and total phosphate were obtained from the U.S. Environmental Protection Agency's STORET database (www.epa.gov/storet/dbtop.html), plotted, and used to visually estimate summer total phosphorus levels in the three branches of the Au Sable River for each year with fish surveys. We considered values obtained as rough estimates since we often had to interpolate values for extended periods (sometimes spanning 10 years or more) for which measurements were unavailable (see Appendix Table 7). We rated general quantity and quality of LWD in each branch on a 0–10 scale (10 being highest) based primarily upon Michigan Department of Natural Resources (MDNR) records of habitat improvement activities during the 1970s and 1980s, LWD counts from 1998 and 1999 (MDNR Fisheries Division, unpublished data), and an opinion survey of six MDNR employees and a habitat improvement crew supervisor well-acquainted with the river. Each employee surveyed had over 20 years of experience working on these river reaches and their periods of work overlapped such that the entire study period could be described. The quality and quantity of the phosphorus and LWD data (Appendix) only allow for coarse assessment of their influence on trout density, growth, and survival.

Other variables were also included to assess their potential for explaining the additional variation in fish population data (Table 2). We developed variables to reflect changes in minimum size limits over the study period and an increase in voluntary release of legal-sized fish by anglers over time (Clark and Alexander 1992). Influence of brown trout as predators on brook trout was assessed by combining estimates of age-3 and older brown trout into a predator variable. We also computed indices of the abundance of the predators mink *Mustela vison* and great blue heron *Ardea herodias* from existing statewide trend information (Table 2).

We developed multiple linear regression (MLR) models to explain variation in numerical density by age-class (up to age 5 for brown trout and age 2 for brook trout), annual growth increment by age-class (up to age 3 for brown trout and age 2 for brook trout), and annual survival (up to age 4 for brown trout and age 3 for brook trout). We did not model these parameters for older age-classes of either species due to their relatively low densities at sample sites. Fish data for each year at a site were treated as an individual record rather than pooled with data from the other sites on that branch because of differences among sites in years when surveys occurred (Table 1). We used Pearson correlations of dependent and predictor variables as well as correlations between predictor variables and model residuals to guide variable selection. When curvilinear relations were evident predictor variables were $\log_{10}$ transformed before being entered into the MLR models. Usually, relatively few predictor variables were significantly correlated with the response variable, but sometimes several variables of a given type (e.g., spring flow or winter severity) were correlated. Occasionally some obviously spurious correlations occurred. To prevent inclusion of spuriously correlated variables in a model, we only entered variables hypothesized to have causal relations with the response variable and variables were entered or removed manually. Variables included in final MLR models were selected based on the existence of plausible causal relations between them and the response variables, the amount of variation they explained, and their significance in the model. All variables included were significant at $P \leq 0.05$.

We evaluated the relative influence of predictor

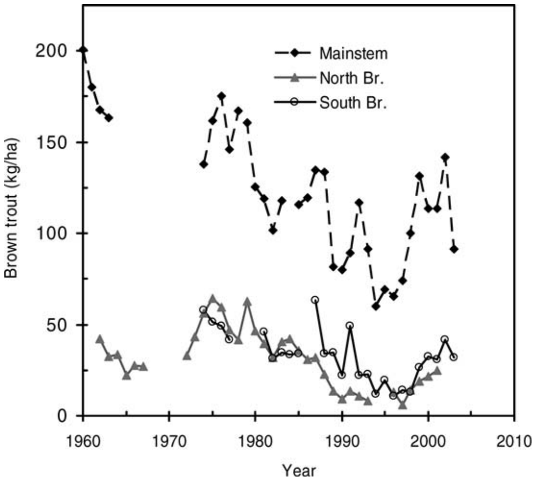

FIGURE 2.—Total fall biomass density of brown trout in three branches of the Au Sable River based on surveys at the following index stations: Stephan Bridge (main stem), Eamon's Landing (North Branch), and Smith Bridge (South Branch). Similar trends occurred for numerical density, but biomass densities are shown because they are less influenced by the annual variation in year-class strength.

variables on the response variable by comparing their standardized regression coefficients. The standardized regression coefficient attempts to standardize the measurement scale of each model variable by estimating the change (in standard deviations) in a response variable for a change of one standard deviation in a predictor (SPSS 1993). Thus, the relative influence of a predictor variable in the regression is proportional to the absolute value of its standardized regression coefficient.

Results

Temporal Trends in Density by Age-Class

Trout populations in the Au Sable River varied considerably over the study period, some sites generally supporting greater trout densities than other sites (Figure 2; Table 3). For example, the mean (range) of age-0 brown trout densities was 1,359 (497–2,253) fish per hectare for the main stem at Stephan Bridge, 532 (164–1,344) fish per hectare for the North Branch at Eamon's, and 470 (124–1,170) fish per hectare in the South Branch at Smith Bridge. However, temporal synchrony in densities among river branches seemed apparent as highest density levels occurred at all sites in the mid-1970s, and lowest densities occurred at all sites in the mid-1990s (Figure 2).

Regression models developed for brown trout emphasized the influences of several factors, the most important being year-class strength and its effect on subsequent densities of all age-groups (Table 4). Density of the year-class the previous year (and potential egg deposition for age-0 fish) was generally the most heavily weighted variable in all models based on standardized regression coefficients. Data from these sites and other Michigan rivers suggest that spawning stock can limit density of age-0 brown trout (Figure 3). The magnitude of deviation from average spring flows had a significant negative effect on fall density of age-0 brown trout, though the model explained only 18% of fall density of age-0 fish. However, inclusion of the age-0 density of the previous year in the model to predict age-1 brown trout density enabled 75% of variation to be explained (Table 4). Similarly, models that incorporated year-class strength explained 71% and 65% of the variation in age-2 and age-3 density, respectively. Less variation could be explained for older age-groups, probably reflecting variability due to uncertainty in estimates, fish movements, and other factors. Nevertheless, flow-induced effects on year-class strength and its subsequent influence on older age-classes of brown trout may explain shared temporal trends in brown trout abundance in the three branches of the Au Sable River (Figure 2).

Several variables had recurring and consistent influences in the six models for density of brown trout age-classes. Large woody debris had a positive influence on age-1 and age-2 densities, while different measures of winter severity (colder winter air temperatures) were negatively related to year-class density in three models.

Significant models were developed for age-0, age-1, and age-2 brook trout densities, up to 54% of variation being explained by these models (Table 4). Density of the year-class during the previous year (and potential egg deposition for age-0 fish) was the most heavily weighted variable in all models based on standardized regression coefficients. Large woody debris had a positive influence on age-1 and age-2 brook trout densities, while density of "predator-sized" brown trout was negatively associated with age-0 and age-1 fish densities.

Temporal Trends in Growth and Annual Survival

Annual growth increments of brown trout and brook trout were influenced by several common factors, up to 44% of the variation in growth being explained (Table 5). Density of brown trout or brook trout in the same age-class had a negative "density-dependent" effect on growth of brown trout and brook trout age-classes in six of seven models. Large woody debris had consistent negative effects on growth in five models and was the most heavily weighted variable in three of

TABLE 3.—Mean, minimum (min), maximum (max), and coefficient of variation (CV) of density, annual growth increment, and annual survival of brook and brown trout in the main-stem, North Branch, and South Branch Au Sable River. The CV for a parameter was equal to its standard deviation divided by its mean.

Species and age	Main stem				North Branch				South Branch			
	Mean	Min	Max	CV	Mean	Min	Max	CV	Mean	Min	Max	CV
Density (number/ha)												
Brook trout												
Age 0	752	177	1,723	0.4	1,809	530	4,593	0.5	536	8	1,471	0.6
Age 1	174	22	775	0.7	320	100	893	0.5	104	4	452	0.7
Age 2	19	0	115	1.1	31	2	190	1.0	6	0	24	0.8
Brown trout												
Age 0	944	142	2,253	0.6	815	73	3,156	0.7	577	34	1,420	0.6
Age 1	378	118	775	0.5	171	37	442	0.5	155	38	399	0.5
Age 2	200	30	537	0.6	67	3	214	0.7	60	9	160	0.6
Age 3	96	9	368	0.8	20	0	112	1.1	29	2	90	0.7
Age 4	11	0	46	0.9	4	0	18	1.1	9	0	45	1.0
Age 5	1	0	8	2.0	0	0	6	2.4	1	0	14	2.3
Annual growth increment (mm)												
Brook trout												
Age 0	85	75	99	0.1	84	73	98	0.1	92	79	112	0.1
Age 0 to age 1	69	37	95	0.2	79	56	99	0.1	73	55	99	0.1
Age 1 to age 2	63	29	117	0.3	54	30	84	0.2	64	27	107	0.3
Brown trout												
Age 0	94	77	106	0.1	95	82	109	0.1	99	85	113	0.1
Age 0 to age 1	83	60	116	0.1	101	75	134	0.1	89	67	105	0.1
Age 1 to age 2	67	43	108	0.2	76	46	124	0.2	80	45	115	0.2
Age 2 to age 3	59	33	102	0.3	66	7	126	0.3	67	15	120	0.3
Annual survival (proportion)												
Brook trout												
Age 0 to age 1	0.26	0.05	1.05	0.7	0.19	0.07	0.46	0.4	0.26	0.04	1.23	0.9
Age 1 to age 2	0.13	0.00	0.89	1.1	0.11	0.00	1.03	1.1	0.08	0.00	0.50	1.1
Age 2 to age 3	0.07	0.00	1.33	3.3	0.04	0.00	1.00	3.3	0.08	0.00	1.50	3.3
Brown trout												
Age 0 to age 1	0.47	0.12	1.12	0.5	0.26	0.06	1.45	0.7	0.30	0.11	1.12	0.6
Age 1 to age 2	0.51	0.23	0.93	0.4	0.38	0.07	0.90	0.5	0.37	0.11	0.95	0.5
Age 2 to age 3	0.46	0.06	0.96	0.5	0.29	0.00	1.10	0.7	0.53	0.07	1.37	0.6
Age 3 to age 4	0.16	0.00	0.81	1.0	0.26	0.00	1.32	1.0	0.36	0.00	1.00	0.8

them. Total phosphorus had a positive effect on growth of age-0 and age-1 fish of both species. Relatively warm winters were associated with better growth for age-2 and age-3 brown trout, while warm summers were related to poorer growth of trout in three of seven models. Coefficients of variation (standard deviation divided by the mean) in annual growth increments were several times lower than those for age-class density (Table 3) suggesting there was less variation to explain in the growth data.

Our models explained up to 68% of the variation in annual survival of age-0 to age-3 brook trout and that of age-0 to age-4 brown trout (Table 6). Year-class density had negative effects on survival in all models (Table 6), suggesting that intraspecific (and sometimes interspecific) interactions influenced survival. Plots of year-class density versus survival to the next year (e.g., Figure 4) suggested that high densities may limit survival or trigger emigration from the reach. Likewise, estimates of survival for very small year classes exceeded 100% in some years, probably indicating immigration into the reach between years (Figure 4). Annual survival of age-0 and age-1 brown trout and age-1 brook trout was positively associated with levels of LWD (Table 6). Higher minimum size limits for angler harvest appeared to enhance survival of age-2 brown trout. Increased catch-and-release behavior of anglers was associated with reduced age-1 brook trout survival (Table 6). Less variation in annual survival could be explained for older age-classes of each species.

Discussion

Regional Influences on Population Dynamics

Our analyses suggest that the density, growth, and survival of brown trout and brook trout in Michigan's low-gradient streams are influenced by a combination of population-level processes and local and regional habitat factors. For example, the variation in age-0 year-class density was difficult to explain but was

TABLE 4.—Multiple linear regression models developed for the densities (number/ha) of brown and brook trout in the Au Sable River system. All regression models and standardized coefficients shown were significant at the 0.05 level. See Table 2 for variable descriptions.

Age	Total df	Adjusted R^2	SE of model estimates	Variables	Standardized coefficients
Brown trout					
Age 0	204	0.18	490	BRNEGGS	0.39
				A10M10QD	−0.20
Age 1	169	0.75	79	LWD	0.48
				BNAGE0P	0.42
				TOTAL_P	0.32
				MINUS10	−0.09
Age 2	169	0.71	53	BNAGE1P	0.74
				LWD	0.22
				TOTAL_P	−0.12
Age 3	201	0.65	30	BNAGE2P	0.81
				MINUS20	−0.13
Age 4	201	0.24	7	BNAGE3P	0.36
				BNTSIZE	0.27
				MINUS15	−0.16
Age 5	201	0.06	2	BNAGE4P	0.25
Brook trout					
Age 0	207	0.39	672	BKEGGYR-1	0.52
				PREDATORS	−0.21
Age 1	170	0.54	109	BKAGE0P	0.64
				PREDATORS	−0.29
				LWD	0.25
Age 2	170	0.47	20	BKAGE1P	0.69
				LWD	0.16

positively associated with spawner (or egg) density the previous fall and negatively influenced by high flow conditions at or near the time of fry emergence in spring (Table 4). Once age-class strength was determined, densities of several subsequent age-classes could be predicted with reasonable accuracy.

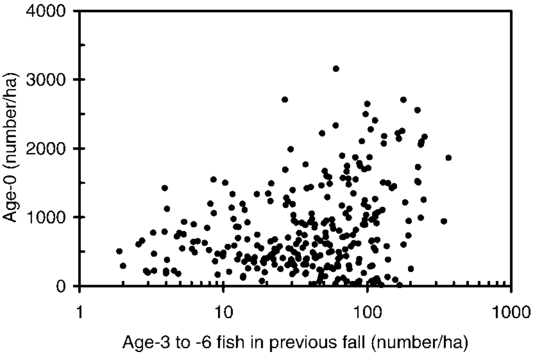

FIGURE 3.—Relationship between the density of fall age-0 brown trout and that of age-3 to age-6 brown trout (spawning-age fish) the previous fall. Data are from electrofishing surveys of 17 Michigan rivers conducted between 1957 and 2003 by state agency personnel. Surveyed rivers are as follows: South Branch Paint River; main-stem, North Branch, and South Branch Au Sable River; Hunt Creek; Gilchrist Creek; Manistee River; North Branch and South Branch Boardman River; Baldwin River; Houghton Creek; Hersey River; Platte River; Spring Brook and Silver Creek (Kalamazoo River tributaries); and main-stem and Little South Branch Pere Marquette River.

Hydrologic influences on brown trout year-class strength have been observed mostly in high-gradient, mountainous streams in the United States and Europe (e.g., Strange et al. 1992; Nehring and Anderson 1993; Spina 2001; Cattanéo et al. 2002, 2003; Lobón-Cerviá 2004; Lobón-Cerviá and Rincón 2004). Aside from our study and Nuhfer et al.'s (1994) study on the South Branch Au Sable River, such relationships have not been noted for low-gradient trout streams in glaciated Midwestern states. While other studies have attributed negative flow effects to redd scouring, we think the displacement and mortality of recently emerged fry is a more plausible explanation for the negative relationship between 10 April–10 May discharge and brown trout recruitment in the Au Sable River because the period corresponds to predicted fry emergence (Zorn and Nuhfer 2007, this issue). Water velocities sufficient to displace brown trout alevins and fry (Ottaway and Forrest 1983) are common in unprotected microhabitats in Michigan streams during spring floods. In addition, spring observations of gravel riffles in the Au Sable River system and in Hunt and Gilchrist creeks reveal only localized areas of gravel scour due to spring floods.

The relatively weak effect of flow in the MLR models may result from several factors. First, the Au

TABLE 5.—Multiple linear regression models developed for annual growth increments (mm) of brown and brook trout in the Au Sable River system. All regression models and standardized coefficients shown were significant at the 0.05 level. See Table 2 for variable descriptions.

Age	Total df	Adjusted R^2	SE of model estimates	Variables	Standardized coefficients
Brown trout					
Age 0	183	0.36	4.8	LWD	−0.45
				BKAGE0	−0.42
				TOTAL_P	0.36
				APRAVEQD	0.16
Age 1	168	0.32	9.0	TOTAL_P	0.57
				LWD	−0.33
				BNAGE1	−0.28
Age 2	168	0.23	12.5	BNAGE2	−0.30
				MINUS25	−0.25
				LWD	−0.23
				MAYAUGC	−0.20
Age 3	198	0.14	17.9	BNAGE3	−0.38
				MAYAUGC	−0.20
				MINUS25	−0.20
Brook trout					
Age 0	186	0.44	4.9	LWD	−0.52
				BKAGE0	−0.51
				TOTAL_P	0.29
				MAYAUGC	−0.27
Age 1	169	0.11	9.9	LWD	−0.36
				TOTAL_P	0.22
Age 2	161	0.12	15.8	BKAGE2	−0.36

Sable River, like many Michigan trout streams, is among the most hydrologically stable rivers in the United States, being 10 or more times stable than trout streams in mountainous areas (Zorn and Sendek 2001). For example, 10% annual exceedance flow of the main-stem Au Sable River is only about 1.9 times greater than the 90% annual exceedance flow, and in the South Branch Au Sable River, the least stable hydrologically, the 10% exceedance flow is only 3.1 times higher than the 90% exceedance flow. As such, spring flow conditions (i.e., those emerging trout must contend with) vary relatively little from year to year. Flow effects may have been further masked since the estimated time when most brown trout fry were predicted to emerge from redds in the Au Sable River

TABLE 6.—Multiple linear regression models developed for annual survival (surviving fraction) of brown and brook trout in the Au Sable River system. An “L” preceding the name of a fish density variable indicates the variable was $\log_{10}$ transformed. All regression models and standardized coefficients shown were significant the 0.05 level. See Table 2 for variable descriptions.

Age interval	Total df	Adjusted R^2	SE of model estimates	Variables	Standardized coefficients
Brown trout					
Age 0 to 1	167	0.68	0.11	LBNAGE0	−0.64
				LWD	0.54
				TOTAL_P	0.21
				LBKAGE0	−0.15
Age 1 to 2	167	0.20	0.17	LWD	0.41
				LBKAGE1	−0.16
Age 2 to 3	200	0.10	0.24	BNTSIZE	0.23
				LBKAGE2	−0.19
Age 3 to 4	196	0.13	0.26	LBNAGE3	−0.36
Brook trout					
Age 0 to 1	198	0.23	0.12	LBKAGE0	−0.53
				PREDATORS	−0.25
Age 1 to 2	169	0.12	0.10	LBKAGE1	−0.23
				PERRELEA	−0.22
				LWD	0.16
Age-2 to 3	188	0.03	0.12	LBKAGE2	−0.19

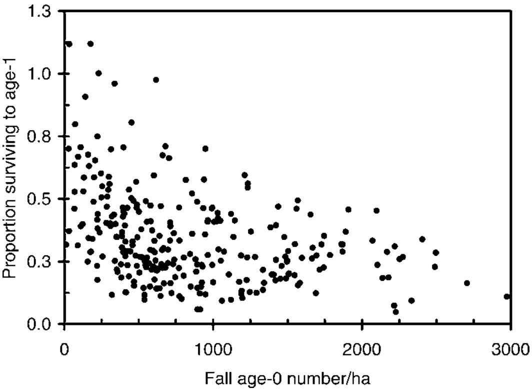

FIGURE 4.—Relationship between fall age-0 density of brown trout and the proportion of fish surviving to age 1 the following fall for 17 Michigan rivers (see Figure 3 for data sources).

was usually after peak spring runoff (Zorn and Nuhfer 2007, this issue).

We hypothesize that water velocity conditions have a proximal effect on the survival of emerging trout fry and subsequent reproductive success of trout in Michigan streams. We also suspect that velocity conditions do not change dramatically, even in years when flows are relatively high at emergence time, owing to the low-gradient nature of most Michigan trout streams. Since effects of spring discharge are most evident during years with extremely high or low spring discharges (which occur infrequently in stable rivers), population estimates need to span long periods to capture these events and enable separation of flow effects from other stochastic processes. Further research into the relationships among current velocity, stream discharge, channel gradient, velocity refuges (e.g., LWD, riparian wetlands, or other edge habitats), and their influences on brown trout fry survival would be beneficial. Finally, the statistically weak effects of spring flows on year-class strength could potentially be strengthened if stream discharge gauges occurred at each index station and if electrofishing stations were longer, both of which were beyond our control. Nevertheless, we confirmed the importance of spring flows to brown trout reproduction in low-gradient Midwestern streams.

We are unaware of other studies demonstrating the effects of flow conditions during fry emergence on brook trout reproductive success, and our regression analyses for brook trout in the Au Sable River did not identify such flows as predictors of age-0 brook trout density (Table 4). However, temporal synchrony in densities of brook trout age-groups among hydrologically stable Michigan rivers suggest that regional effects of climate on stream hydrology may influence year-class strength similarly across large portions of Michigan (Zorn and Nuhfer 2007, this issue).

The regional-scale effects of climate were not only evident on trout year-class strength. We found that abundance of age-1, age-3, and age-4 brown trout was adversely affected by winter severity, as measured by the number of days with air temperatures below −10, −15, and −20°C (Table 4). Declines in condition and lipid levels during winter that could lead to reduced survival have been documented for brown trout and brook trout in Canadian rivers (Cunjak and Power 1986, 1987a; Cunjak 1988) and for brook trout and rainbow trout *Oncorhynchus mykiss* in Appalachian streams (Whitworth and Strange 1983). Winter ice conditions may also cause mortality of fishes through a variety of mechanisms including suffocation, stranding, and displacement from resting positions (Power et al. 1993). Benson (1955) documented anchor ice formation in a Michigan trout stream when air temperatures fell below about −15°C. Likewise, growth of several age-classes of brown trout and brook trout in the Au Sable River was reduced when warm summer or severe winter conditions occurred (Table 5). It is likely that reduced growth during warm summers occurred because metabolic demands exceeded caloric intake at the higher temperatures. Reduced summer growth rates for trout have been attributed to limited food supplies in several Michigan rivers (Cooper 1953; Ellis and Gowing 1957) as well as in Canadian and Appalachian streams (Cunjak et al. 1987; Ensign et al. 1990). Cunjak et al. (1987) suggested that energy intake during colder winters was reduced by a combination of lower food consumption rates and slower gastric evacuation rates. Survival of brook trout may be enhanced indirectly when thermal conditions are adverse for its competitor and predator, brown trout (Table 4; Table 6). Brook trout comprised 42% of winter diets of brown trout at least 300 mm total length in the special regulations waters of the North Branch Au Sable River during the 1960s (Alexander 1977). Colder winters would lower both consumption and digestion rates of brown trout.

Local Influences on Population Dynamics

In addition to looking at regional influences, our study demonstrated the importance of local-scale factors to trout population density, growth, and survival. Density of older age-classes for both species was heavily influenced by year-class strength, which ultimately was most strongly associated with adult density the previous fall or its surrogate egg density. Localized effects of estimated egg deposition intensity were the most influential variables explaining variation in age-0 density of both brown trout and brook trout in the Au Sable River (Table 4). Since our fish surveys occurred about a month before the spawning season, one may infer that mature fish were near their spawning areas, and our estimates of egg (spawner) density provided a reasonable index of actual densities of eggs deposited in study reaches. Positive relationships between redd density and density of age-0 and age-1 and older trout have previously been reported for brown and brook trout in the Pigeon River, Michigan (Benson 1953) and brown trout in a Pennsylvania stream (Beard and Carline 1991). Both studies suggest that young trout show limited dispersal from spawning sites, which in turn implies positive associations among spawner, redd, egg, and young trout densities and overall differences in trout abundance at various locations along a stream.

The positive relation between our relatively coarse index of LWD and the density of several age-classes of brown trout and brook trout (Table 4) may relate the ability of LWD to diversify depth, velocity, substrate, and cover conditions in rivers, thereby creating additional edge habitat for many size-classes of fish (Keller and Swanson 1979; Maser and Sedell 1994). The additional "packing" of the stream with fish that occurred when LWD was abundant may have led to enhanced survival (Table 6), but less food resources being available per fish resulting in reduced growth (Table 5). The importance of LWD here and in other studies (e.g., Cunjak and Power 1987b; Flebbe and Dolloff 1995; Dolloff and Warren 2003) suggests it is worthy of quantification in long-term studies of trout population dynamics.

Total phosphorus also had consistent effects on brown trout and brook trout growth. Growth of age-0 and age-1 fish of both species was positively associated with total phosphorus, possibly reflecting increased food (i.e., invertebrate) production associated with higher nutrient levels (Eyman 1969; Johnston et al. 1990; Perrin and Richardson 1997; Biggs et al. 2000). The positive influence of total phosphorus on survival of brown trout from age 0 to age 1 (Table 6) may reflect increased food availability for age-0 fish that subsequently enabled them to be in better condition before winter. Hunt (1969) observed that overwinter survival of fingerling brook trout in a Wisconsin stream generally increased when fingerlings were large. Brown trout from more fertile streams grew faster, became sexually mature earlier, exhibited higher fecundity at a given age and produced larger eggs than trout from less fertile systems (McFadden et al. 1965). In the main-stem Au Sable River the mean length of age-3 brown trout (at annulus formation) during a period of high nutrient loading was 54 mm longer than during a period after discharges were diverted (Merron 1982). More and larger spawners would result in greater egg deposition, which in turn could potentially result in a greater density of age-0 fish, and these larger year-classes would lead to more fish in older age-groups. Thus, changes in river nutrient levels can cascade throughout the system, substantially affecting overall population abundance. Such effects were documented when sewage discharges into the main-stem and South Branch Au Sable River were discontinued (Merron 1982). The relatively modest effects of phosphorus in many of our regression models probably occurred because only a small proportion of our total number of population estimates were made during years when nutrient loadings were notably high. Clearly, nutrient conditions should be considered part of habitat and included in programs designed to monitor stream fish population levels.

Our analyses also demonstrated the importance of biotic interactions to understanding the population dynamics of these species. Effects were most apparent for brook trout where age-0 and age-1 densities and survival were tempered by densities of predator-sized (i.e., age-3 and older) brown trout (Table 4; Table 6). In addition, increased catch-and-release behavior of anglers appeared to be detrimental to age-1 brook trout survival, possibly because increased release activities limited depletion of populations of large, predatory brown trout (Table 6). Negative effects of brown trout on co-existing brook trout stocks have been shown previously by Waters (1983) and Grant et al. (2002). Negative effects of intra- and interspecific competition were quite apparent in growth and survival models with significant negative coefficients occurring for competitors in models developed for both species and all age-classes, except growth of age-1 brook trout (Table 5). Again, such findings have been previously documented (e.g., Jenkins et al. 1999) and our results support their findings. Density-dependent effects of intraspecific competition on annual survival were apparent in five of seven models, and interspecific competition was related to variation in annual survival of brown trout from age 0 to age 3 (Table 6). In fact, cohort densities had the strongest effect (i.e., standardized regression coefficient) in five of seven models for age-class survival. Higher mortality rates of dominant brown trout cohorts have also been demonstrated in a Spanish river (Lobón-Cerviá 2005). Inverse density-dependent survival of older brook trout in Hunt Creek, Michigan was reported by McFadden et al. (1967). Elliott (1994) noted that density-dependent regulation of older age-groups of brown trout was unlikely to occur in harsh environments. Density-dependent mechanisms may have operated in our study streams because conditions were relatively benign, except during the winter (Cunjak 1996).

Limitations of the Models

Several attributes of the fish and habitat data used in this study limit the robustness of our findings. Trout population estimates were made in relatively short (<400 m) reaches and may not have always provided an accurate index of actual population density. Inaccurate age-class density estimates might have occurred occasionally, particularly when densities were low for older age-classes. We tried to minimize this effect by excluding the oldest age-classes from our models, although estimation error may have occurred for some age-classes modeled.

The LWD and total phosphorus data represented a mix of expert opinion and quantitative data. The LWD indices were almost entirely subjective, but were based upon opinions of reliable persons well acquainted with the Au Sable River for several decades and were supported by limited habitat improvement records and LWD counts. Thus, we have reasonable confidence in these data. The total phosphorus trends also represent a combination of real data and projections, including a review by water quality specialists with the Michigan Department of Environmental Quality Surface Water Quality Division. Projections before the period of data collection were primarily speculative, but influenced by retired biologists (e.g., G. Alexander, MDNR, personal communication) with historical insight into past river conditions. In summary, LWD and total phosphorus values were determined independently of our analyses and though their accuracy could be questioned, we had no reason to discount them as being intentionally biased. That these variables were significant in our study and in work of other researchers supports their importance and underscores the need for including them in long-term studies of fish population dynamics.

The strong effects of some habitat variables (e.g., total phosphorus) may not be as striking in future analyses as in our study because of the historic changes in river conditions that occurred during our study period. For example, roughly 10-fold reductions in estimated phosphorus levels occurred in portions of the Au Sable River (Appendix). Major changes in water quality in the Au Sable River during the course of this study were associated with several events: (1) a state hatchery that discharged nutrients into the East Branch Au Sable River about 1 km from the main-stem Au Sable River was phased out in 1966 (Figure 1); (2) discharge of effluent from the Grayling wastewater treatment plant into the main-stem Au Sable River was stopped in 1971; (3) a major upgrade to the Roscommon wastewater treatment plant, which discharged into the South Branch Au Sable River, in 1974 (Figure 1); (4) activities at a military base that may have influenced nutrient levels in the North Branch Au Sable River; and (5) other changes resulting from passage of the Clean Water Act in 1972 (Coopes et al. 1974). Changes of similar magnitude may not occur in the foreseeable future. Similar changes in LWD occurred in portions of the river during major habitat construction periods in the late 1970s and late 1990s (Appendix).

Lack of data for some variables limited our ability to examine their importance. Stream discharge data were missing for some years on the main-stem Au Sable River, but could be readily predicted from adjacent gauges. Use of data from the main-stem Au Sable River as a surrogate for flow conditions on the North Branch Au Sable River was not an ideal solution but seemed reasonable, especially given the high correlations in flow among rivers in the area. However, site-specific data may have resulted in tighter linkages between spring flow and age-0 trout density.

We explored other variables that also changed over time that we thought might have significant effects on trout population dynamics. These included indices of avian and mammalian predator (mink and great blue heron) density, changes in angler harvest and release practices, and changes in minimum size limits. Predator data were not locally based but rather reflected long-term trends at the state or multistate level. We considered these data to be of limited reliability and included them in the initial analysis, but found only one instance of significance in a model (great blue heron in the age-1 brook trout density model). Thus, we excluded them from the final models. Minimum size limits were only significant in the model of age-4 brown trout density and for survival of age-2 brown trout. However, we consider this an inadequate evaluation of the importance of size limits because the relatively short length of reaches sampled limited our ability to accurately quantify abundance of older trout. Still, this finding suggests that more restrictive regulations (e.g., increasing the minimum size limit from 20 to 30 cm) may favor increased brown trout populations in the Au Sable River.

Management Implications

Our study underscores several key points of interest to fishery managers. First, it emphasized the strong positive relationship between abundance of younger and older age-classes of trout and the importance of having dense populations of age-0 trout. Age-0 trout densities were positively influenced by egg density and negatively associated with high spring flows roughly at the time of fry emergence. Thus, management should support actions that protect spawning stocks and a river's natural flow patterns, while discouraging those that will decrease its hydrologic stability. Obviously, streamflow monitoring is needed to document its influence on trout reproduction as well as human influences on a river's flow characteristics. Second, it showed the strong influence of regional climatic factors beyond direct management control that must be considered when examining fish population trends. Third, it highlighted potential influences of LWD on trout density, growth, and survival, and supported the use of quantitative LWD inventory work in fish habitat surveys. It also stressed the potentially significant effects of nutrient levels on trout populations, acknowledged the importance of historic water quality changes to present fish community conditions, and emphasized the need for continued nutrient monitoring. The potential effects of natural and human predators were noted along with the need for specialized data to assess their influences. In summary, maintaining self-sustaining trout populations for the long term will require an integrated ecosystem approach to management involving multiple perspectives (e.g., regional climate, land use and river hydrology, local habitat influences, water quality, angling, and other biota).

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Appendix: Large Woody Debris and Total Phosphorus Concentrations

TABLE A.1.—Hypothesized ratings of quality and quantity of large woody debris (LWD) and estimated total phosphorus concentrations in the main-stem, North Branch, and South Branch Au Sable River for years when brook and brown trout population estimates were made. Scores for LWD ranged from 0 to 10, with 10 indicating the best conditions among branches during the study period. Total phosphorus estimates were derived from the U.S. Environmental Protection Agency's STORET database.

	LWD			Total phosphorus (mg/L)		
Year	Main stem	North Branch	South Branch	Main stem	North Branch	South Branch
1957		5.3			0.019	
1958		5.2			0.020	
1959		5.1			0.020	
1960	9.0	5.0		0.108	0.021	
1961	8.8	4.9		0.112	0.022	
1962	8.7	4.8		0.114	0.023	
1963	8.6	4.7		0.116	0.025	
1964	8.5	4.6		0.118	0.026	
1965	8.4	4.5		0.118	0.027	
1966	8.3	4.4		0.117	0.030	
1967	8.2	4.3		0.111	0.032	
1968	8.0	4.2		0.100	0.034	
1969	7.9	4.1		0.087	0.036	
1970	7.8	4.0		0.081	0.038	
1971	7.7	4.5		0.079	0.041	
1972	7.6	4.4		0.077	0.043	
1973	7.5	4.3		0.070	0.045	
1974	7.7	4.2	4.1	0.064	0.046	0.038
1975	8.0	4.1	4.0	0.055	0.046	0.034
1976	8.3	4.0	3.9	0.046	0.044	0.030
1977	8.5	4.0	3.8	0.040	0.042	0.026
1978	8.8	3.9	3.7	0.034	0.040	0.022
1979	9.0	3.8	3.5	0.031	0.037	0.020
1980	8.9	3.7	3.4	0.030	0.034	0.018
1981	8.8	3.6	3.3	0.027	0.031	0.017
1982	8.7	3.5	3.2	0.026	0.028	0.016
1983	8.5	3.4	3.1	0.024	0.026	0.016
1984	8.4	3.3	3.0	0.023	0.023	0.016
1985	8.3	3.2	2.9	0.022	0.022	0.015
1986	8.1	3.1	2.8	0.020	0.020	0.015
1987	8.0	3.0	2.7	0.019	0.019	0.014
1988	7.9	2.9	2.5	0.018	0.017	0.014
1989	7.8	2.8	2.4	0.016	0.016	0.014
1990	7.7	2.8	2.3	0.015	0.016	0.013
1991	7.5	2.7	2.2	0.014	0.015	0.013
1992	7.4	2.6	2.1	0.013	0.014	0.013
1993	7.3	2.5	2.0	0.012	0.014	0.013
1994	7.1	2.4	1.9	0.011	0.013	0.013
1995	7.0	2.3	1.7	0.011	0.013	0.013
1996	8.0	2.2	1.6	0.011	0.012	0.013

TABLE A.1.—Continued.

Year	LWD			Total phosphorus (mg/L)		
	Main stem	North Branch	South Branch	Main stem	North Branch	South Branch
1997	9.0	2.1	1.5	0.011	0.012	0.013
1998	8.9	2.0	2.0	0.011	0.012	0.013
1999	8.8	2.9	2.0	0.011	0.012	0.013
2000	8.6	3.8	1.9	0.011	0.012	0.013
2001	8.5	4.6	1.8	0.011	0.012	0.013
2002	8.4		1.6	0.011		0.013
2003	8.2		4.5	0.011		0.013