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ARTICLE

Fish Distributions and Habitat Associations in Manistee River, Michigan, Tributaries: Implications for Arctic Grayling Restoration

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Abstract
Restoration and enhancement of North American native freshwater fishes have for several decades been the subject of growing interest among fisheries biologists, natural resource managers, non-governmental organizations, and the sportfishing public. The Little River Band of Ottawa Indians (LRBOI) and the Michigan Department of Natural Resources (MDNR), along with universities and public interest groups, are re-examining the potential for re-introduction of the Arctic Grayling *Thymallus arcticus*, a species that has been extirpated in Michigan since the 1930s. The Manistee River, Michigan, flows through the LRBOI's reservation and once supported the last known native Arctic Grayling population in the state's Lower Peninsula. The objectives of this study were to (1) identify potential biotic limitations, such as competition and/or predation from other fish species, that may interfere with Arctic Grayling re-introduction in the Manistee River watershed; and (2) describe how instream habitat features currently relate to populations of potentially interacting species. Field surveys conducted during June–August 2012 in eight Manistee River tributaries identified suitable abiotic habitat for Arctic Grayling in 20 of 22 sampling reaches. However, high densities of Brown Trout *Salmo trutta* (a nonnative salmonid) may have influenced some of the habitat associations observed for Brook Trout *Salvelinus fontinalis* and Slimy Sculpin *Cottus cognatus*, two species that currently and historically co-occurred in Arctic Grayling habitats. These two species were the most abundant in river reaches with Brown Trout densities less than 0.10 fish/m^2. Based on habitat conditions and Brown Trout densities, there appear to be four distinct tributary regions for which management strategies could be developed to enhance the success of Arctic Grayling re-introduction efforts. Re-introduction of Arctic Grayling in the Manistee River watershed would support LRBOI and MDNR goals for native species restoration and would provide a unique and historic angling opportunity that has been absent in Michigan for nearly 100 years.

Restoration and protection of native fish species have become increasingly important concerns for fisheries researchers and managers throughout North America, as many populations of native fishes are under threat from factors such as water withdrawals, habitat destruction, overharvest, and introductions of nonnative species (Angermeier 1995; Rahel 2000). Members of the family Salmonidae appear to be particularly susceptible to these factors, with 35 of the 80 salmonid species or subspecies in North America currently identified as species of

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concern, threatened, endangered, or extinct (NANFA 2015). Programs such as the National Fish and Wildlife Association's Bring Back the Natives and the North American Native Fishes Association's Conservation Research Grant are evidence of the broad and growing support for preserving North America's native ichthyofauna. Arctic Grayling *Thymallus arcticus* are native to Arctic Ocean drainages in North America, Asia, and Europe; the upper Missouri River system in Montana; and much of Michigan's Lower Peninsula (Northcote 1995). However, the current distribution of native fluvial Arctic Grayling in the contiguous United States has been reduced to less than 5% of the historic range, with the only known populations occurring in the headwaters of the Missouri River system in Montana (Steed et al. 2010). Historically, Arctic Grayling and Brook Trout *Salvelinus fontinalis* were the only native salmonids that were known to live in rivers and streams of Michigan, although the extent to which they coexisted remains unknown. Arctic Grayling are believed to have been the dominant (and likely only) native fluvial salmonid species in the major river systems throughout the northern half of the Lower Peninsula, with abundant populations occurring in the Manistee, Au Sable, Jordan, and Boardman rivers (Vincent 1962). Historical records are somewhat conflicting on the native distribution of Brook Trout in Michigan. Smedley (1938) stated that Brook Trout were widely distributed throughout the Upper Peninsula but were not present in the Lower Peninsula prior to approximately 1870. Similarly, Hubbard (1887) described an apparent absence of Brook Trout in all Lower Peninsula streams during his explorations with Douglas Houghton in the early 19th century. However, other authors have provided evidence that Brook Trout were either native to or dispersing south through the Lower Peninsula since the mid-1800s (Strang 1855; Hubbard 1887; Vincent 1962). The Michigan Department of Natural Resources (MDNR) stated that "Brook Trout may have been native to the Manistee River," citing an early newspaper report of "speckled brook trout" being caught in 1869 from Pine Creek, which is located in the Manistee River watershed below Tippy Dam (Rozich 1998).

Arctic Grayling were extirpated from Michigan (the last population occurred in the Upper Peninsula's Otter River, Houghton County) and last detected in 1936 (McAllister and Harington 1969); the last recorded captures in the Lower Peninsula occurred at least 30 years earlier (Mershon 1916). Several factors are believed to have contributed to the declines in the Arctic Grayling population, including overharvest, habitat destruction, and competition with and/or predation by nonnative fish species (Leonard 1949; Taylor 1954; Vincent 1962). Records indicate that large numbers of Arctic Grayling were harvested from many Lower Peninsula rivers in the mid- to late 1800s, with recreational catches often measured in the hundreds of fish per day and commercial harvest supplying markets in large cities, such as Milwaukee, Wisconsin, and Chicago, Illinois (Norris 1879). By the 1870s, many riverine habitats were undergoing drastic alteration by large-scale timber harvesting practices and increasing agricultural development (Vincent 1962). Harvested logs were often transported to mills by floating them down rivers, which increased bank erosion, sediment deposition, and scouring of the riverbeds during the Arctic Grayling spawning season in early spring (Harris 1905; Mershon 1916; Leonard 1939). Taylor (1954), summarizing the field notes of biologist John Lowe, suggested that bank erosion and increased sediment loads attributed to deforestation were primarily responsible for the decline of the Arctic Grayling population in the Otter River. The introduction of nonnative salmonids in Michigan began in the 1870s, with plantings of Rainbow Trout *Oncorhynchus mykiss* in the Au Sable River in 1876 (Bower 1910) and Brown Trout *Salmo trutta* in the Pere Marquette River in 1884 (Luton 1985). Both of these Lower Peninsula rivers had contained Arctic Grayling until the late 1890s to early 1900s (Vincent 1962; MDNR 1978).

Attempts to supplement Arctic Grayling stocks in Michigan began as early as the 1870s (Metcalf 1961) through egg and broodstock collections from Lower Peninsula rivers, such as the Manistee and Au Sable rivers (Jerome 1879; Mather 1923; Norris 1923). As Arctic Grayling stocks in the Lower Peninsula became depleted to the point where in-state collection of gametes was no longer a viable option, eggs and fry were transported from Montana in an attempt to re-establish the species in Michigan (Creaser and Creaser 1935). The early efforts to stock Arctic Grayling from Montana began in 1900, and attempts continued regularly until 1936 (Leonard 1949), after which most Arctic Grayling restoration activities ceased in the Lower Peninsula for the next 50 years. The most recent attempt to re-establish Arctic Grayling in Michigan occurred between 1987 and 1991, when the MDNR stocked approximately 250,000 Arctic Grayling fry, fingerlings, and yearlings in rivers and lakes throughout the state (Nuhfer 1992). As with all previous attempts, these efforts were unsuccessful (due to a variety of factors) in establishing self-sustaining Arctic Grayling populations in the state (Nuhfer 1992).

Although most of Michigan's Lower Peninsula rivers may have been devoid of Arctic Grayling by the 1890s, the Manistee River was home to one of the last known populations, with captures documented into the early 1900s (Vincent 1962). This river flows through the reservation of the Little River Band of Ottawa Indians (LRBOI), who have shown great interest in protecting and restoring native and culturally significant species, such as the Arctic Grayling, Lake Sturgeon *Acipenser fulvescens*, and elk

Cervus canadensis, within the 1836 Treaty area (Auer et al. 2013; Holtgren and Auer 2016). As part of the tribe's native species restoration goals, LRBOI and Michigan Technological University (MTU) partnered to develop habitat assessment criteria for determining whether current conditions in the Manistee River and its tributaries would be suitable for potential Arctic Grayling re-introductions (Auer et al. 2013). Danhoff et al. (2017) compared abiotic conditions in tributaries of the Manistee River to conditions at locations with extant Arctic Grayling populations in Montana, Alaska, and northern Canada; they identified suitable Arctic Grayling habitat in seven of eight surveyed tributaries of the Manistee River. The findings of Danhoff et al. (2017) indicate that there remains supportive habitat for Arctic Grayling re-establishment in the Manistee River watershed (MRW); the findings also provide necessary assessment criteria and background information and lay the groundwork for future re-introduction efforts.

The LRBOI is not alone in the desire to restore Arctic Grayling populations in Michigan. Based in part on findings from the 2011–2013 research by LRBOI and MTU (J. M. Holtgren, MDNR, personal communication), a statewide restoration initiative was formed in 2016 with the goal of re-introducing this species to Michigan. The LRBOI has partnered with MDNR, MTU and other universities, federal agencies, and non-governmental organizations to move forward with the goal of re-establishing Arctic Grayling populations in the state. Interest in establishing this species throughout North America is seen in the U.S. Geological Survey's species profile for Arctic Grayling (Fuller et al. 2017). Introductions of Arctic Grayling have occurred in 26 states (23 of which are outside of the species' native range), with established populations persisting in at least six of those states: Alaska, Arizona, Colorado, Montana, Utah, and Wyoming (Fuller et al. 2017). A more thorough understanding of the relationships between abiotic habitat features and the life history dynamics of co-occurring fish species that currently occupy potential Arctic Grayling habitats can help to guide future introduction and restoration efforts throughout North America.

The extent to which interactions with other fish species, which may outcompete or prey upon Arctic Grayling, could impact re-introduction efforts remains unknown. Although Arctic Grayling were historically the most abundant and likely the only (Harris 1905) fluvial salmonid species found in the Manistee River and its tributaries (Babbitt 1900; Creaser and Creaser 1935), the Brown Trout, Brook Trout, and Rainbow Trout are now widely distributed throughout much of the watershed (Rozich 1998; Burroughs et al. 2010). Here, we present univariate and multivariate regressions describing habitat associations and interspecific relations of three fish species (Brook Trout, Brown Trout, and Slimy Sculpin *Cottus cognatus*) that have the potential to compete with and/or prey upon various life stages of Arctic Grayling in the MRW. Many fluvial salmonids are thought to be primarily insectivorous drift feeders throughout much of their life cycle (Harvey and Railsback 2014); however, Brook Trout, Brown Trout, and Rainbow Trout are also known to transition to diets that include varying levels of piscivory as they grow and mature (East and Magnon 1991; L'Abée-Lund et al. 1992; Turek 2014), indicating the possibility of competition with and predation upon Arctic Grayling if re-introduction occurs. Previous research into the effects of competition and predation between fluvial salmonids has indicated that competition for food and space and high predator densities can influence the abundance and habitat associations of native salmonids (Fausch and White 1981; Quist and Hubert 2005). For this study, it was hypothesized that in Manistee River tributaries, reach-scale abundances of potential Arctic Grayling competitors or predators would not be significantly related to abiotic habitat conditions or heterospecific fish densities. The objectives of this study were to (1) determine which abiotic habitat features and/or interspecific relationships were associated with populations of co-occurring fish species in tributaries of the Manistee River and (2) evaluate how these relationships might influence potential Arctic Grayling re-introduction strategies.

STUDY AREA

The MRW is one of the largest watersheds in Michigan, with an area of 4,610 km^2, and the Manistee River has a main-stem length of 373 river kilometers (rkm; Chiotti et al. 2008). Data for this study were collected from eight Manistee River tributaries located between Tippy and Hodenpyl dams (Appendix Table A.1; Figure 1). Tippy Dam is situated approximately 47 rkm upriver of Lake Michigan and blocks all upstream fish movement. Hodenpyl Dam, which is located approximately 68 rkm upriver of Lake Michigan, forms a second barrier, marking the upper boundary of the 21-rkm study area. The Manistee River in this 21-rkm segment is characterized by a deeply incised valley, a moderately high gradient (1.3 m/km), and predominately gravel and cobble substrates (Rozich 1998). Within this segment, eight-first- through third-order, groundwater-fed tributaries discharge into the main stem, providing an additional 50.8 rkm of connected fluvial habitat.

METHODS

Instream habitat and fish population surveys were conducted monthly during June–August 2012 in 22 sampling reaches of the eight tributaries (see Figure 1 for tributary names and reach locations). Reaches were selected that represent a range of abiotic conditions found in the

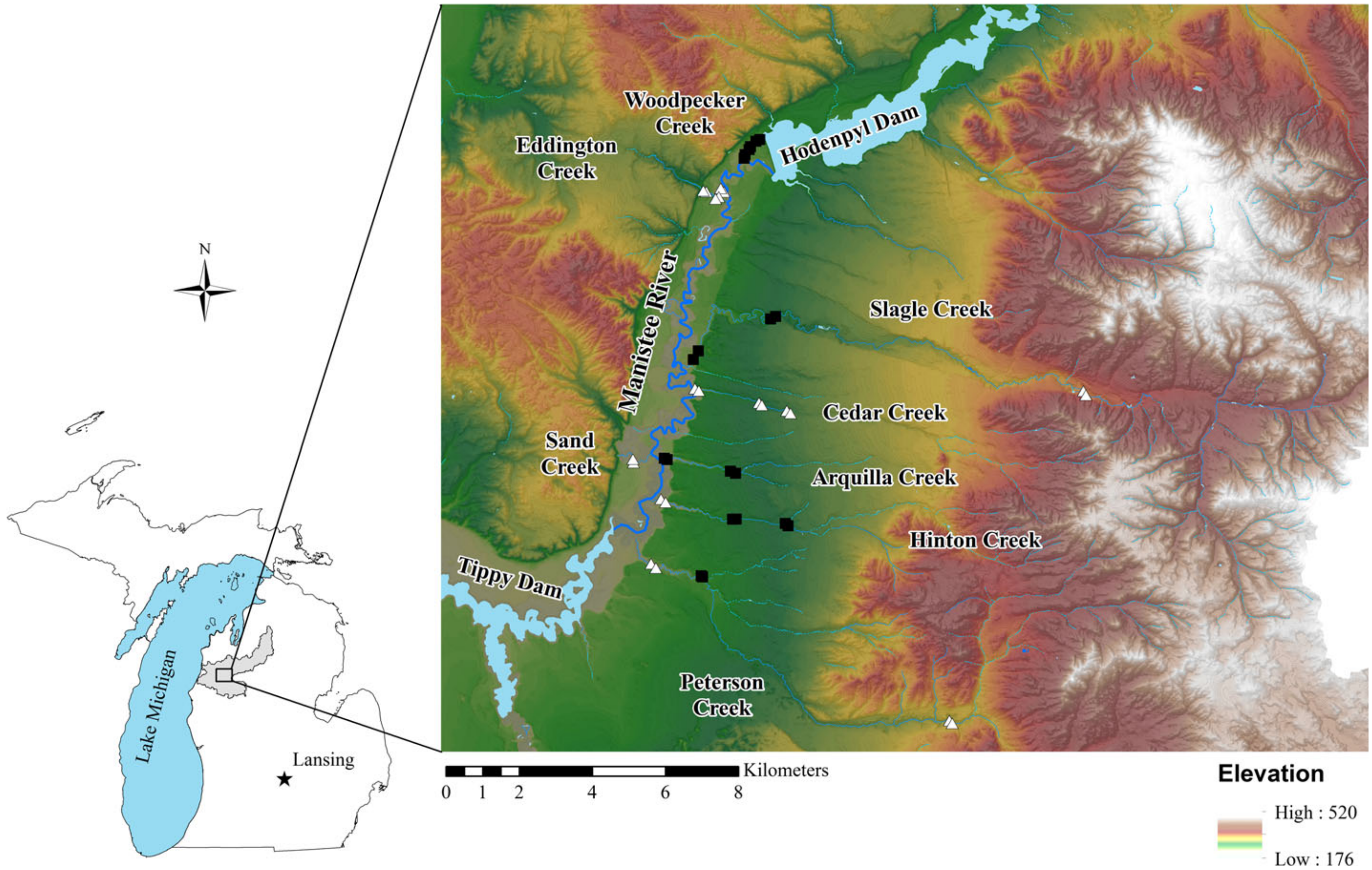

FIGURE 1. Location of the Manistee River watershed in the state of Michigan and locations of 22 tributary reaches sampled during June–August 2012. White triangles indicate reaches with Brown Trout densities less than 0.10 fish/m^2; black squares indicate reaches with Brown Trout densities greater than 0.10 fish/m^2. [Color figure can be viewed at afsjournals.org.]

watershed. Each reach was classified as "Lower" (closest to main stem), "Middle," or "Upper" (most upstream) based on its distance from the tributary confluence relative to the overall length of the stream. Following Environmental Monitoring and Assessment Program (U.S. Environmental Protection Agency) protocols for wadeable streams (Lazorchak et al. 2000), reach lengths were set at 40 times the mean wetted stream width or a minimum length of 120 m for reaches averaging less than 3 m wide. For detailed descriptions and methods for abiotic features of tributaries in this study (e.g., substrate size structure, temperature, etc.), see Danhoff et al. (2017).

Instream habitat and water parameters.— A channel morphology profile was developed for each reach using field measurements of linear lengths and widths for each unique habitat type or channel geomorphic unit (CGU) following the classifications of Hawkins et al. (1993). Transitions between unique CGUs were marked with a handheld GPS unit and referenced with hip-chain measurements collected in summer 2011. Each reach was divided into transects, spaced approximately 2 m apart, where the wetted stream width (nearest 0.5 m), water depth (m), bottom velocity (m/s), and 60% column velocity were measured (see Danhoff et al. 2017 for detailed methods) and used to calculate mean (and maximum) depth and velocity for each reach. All measures of water depth and velocity were conducted under summer baseflow conditions to ensure comparability between sites.

The gradient (percent slope) of each reach was calculated using ArcMap version 10.1 and referenced to field measurements. Elevation data for each tributary channel were derived from 10-m-resolution U.S. Geological Survey digital elevation models (DEMs) by extracting the DEM pixels masked by the stream layer of the National Hydrography Dataset (U.S. Department of Agriculture, Natural Resources Conservation Service, National Geospatial Management Center). Each 10-m pixel was converted from elevation to a percent gradient using the slope function of the Spatial Analyst toolbox (Environmental Systems Research Institute), and the mean of all pixels was calculated for each reach. Field reference data were collected by marking a 33-m section of each reach and measuring the percent incline between two 1.5-m posts with a Suunto M-5/360 PC Clinometer.

Large woody debris (LWD; defined as wood pieces >50 cm in length, > 10 cm in diameter, and in contact with the water) was identified as the primary source of instream overhead cover in most reaches. The amount of available LWD cover was quantified by counting, measuring, and calculating the surface area of LWD structures within each reach. When multiple pieces of LWD were clustered (i.e., logjams), the cluster was measured as a single structure, and its overall surface area, rather than the surface area of individual pieces, was calculated. As with the areal CGU measurements, LWD surface area was standardized as a proportion of the overall reach area.

A modification of the Wolman pebble count (Wolman 1954), wherein the intermediate axis of a randomly selected substrate particle was measured at 100 points throughout each reach, was used to estimate substrate compositions. Substrate particles were categorized for analyses as coarse (>2.0 mm), sand (0.06–2.0 mm), and silt/clay (<0.06 mm) in order to calculate the relative frequencies of different substrate types within each reach. Discharge, water temperature, dissolved oxygen (DO) concentration, pH, and turbidity were measured monthly on the same day that fish population surveys were conducted (see Danhoff et al. 2017 for detailed summaries of methods for pebble counts and water parameter measurements).

Fish population surveys.— One multi-pass depletion electrofishing survey (in June 2012; following the methods of Hayes et al. 2007) and two single-pass electrofishing surveys (one in July 2012 and one in August 2012; MDEQ–SWQD 2000) were conducted in each of the 22 reaches. Surveys were performed by using a Smith-Root LR-14 backpack electrofishing unit that was initially set to output pulsed DC at 30 Hz and a peak voltage of 275 V and was adjusted as needed to maintain a duty cycle of 12% or less depending on conductivity and water temperature. During the multi-pass survey, a 6.35-mm-mesh block net was placed at both the downstream and upstream reach boundaries to prevent fish from escaping or entering the reach; this allowed us to meet the closed-population assumption required for estimating abundance (Hayes et al. 2007). Three passes were conducted back to back in all but two reaches (Eddington Creek Middle and Peterson Creek Upper), where two passes yielded depletions over 80% and a third pass was deemed unnecessary (Lockwood and Schneider 2000). All fish captured were identified to species, counted, measured to the nearest 1.0 mm TL, weighed to the nearest 0.1 g, and placed into an instream holding tank to prevent recaptures for the duration of the survey. To account for differences in electrofishing effort between reaches of different sizes, all species counts from the first electrofishing pass were standardized as the number of fish captured per minute of electrofishing (CPUE), and the mean CPUE for each species across the three sampling occasions was calculated. A $\log_e(x + 1)$ transformation (Hubert and Fabrizio 2007) was performed on all CPUE values due to non-normality (Kolmogorov–Smirnov test: $P > 0.05$) and significantly improved the normality of the data ($P < 0.05$).

Based on previous age and growth information from this part of the MRW (LRBOI, unpublished data), salmonids smaller than 100 mm TL were classified as young of the year or juveniles, and 100-mm TL or larger salmonids were classified as subadults or adults for analyses. Population estimates from the multi-pass surveys were computed for each species and age-group of salmonids (i.e., Brook Trout juveniles and adults; Brown Trout juveniles and adults) and both age-groups combined (i.e., all Brook Trout; all Brown Trout) using the Carle–Strub k-pass maximum likelihood estimator (Carle and Strub 1978) under the “removal” function in the Fisheries Stock Assessment package (Ogle 2015) for program R (R Development Core Team 2015). All sizes of Slimy Sculpin were pooled for population estimates. Density estimates (fish/m^2) were calculated by dividing the numerical population estimates by the total area of each reach. Similarly, biomass (g/m^2) was calculated as the product of the numerical population estimate and the mean weight of the species in each reach divided by the reach area. Correlations were tested among 19 habitat variables and mean salmonid and sculpin CPUE, density, and biomass. Where significant correlations ($P \leq 0.05$) among habitat variables were identified, the variables that displayed the largest correlation coefficients (r) with the fish population indices were retained for further regression analyses, and those with lower r-values were removed (Hubert and Rahel 1989). Species richness (N) and the Shannon diversity index (H') were also calculated for each reach. Both species richness and H' were calculated while excluding Brown Trout in order to compare the fish community between reaches with high densities of Brown Trout and those with low (or zero) Brown Trout densities. An exponential transformation was used to convert Shannon H' values to their effective numbers ($\exp H'$; Jost 2006). Univariate and stepwise multiple regression models were developed using SAS version 9.2 for Windows (SAS Institute 2008) to describe the variation in population indices for each species.

RESULTS

In total, 10,090 fish representing 22 species were captured throughout the fish population surveys in 2012 (Table 1). Species richness across all reaches ranged from two species captured in the Cedar Creek Middle and Upper reaches to 12 species captured in the Hinton Creek Lower reach (Table A.1). The most widely distributed and abundant species were Brook Trout, Brown Trout, and

Slimy Sculpin, which were captured in all tributaries and accounted for over 96% of the overall number of fish caught (Table 1). Each of the other 19 species accounted for less than 1% of the overall catch, and six of those species were captured only from single streams (Table 1). Brook Trout were captured in 21 of 22 reaches, with mean CPUE ranging from 0.03 to 4.04 fish/min, density ranging from less than 0.01 to 1.31 fish/m^2, and biomass ranging from 0.05 to 20.83 g/m^2 (Table 2; includes SDs of CPUE). Brown Trout were captured in 19 of 22 reaches, with mean CPUE ranging from 0.04 to 2.84 fish/min, density ranging from less than 0.01 to 0.39 fish/m^2, and biomass ranging from less than 0.01 to 12.48 g/m^2 (Table 2). Slimy Sculpin were captured in 21 of 22 reaches; mean CPUE of Slimy Sculpin ranged from 0.01 to 3.25 fish/min, density ranged from less than 0.01 to 1.22 fish/m^2, and biomass ranged from less than 0.01 to 4.82 g/m^2 (Table 2). Rainbow Trout were infrequently captured during 2012 surveys (62 fish, accounting for <1% of the overall catch) and were not included in further analyses.

Of the 19 habitat variables measured, 9 were found to be significantly ($P < 0.05$) correlated with Brook Trout CPUE (Table 3). After removing intercorrelated habitat variables (retaining the variables with the highest correlation coefficients; see Methods), we retained three variables for regression modeling: mean wetted width, water temperature, and proportion of run habitat (Table 4). Brown Trout CPUE was found to have a significant negative correlation with Brook Trout CPUE (Table 3) and was added to create a second multiple regression model incorporating the interspecific relationship. When Brown Trout CPUE was excluded from the model, multiple regression yielded a two-variable model (equation 1), with wetted width (partial $r^2 = 0.42$, $P < 0.01$) and water temperature (partial $r^2 = 0.14$, $P = 0.02$) accounting for 56% of the observed variation in Brook Trout CPUE (Figure 2):

$$\text{Brook Trout } CPUE_{lt} = 2.41 - 0.13(\text{wetted width}) - 0.12(\text{water temperature}), \quad (1)$$

TABLE 1. Total number of fish captured in Manistee River tributaries and proportion of the total catch represented by each species throughout the 2012 fish population surveys (species are listed in order of their proportional contribution to the overall catch).

Species	Streams	Count	Percentage of total catch
Slimy Sculpin *Cottus cognatus*	All	3,915	38.80
Brown Trout *Salmo trutta*	All	3,836	38.02
Brook Trout *Salvelinus fontinalis*	All	1,982	19.64
Blacknose Dace *Rhinichthys atratulus*	Peterson Creek	95	0.94
Rainbow Trout *Oncorhynchus mykiss*	Arquilla, Cedar, Eddington, Hinton, Slagle, and Woodpecker creeks	62	0.61
Chestnut Lamprey *Ichthyomyzon castaneus*	Arquilla, Cedar, Peterson, Slagle, and Woodpecker creeks	51	0.51
Blackside Darter *Percina maculata*	Arquilla and Hinton creeks	31	0.31
Johnny Darter *Etheostoma nigrum*	Arquilla, Hinton, and Sand creeks	21	0.21
Lamprey species	Arquilla, Hinton, Peterson, and Slagle creeks	21	0.21
Black Bullhead *Ameiurus melas*	Arquilla, Hinton, and Sand creeks	14	0.14
Creek Chub *Semotilus atromaculatus*	Peterson Creek	13	0.13
Brook Stickleback *Culaea inconstans*	Sand and Woodpecker creeks	11	0.11
Silver Lamprey *I. unicuspis*	Arquilla, Hinton, and Slagle creeks	8	0.08
American Brook Lamprey *Lethenteron appendix*	Hinton, Peterson, and Slagle creeks	7	0.07
Longnose Dace *Rhinichthys cataractae*	Woodpecker Creek	5	0.05
Northern Redbelly Dace *Chrosomus eos*	Eddington and Peterson creeks	5	0.05
White Sucker *Catostomus commersonii*	Sand and Slagle creeks	4	0.04
Northern Brook Lamprey *I. fossor*	Hinton, Sand, and Slagle creeks	3	0.03
Bluegill *Lepomis macrochirus*	Hinton and Slagle creeks	2	0.02
Fathead Minnow *Pimephales promelas*	Sand Creek	2	0.02
Pumpkinseed *Lepomis gibbosus*	Hinton Creek	1	0.01
Smallmouth Bass *Micropterus dolomieu*	Hinton Creek	1	0.01
Total		10,090	

($r^2 = 0.56$, $P < 0.01$), where $CPUE_{lt}$ represents the $\log_e(x + 1)$-transformed CPUE. The addition of Brown Trout CPUE resulted in the removal of all habitat variables during the stepwise model development and yielded a univariate regression of Brook Trout CPUE and Brown Trout CPUE that accounted for 47% of the observed variation (Table 4). In general, Brook Trout were most abundant in the narrow and relatively cold reaches, and this was reflected in the strongest correlations occurring with measures of stream size (i.e., reach area, wetted width, and width : depth ratio) and water temperature.

Nine habitat variables were significantly ($P < 0.05$) correlated with Brown Trout CPUE (Table 3). After removing intercorrelated habitat variables, we retained two variables for regression modeling: reach area and the proportion of coarse substrate (Table 4). Brook Trout CPUE and Slimy Sculpin CPUE were found to have significant negative correlations with Brown Trout CPUE (Table 3). Univariate regression identified two habitat variables and two species interaction variables as significantly related to Brown Trout CPUE. However, the stepwise multiple regression procedure excluded both reach area and Slimy Sculpin CPUE, thus producing a two-variable model (equation 2) containing Brook Trout CPUE (partial $r^2 = 0.47$, $P < 0.01$) and the proportion of coarse substrate (partial $r^2 = 0.21$, $P < 0.01$). The resulting model accounted for 68% of the observed variation in Brown Trout CPUE (Figure 2):

$$\text{Brown Trout } CPUE_{lt} = 0.38 - 0.60(\text{Brook Trout } CPUE_{lt}) + 0.01(\text{proportion of coarse substrate}), \tag{2}$$

($r^2 = 0.68$, $P < 0.01$). Brown Trout CPUE was the only variable that was significantly ($P < 0.05$) correlated with Slimy Sculpin CPUE, with a negative association that accounted for 24% of the observed variation (Tables 3, 4). Brown Trout were generally most abundant in the large, deep, and relatively warm reaches and were also positively associated with the proportion of coarse substrate.

Brook Trout size-classes did not differ in terms of variables that were significantly ($P < 0.05$) correlated with density or biomass; therefore, regression analyses were performed using pooled density and biomass estimates for all sizes of Brook Trout. Two habitat variables—wetted width and the ratio of wetted width to depth—were found to have significant ($P < 0.05$) negative correlations with Brook Trout density and biomass. Brook Trout density (but not biomass) was positively correlated with the density of Slimy Sculpin (Table 3). Univariate regression models of Brook Trout density with Slimy Sculpin density and Brook Trout biomass with width : depth ratio accounted for 21% and 27% of the observed variation in density and biomass, respectively (Table 4). As with Brook Trout, no differences between size-classes were observed for Brown Trout density or biomass, so regression analyses were performed for all sizes combined. Proportion of coarse substrate was positively correlated with and accounted for 32% of the observed variation in Brown Trout density, whereas it was negatively correlated with and accounted for 26% of the observed variation in Slimy Sculpin density (Tables 3, 4). A two-variable regression model (equation 3) was developed with mean depth (partial $r^2 = 0.38$, $P < 0.01$) and the proportion of coarse substrate (partial $r^2 = 0.21$, $P < 0.01$), accounting for 59% of the observed variation in Brown Trout biomass (Figure 3):

$$\text{Brown Trout biomass} = -5.73 + 31.76(\text{mean depth}) + 0.08(\text{coarse substrate}), \tag{3}$$

($r^2 = 0.59$, $P < 0.01$). Three variables were retained for assessing Slimy Sculpin density: Brook Trout density, Brown Trout density, and mean bottom velocity (Table 4). A two-variable multiple regression model (equation 4) was developed with Brown Trout density (partial $r^2 = 0.26$, $P = 0.02$) and mean bottom velocity (partial $r^2 = 0.18$, $P = 0.02$) and accounted for 44% of the observed variance in Slimy Sculpin density (Figure 3):

$$\text{Slimy Sculpin density} = 0.69 - 1.17(\text{Brown Trout density}) - 1.45(\text{mean bottom velocity}), \tag{4}$$

($r^2 = 0.44$, $P < 0.01$). The proportion of coarse substrate in a reach was the only variable found to be significantly correlated with Slimy Sculpin biomass, exhibiting a negative association that accounted for 31% of the observed variation (Tables 3, 4). Slimy Sculpin abundance was not significantly related to stream size but was negatively associated with both bottom velocity and the proportion of coarse substrate.

Of the 21 tributary reaches surveyed, gradients ranged from 0.3% to 8.6% (Tables 5, A.1) and were generally greatest in the downstream, low-elevation reaches on the east side of the Manistee River (Table 5, section B). The steepest gradient (8.6%) across all reaches was found near the mouth of Cedar Creek due to a large cascade that marked the upstream reach boundary (see Danhoff et al. 2017). The mid-elevation and upper-elevation reaches on the east side were lower gradient (average = 1.1% and 0.6%, respectively; Table 5, sections C and D), as were most reaches on the west side of the river (average = 1.5%; Table 5, section A). Mean values of discharge, DO concentration, pH, and turbidity were calculated across all three sampling events (June, July, and August) because no significant differences between sampling events were detected (ANOVA: $P > 0.05$ for

TABLE 2. Mean CPUE (number of fish captured per minute of electrofishing), density, and biomass of Brook Trout, Brown Trout, and Slimy Sculpin in 22 Manistee River tributary sampling reaches. Standard deviations of CPUE are presented in parentheses.

		Brook Trout			Brown Trout			Slimy Sculpin		
Tributary	Reach	CPUE (fish/min)	Density (fish/m²)	Biomass (g/m²)	CPUE (fish/min)	Density (fish/m²)	Biomass (g/m²)	CPUE (fish/min)	Density (fish/m²)	Biomass (g/m²)
Arquilla Creek	Lower	0.15 (0.12)	0.01	0.11	1.28 (0.17)	0.11	4.94	0.50 (0.08)	0.09	0.43
	Upper	1.63 (0.36)	0.21	2.59	1.42 (0.31)	0.16	4.82	1.38 (0.34)	0.23	1.52
Cedar Creek	Lower	1.21 (0.11)	0.27	4.17	0.33 (0.25)	0.06	2.22	0.68 (0.21)	0.14	0.50
	Middle	4.04 (0.48)	1.31	20.83	0.00	0.00	0.00	1.05 (0.69)	0.78	3.03
	Upper	2.58 (0.57)	0.43	5.41	0.00	0.00	0.00	0.65 (0.33)	0.32	1.20
Eddington Creek	Lower	1.55 (0.51)	0.15	1.97	0.18 (0.08)	0.06	1.06	2.17 (0.04)	0.49	3.00
	Middle	1.18 (0.16)	0.11	2.63	0.11 (0.15)	0.00	0.00	0.51 (0.37)	0.25	1.27
	Upper	2.07 (0.27)	0.26	3.51	0.00[b]	0.00	0.00	0.55 (0.16)	0.08	0.49
Hinton Creek	Lower	0.44 (0.06)	0.03	0.27	1.18 (0.19)	0.08	2.74	1.00 (0.23)	0.12	0.57
	Middle	0.33 (0.13)	0.09	2.67	1.74 (0.46)	0.28	10.72	0.21 (0.06)	0.07	0.50
	Upper	0.62 (0.20)	0.07	1.49	1.92 (0.01)	0.39	9.26	0.00	0.00	0.00
Peterson Creek	Lower	0.06 (0.05)	<0.01	0.15	0.47 (0.18)	0.04	2.25	0.62 (0.15)	0.05	0.20
	Middle	0.03 (0.03)	<0.01	0.12	1.55 (0.65)	0.13	6.61	1.06 (0.53)	0.09	0.58
	Upper	0.30 (0.10)	0.07	2.64	0.00	0.00	0.00	1.71 (0.43)	0.49	4.62
Sand Creek	Middle	0.98 (0.53)	0.20	3.42	0.13 (0.07)	0.01	0.18	1.26 (0.93)	0.51	1.69
	Upper	0.77 (0.27)	0.14	2.25	0.04 (0.01)	<0.01	0.15	1.85 (0.33)	1.22	4.48
Slagle Creek	Lower	0.00[a]	<0.01	0.05	1.47 (0.22)	0.11	6.94	1.33 (0.35)	0.14	2.11
	Middle	0.00	0.00	0.00	2.84 (0.06)	0.21	12.48	1.05 (0.31)	0.10	1.12
	Upper	0.14 (0.10)	0.01	0.52	0.79 (0.07)	0.06	7.11	3.25 (0.81)	0.38	4.82
Woodpecker Creek	Lower	0.14 (0.05)	0.01	0.08	1.74 (0.30)	0.16	6.05	1.02 (0.25)	0.16	0.82
	Middle	0.10 (0.05)	0.01	0.37	2.11 (0.03)	0.34	10.75	0.52 (0.03)	0.10	0.58
	Upper	0.10 (0.06)	0.02	0.78	1.86 (0.61)	0.12	1.81	0.01 (0.02)	<0.01	<0.01

[a]No Brook Trout were collected on the first electrofishing pass from which CPUE was calculated; two were collected on subsequent passes.
[b]No Brown Trout were collected on the first electrofishing pass from which CPUE was calculated; one was collected on subsequent passes.

TABLE 3. Interspecific relationships and habitat features that were correlated ($P \leq 0.05$) with the CPUE (fish/min), density (fish/m^2), and biomass (g/m^2) of Brook Trout, Brown Trout, and Slimy Sculpin in 22 Manistee River tributary sampling reaches ("+" indicates a positive correlation; "–" indicates a negative correlation).

	CPUE			Density			Biomass		
Variable	Brook Trout	Brown Trout	Slimy Sculpin	Brook Trout	Brown Trout	Slimy Sculpin	Brook Trout	Brown Trout	Slimy Sculpin
Biota									
Brook Trout		–				+			
Brown Trout	–		–			–			
Sculpin *Cottus* sp.		–		+	–				
Habitat									
Mean wetted width	–	+		–		–	–	+	
Site area	–	+						+	
Pool (%)									
Riffle (%)	–	+				–		+	
Run (%)	+								
Discharge	–	+						+	
Mean depth	–	+						+	
Maximum depth	–	+						+	
Width : depth ratio				–			–		
Mean bottom velocity						–			
Maximum bottom velocity								+	
Mean column velocity	–					–		+	
Maximum column velocity		+				–		+	
Large woody debris (%)									
Coarse substrate (%)		+			+	–		+	–
Water temperature	–	+							
pH									
Turbidity									
Dissolved oxygen									

all). Mean July water temperatures near each tributary confluence in 2012 ranged from 10.7 ± 1.2°C to 15.0 ± 1.5°C, and maximum summer (June–August) water temperatures observed in each tributary mouth occurred on July 25 and ranged from 16.1°C in Cedar Creek to 19.2°C in Sand Creek (Figure 4). Although water temperatures did differ between sampling events (temperatures were highest during July sampling), the "average summer value" of this variable is reported to provide comparisons similar to those presented for other water quality and physical habitat variables (Table A.1).

DISCUSSION

Since Brown Trout, Brook Trout, and Slimy Sculpin together accounted for approximately 96% of the overall catch (Table 1), modeling of biotic and abiotic interactions of these species has implications for potential Arctic Grayling restoration in the MRW. All three species occurred in all of the Manistee River tributaries surveyed, but there was variation in their abundance at the reach scale (120–325 m), indicating that localized habitat conditions (see Danhoff et al. 2017) and/or biotic interactions could be influencing fish community and population characteristics in these tributaries. In general, Brook Trout were most abundant in the small and relatively cold upper-elevation reaches, while Brown Trout were most abundant in the large, deep, and relatively warm mid-elevation reaches. Brown Trout abundance appears to be influencing some of the observed habitat associations and fish community compositions in the study reaches. For example, Brown Trout CPUE was the best explanatory variable for both Brook Trout CPUE and Slimy Sculpin CPUE, and Brown Trout density was the best explanatory variable for Slimy Sculpin density (Table 4). Brook Trout abundance was greatest and most variable in the narrowest reaches, which had the lowest abundance of Brown Trout (Figure 5). Species diversity (excluding

TABLE 4. Univariate regression equations describing interspecific relationships and abiotic habitat factors associated with the CPUE (fish/min), density (fish/m^2), and biomass (g/m^2) of Brook Trout, Brown Trout, and Slimy Sculpin in 22 Manistee River tributary sampling reaches (CPUE$_{lt}$ = log$_e$[x + 1]-transformed CPUE).

Regression equation	r^2	P
Brook Trout CPUE$_{lt}$		
0.89 − 0.69(Brown Trout CPUE$_{lt}$)	0.47	<0.01
1.08 − 0.16(wetted width)	0.42	<0.01
1.57 − 0.09(water temperature)	0.29	0.01
−0.0002 + 0.88(% run)	0.20	0.04
Brook Trout density		
0.04 + 0.44(Slimy Sculpin density)	0.21	0.03
0.60 − 0.02(width : depth ratio)	0.18	0.04
Brook Trout biomass		
6.45 − 1.07(width : depth ratio)	0.27	0.01
Brown Trout CPUE$_{lt}$		
0.91 − 0.68(Brook Trout CPUE$_{lt}$)	0.47	<0.01
−0.02 + 0.01(% coarse substrate)	0.32	<0.01
0.33 + 0.0004(site area)	0.29	0.01
0.97 − 0.58(Slimy Sculpin CPUE$_{lt}$)	0.24	0.02
Brown Trout density		
−0.04 + 0.003(% coarse substrate)	0.32	<0.01
0.16 − 0.20(Slimy Sculpin density)	0.26	0.02
Brown Trout biomass		
−2.50 + 38.69(mean depth)	0.38	<0.01
−1.42 + 0.11(% coarse substrate)	0.35	<0.01
Slimy Sculpin CPUE$_{lt}$		
0.75 − 0.20(Brown Trout CPUE$_{lt}$)	0.06	0.04
Slimy Sculpin density		
0.40 − 1.31(Brown Trout density)	0.26	0.02
0.61 − 1.66(mean bottom velocity)	0.24	0.02
0.19 + 0.47(Brook Trout density)	0.21	0.03
Slimy Sculpin biomass		
3.44 − 0.04(% coarse substrate)	0.31	<0.01

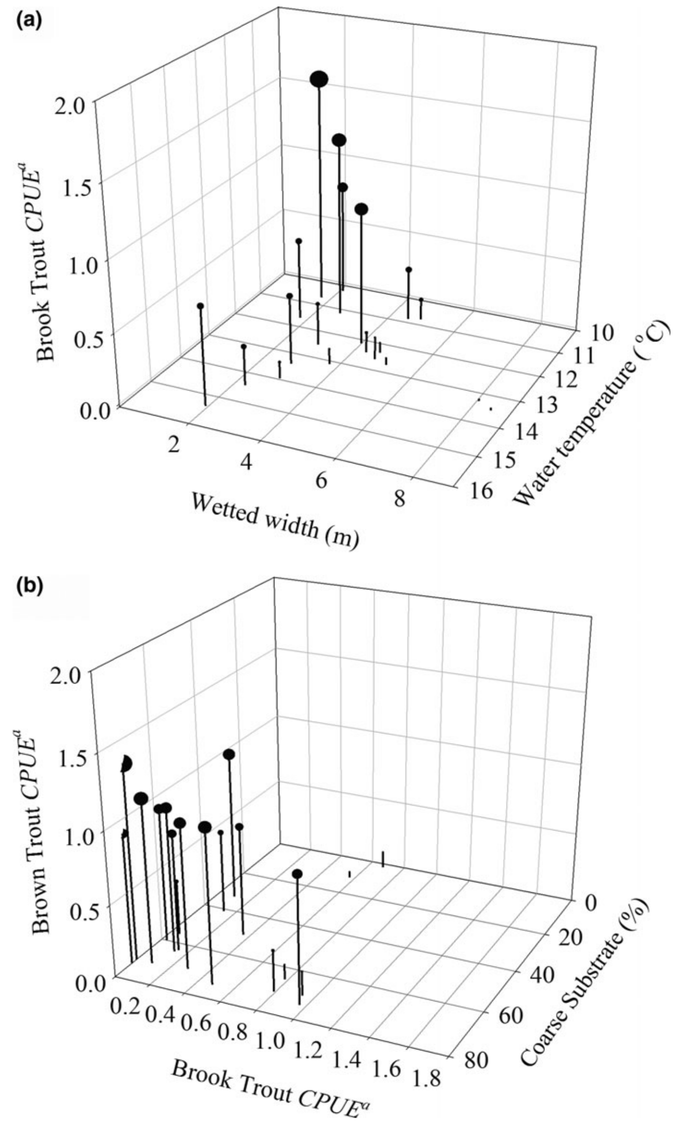

FIGURE 2. Relationships between **(A)** Brook Trout CPUE (fish/min), stream wetted width (m), and average water temperature (°C); and **(B)** Brown Trout CPUE, Brook Trout CPUE, and the percentage of substrate particles larger than 2 mm (coarse substrate) during three sampling occasions in 22 Manistee River tributary reaches (CPUE^a = log$_e$[x + 1]-transformed CPUE).

Brown Trout) was greater in the tributary regions where Brown Trout densities were less than 0.10 fish/m^2.

Researchers and the public have become increasingly aware that introductions of salmonid species outside of their native ranges can have deleterious effects on native salmonids (Rahel 1997; Fausch 2008). Examples can be seen in the western United States, where introductions of nonnative Brook Trout have displaced native salmonids, such as the Cutthroat Trout *O. clarkii* (Krueger and May 1991; Dunham et al. 2002; Peterson et al. 2004), and Bull Trout *Salvelinus confluentus* (Gunckel et al. 2002; Rieman et al. 2006). Similarly, introduced Brown Trout are known to outcompete Brook Trout for energetically profitable microhabitats (Fausch and White 1981), spawning locations (Essington et al. 1998), and food (Dewald and Wilzbach 1992). Brown Trout and Brook Trout are known to consume small fish (East and Magnon 1991; L'Abée-Lund et al. 1992), and Slimy Sculpin are known egg predators with the potential to negatively impact salmonid recruitment (Bunnell et al. 2014). The biotic–abiotic constraining hypothesis (BACH) first proposed by Quist et al. (2003) may explain the apparent influence of biotic interactions in Manistee River tributaries. The premise of the BACH is that a species' abundance is determined by habitat conditions unless predator and/or competitor abundance is high, in which case negative biotic interactions override suitable habitat conditions and are the primary limiting factor (Quist et al. 2003). Quist and Hubert (2005) tested

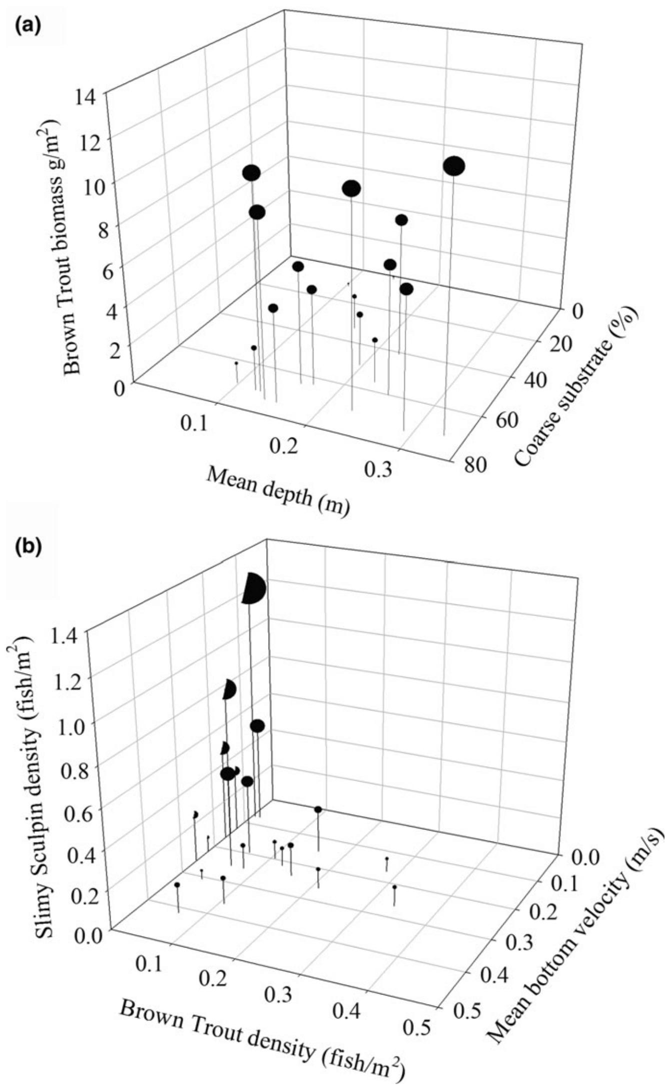

FIGURE 3. Relationships between **(A)** Brown Trout biomass (g/m^2), mean water depth (m), and the percentage of substrate particles larger than 2 mm (coarse substrate); and **(B)** Slimy Sculpin density (fish/m^2), Brown Trout density, and mean bottom velocity (m/s) in 22 Manistee River tributary reaches.

TABLE 5. Gradients (% slope) of Manistee River tributary sampling reaches in four elevation regions: (A) west side (all reaches), (B) low-elevation reaches on the east side, (C) mid-elevation reaches on the east side, and (D) high-elevation reaches on the east side. Arquilla Creek Middle and Sand Creek Lower are not included due to sampling constraints that prevented full surveys.

Tributary	Reach	Mean gradient (%)
(A) West tributaries, all reaches		
Eddington Creek	Lower	0.8
	Middle	1.8
	Upper	2.7
Sand Creek	Middle	0.3
	Upper	1.6
Woodpecker Creek	Lower	0.9
	Middle	3.4
	Upper	0.5
Overall average		1.5
(B) East tributaries, low-elevation reaches		
Arquilla Creek	Lower	2.4
Cedar Creek	Lower	8.6
Hinton Creek	Lower	2.6
Peterson Creek	Lower	1.2
Slagle Creek	Lower	2.2
Overall average		3.4
(C) East tributaries, mid-elevation reaches		
Arquilla Creek	Upper	1.6
Hinton Creek	Middle	1.4
	Upper	0.9
Peterson Creek	Middle	1.0
Slagle Creek	Middle	0.7
Overall average		1.1
(D) East tributaries, high-elevation reaches		
Cedar Creek	Middle	0.3
	Upper	0.5
Peterson Creek	Upper	0.5
Slagle Creek	Upper	1.2
Overall average		0.6

the BACH on three co-occurring salmonid species—Cutthroat Trout, Brook Trout, and Brown Trout—and found that regardless of habitat conditions, Cutthroat Trout density was always low (<0.05 fish/m^2) when Brook Trout and Brown Trout densities were high (>0.10 fish/m^2).

The four Manistee River tributaries that were identified as most abiotically suitable for Arctic Grayling with regard to abiotic conditions (Arquilla, Hinton, Slagle, and Woodpecker creeks; Danhoff et al. 2017) had Brown Trout densities greater than 0.10 fish/m^2, which are high enough to exert an "overriding effect" (as proposed by Quist et al. 2003 and defined by Quist and Hubert 2005) on Brook Trout and Slimy Sculpin abundance (Figure 6). However, within each tributary, there were reaches with low densities of Brown Trout (i.e., <0.10 fish/m^2; Figure 7), where Brook Trout and Slimy Sculpin were the most abundant fish species and the likelihood of interactions with Brown Trout were lower, suggesting that these reaches could be targeted for Arctic Grayling restoration efforts. In a 2012 survey of the Big Hole River, Montana, and its tributaries, Cayer and McCullough (2013) found the greatest densities (measured as fish/mi) of Arctic Grayling occurred in tributaries where Brook Trout (and/or Rainbow Trout) densities generally exceeded Brown Trout densities. Although there is potential for competitive and predatory interactions between Arctic Grayling, Brook Trout, and Slimy Sculpin, these species are known to co-

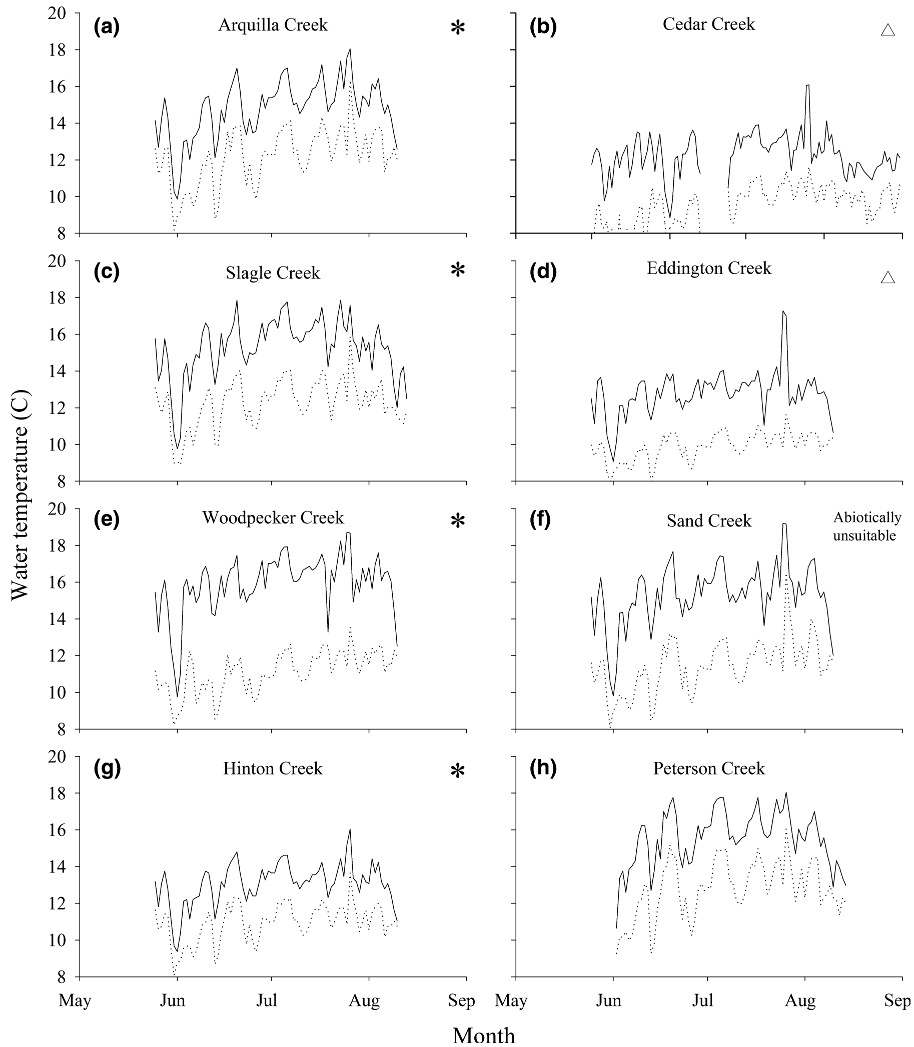

FIGURE 4. Maximum (solid line) and minimum (dashed line) daily water temperatures (°C) recorded in lower reaches of Manistee River tributaries during summer 2012. Asterisks identify the most abiotically suitable tributaries for Arctic Grayling according to Danhoff et al. (2017); open triangles denote tributaries with the lowest abundances of Brown Trout (excluding Sand Creek, which is classified as abiotically unsuitable for Arctic Grayling re-introduction).

occur elsewhere in North America. For example, in the Big Hole River watershed, Byorth and Magee (1998) found evidence of habitat partitioning between Arctic Grayling and Brook Trout, and intraspecific competition appeared to be a more significant factor affecting Arctic Grayling habitat use and growth than interspecific competition. In Michigan, Arctic Grayling naturally co-occurred with Brook Trout in the Otter River (Taylor 1954) and with Slimy Sculpin in the MRW, suggesting that there was potential for each species to find suitable habitat and to partition resources within the fish community.

Water temperature has been suggested as a limiting factor for salmonid species such as the Arctic Grayling, Brook Trout, and Brown Trout (Kaya 1992; Lyons et al. 2010). In each Manistee River tributary, the mean July water temperatures recorded near the confluence were within the optimal temperature ranges for Brook Trout, Brown Trout, and Arctic Grayling growth (11–16, 12–19, and 9.5–16°C, respectively; Raleigh 1982; Hubert et al. 1985; Raleigh et al. 1986; Danhoff et al. 2017). Although maximum summer water temperatures were above the upper optimal bounds for growth of Brook Trout and Arctic Grayling, they were below the suggested lethal levels for each species (25.3°C and 29.3°C, respectively; Raleigh 1982; Lohr et al. 1996). High-temperature events in the streams studied were of short duration rather than representing long-term exposures, and thermal refuges appeared to be present (Figure 4; see Danhoff et al. 2017).

Based on current abiotic conditions (see Danhoff et al. 2017) and Brown Trout densities, there appear to be four

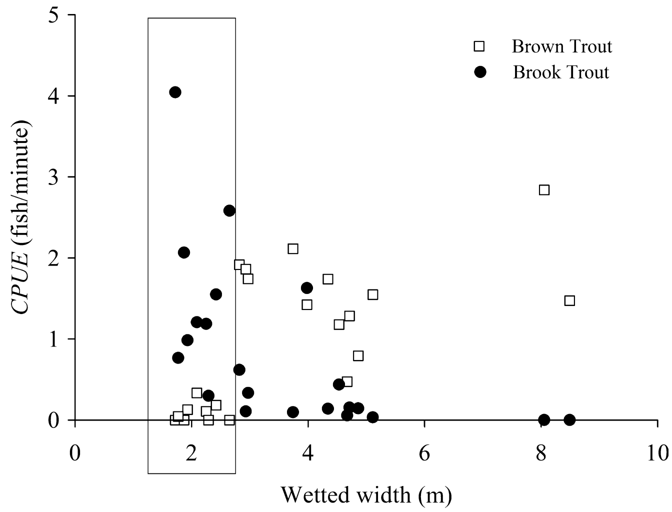

FIGURE 5. Relationship of Brown Trout and Brook Trout CPUE (fish/min) with wetted width (m) in 22 Manistee River tributary reaches. The box indicates reaches where Brown Trout CPUE is the lowest, Brook Trout CPUE is the highest and most variable, and potential predation on Arctic Grayling is expected to be lowest.

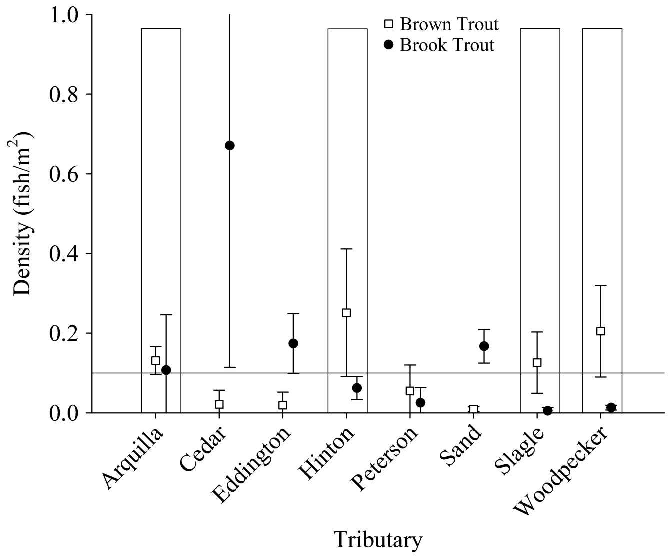

FIGURE 6. Brown Trout and Brook Trout mean density (±SD; fish/m^2) in eight Manistee River tributaries. Boxes indicate tributaries that were identified as most abiotically suitable for Arctic Grayling based on the work of Danhoff et al. (2017). The horizontal line denotes the 0.10-fish/m^2 threshold for a high-density Brown Trout population in Wyoming as proposed by Quist and Hubert (2005).

distinct tributary regions in the MRW that could provide potentially different management strategies and opportunities for Arctic Grayling re-introduction efforts: (1) all west tributaries (Figure 7A); (2) east tributary low-elevation reaches (Figure 7B); (3) east tributary mid-elevation reaches (Figure 7C); and (4) east tributary high-elevation reaches (Figure 7D). The tributaries on the west side of the Manistee River are relatively short (1.0–1.6 rkm), high gradient (average slope = 1.5%), and less thermally stable than tributaries on the east side of the river (Figure 4). With the exception of Woodpecker Creek (the confluence of which is located <50 m from a MDNR Brown Trout stocking site on the Manistee River), the west-side tributaries have low densities (<0.10 fish/m^2) of Brown Trout in all reaches (Figures 1, 7A). On the east side of the Manistee River, there are three elevation regions, and the highest densities (all > 0.10 fish/m^2) of Brown Trout are typically found in the mid-elevation reaches with an average gradient of 1.1% (Figure 7C). Low Brown Trout densities (<0.10 fish/m^2) were observed in seven of nine lower- and upper-elevation reaches (Figure 1; Figure 7B, D). None of the tributaries identified as containing low densities (<0.10 fish/m^2) of Brown Trout overlapped with those identified as "most" suitable at the tributary scale by Danhoff et al. (2017). However, at the reach scale, 4 of the 13 reaches meeting over 80% of the abiotic criteria also had Brown Trout densities less than 0.10 fish/m^2. Based on these results, the most suitable sites for Arctic Grayling re-introduction in this portion of the MRW are as follows: (1) Peterson Creek Lower, (2) Hinton Creek Lower, (3) Eddington Creek Lower, and (4) Eddington Creek Middle. Additionally, Slagle and Woodpecker creeks would provide interesting experimental re-introduction sites, as they rank as the first and second most abiotically suitable tributaries, respectively (Slagle Creek is the largest of the tributaries surveyed; see Danhoff et al. 2017), but five of six reaches exceed the proposed 0.10-fish/m^2 Brown Trout density threshold.

No Arctic Grayling re-introductions are expected to occur in the MRW until 2022–2025, as time is needed to establish an in-state brood population that meets MDNR disease and genetic protocols (T. Zorn, MDNR, personal communication). As such, it is not possible to directly test these models with Arctic Grayling in the MRW at the present time, which leaves uncertainty in predictive capabilities for Arctic Grayling re-introduction in Michigan and elsewhere. However, abiotic relationships for Brook Trout and Arctic Grayling that were documented by McCullough (2017) in the Big Hole River system of Montana are similar to the relationships between Brook Trout and abiotic metrics suggested by this study. Additionally, some of Montana's earlier restoration work has demonstrated that Brook Trout and Arctic Grayling are able to co-exist without significant dietary overlap (McMichael 1990) or microhabitat overlap impacting the growth rates of either species (Byorth and Magee 1998). This suggests that habitats demonstrated as suitable for Brook Trout may also be potentially suitable as Arctic Grayling re-introduction sites (J. Magee, U.S. Fish and Wildlife Service [USFWS], personal communication).

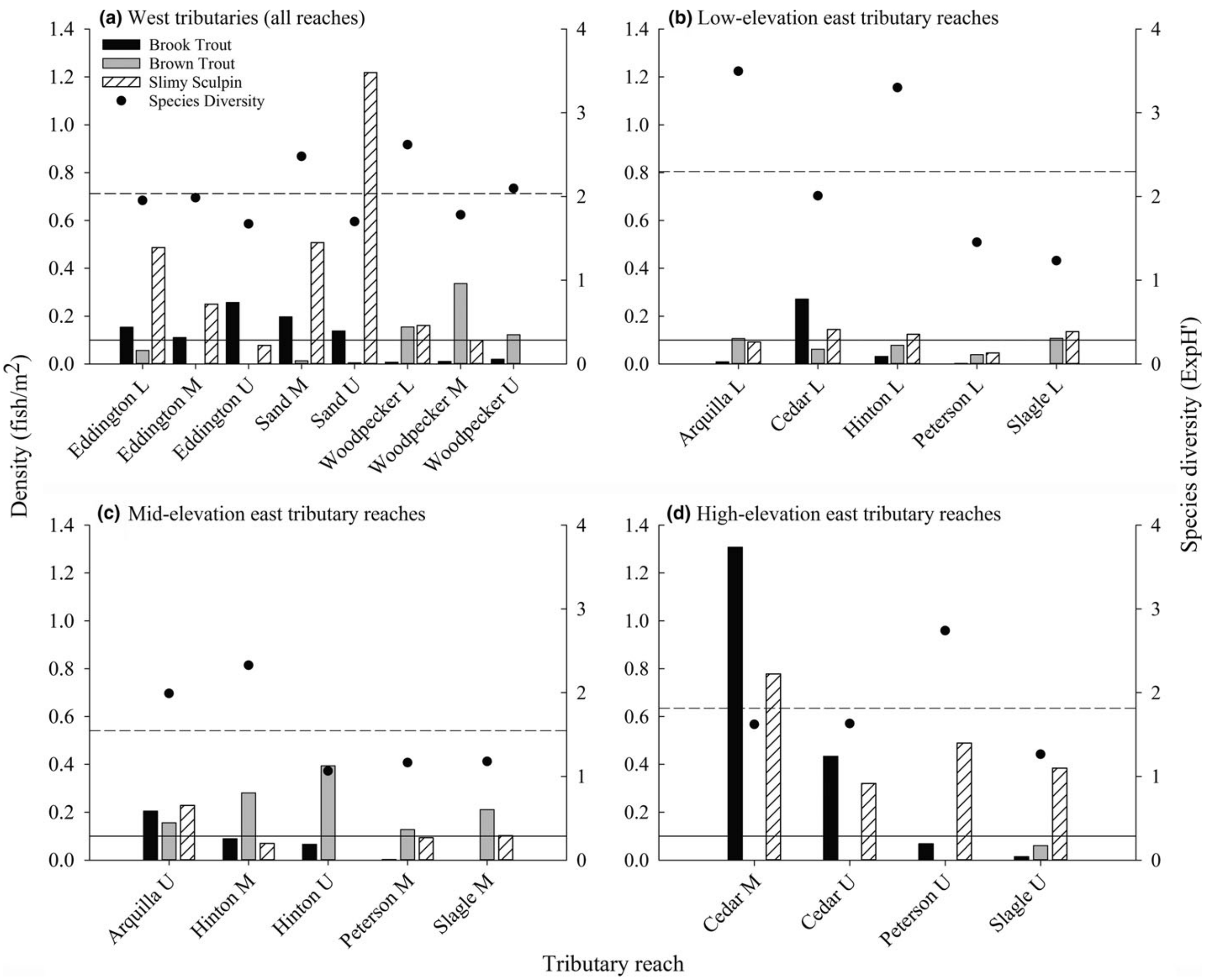

FIGURE 7. Densities (fish/m^2) of Brook Trout, Brown Trout, and Slimy Sculpin and Shannon diversity index (ExpH') values in Manistee River tributary reaches (L = Lower; M = Middle; U = Upper): **(A)** west tributaries (all reaches); **(B)** east tributary low-elevation reaches; **(C)** east tributary mid-elevation reaches; and **(D)** east tributary high-elevation reaches. The solid horizontal line denotes the 0.10-fish/m^2 threshold for a high-density Brown Trout population in Wyoming as described by Quist and Hubert (2005). The dashed horizontal line indicates the mean ExpH' value for each region.

Over the past decade, Brown Trout numbers have been increasing in the Big Hole River basin, and they have replaced Brook Trout as the dominant salmonid species in some streams that support Arctic Grayling (McCullough 2017). The influences of high Brown Trout densities on Brook Trout abundance, as suggested by studies in Montana and by the present research, indicate that Arctic Grayling abundance could be affected in a similar manner, and such a possibility should be taken into consideration when evaluating the restoration potential of proposed Arctic Grayling re-introduction sites within watersheds where Brown Trout are known to occur. McCullough (2017) found a significant negative, non-linear association between the abundances (CPUE; fish/km) of Brown Trout and age-0 Arctic Grayling in the Big Hole River system. Whether that relationship represents direct competition with and/or predation by Brown Trout in Montana streams is unknown, and it appears not to affect age-1 and older (age-1+) Arctic Grayling in the same manner. Brown Trout and Arctic Grayling are currently known to co-occur in portions of the Big Hole River and Ruby River watersheds, suggesting that the mere presence of Brown Trout does not necessarily preclude Arctic Grayling from being successfully established (A. McCullough, personal communication). However, differing influences of Brown Trout on age-0 and age-1+ Arctic Grayling provide evidence supporting the potential for high Brown Trout densities to influence the success of Arctic Grayling re-introduction strategies that utilize eggs or age-0 fish or that rely on natural recruitment. This highlights the importance of habitat heterogeneity, watershed connectivity, and fish community composition that can provide each life stage of Arctic Grayling with unimpeded access to habitats that support their differing biotic and abiotic requirements (e.g., access to spawning and rearing areas with low Brown Trout densities). The proposed Brown Trout threshold of 0.10 fish/m^2 for determining Arctic Grayling re-introduction suitability from this research is a suggested "starting point" that can be adjusted if necessary as new data from ongoing restoration and re-introduction projects throughout the species' range (i.e., Alaska, Michigan, Montana, Canada, etc.) become available.

Re-introduction of Arctic Grayling in the MRW would provide an opportunity for fishery management agencies to examine current goals and adopt strategies focusing on native species in the watershed. Arctic Grayling restoration planning for the MRW should target abiotically suitable locations while considering sites where predation and/or competition (e.g., by Brown Trout) may also be limiting and should develop re-introduction and management strategies that account for this possibility. For example, remote site incubators (RSIs) have been successfully used for Arctic Grayling in Montana (Kaeding and Boltz 2004) and are being considered for possible re-introduction efforts in Manistee River tributaries. The RSIs should enhance survival of early life stages of Arctic Grayling by protecting developing eggs and embryos from sedimentation and from predation by other species prior to hatch and swim-up. Management of nonnative salmonids should also be considered as a potential Arctic Grayling restoration technique. Successful examples of this strategy can be seen in restoration and conservation of other native salmonid species, such as the Colorado River Cutthroat Trout *O. clarkii pleuriticus* and Greenback Cutthroat Trout *O. clarkii stomias*, in western states where moratoria on the stocking of nonnative species have been adopted (USFWS 1998; CDOW 2006). Between 2011 and 2012, nearly 125,000 Brown Trout and Rainbow Trout were stocked in the Manistee River study area by the MDNR (MDNR 2016). If Arctic Grayling restoration proceeds for this watershed, it may be beneficial to reduce or eliminate additional stocking of nonnative species.

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Appendix

TABLE A.1. Physical habitat characteristics and number of fish species captured in 22 sampling reaches within Manistee River, Michigan, tributaries.

Tributary	Reach	Reach length (m)	Reach area (m^2)	Mean gradient (%)	Mean width (m)	Mean depth (m)	Mean discharge (m^3/s)	Mean velocity (m/s)	Average temperature (°C)	Coarse substrate (%)	Woody debris (%)	Fish species (*N*)
Arquilla Creek	Lower	160	809.6	2.4	4.7	0.17	0.14	0.27	12.6	63	20	10
	Upper	198	838.9	1.6	4.0	0.15	0.09	0.22	12.1	74	15	3
Cedar Creek	Lower	133	276.4	8.6	2.1	0.12	0.09	0.51	10.2	71	26	5
	Middle	120	213.3	0.3	1.7	0.18	0.04	0.23	10.7	22	22	2
	Upper	120	343.3	0.5	2.6	0.09	0.03	0.16	11.2	39	13	2
Eddington Creek	Lower	120	299.9	0.8	2.4	0.10	0.05	0.30	9.9	70	21	4
	Middle	120	271.5	1.8	2.3	0.11	0.06	0.32	9.7	65	21	4
	Upper	120	217.8	2.7	1.9	0.10	0.05	0.28	9.9	58	20	3
Hinton Creek	Lower	199	944.9	2.6	4.5	0.20	0.20	0.37	10.9	50	15	12
	Middle	120	359.4	1.4	3.0	0.23	0.07	0.26	12.5	70	15	6
	Upper	123	332.6	0.9	2.8	0.14	0.09	0.28	13.4	74	10	3
Peterson Creek	Lower	247	1,065.4	1.2	4.7	0.23	0.26	0.44	12.3	56	38	5
	Middle	219	1,089.8	1.0	5.1	0.25	0.24	0.33	12.7	60	13	6
	Upper	120	263.9	0.5	2.3	0.16	0.06	0.24	14.4	5	12	6
Sand Creek	Middle	120	228.6	0.3	1.9	0.14	0.02	0.11	15.4	2	18	9
	Upper	120	202.8	1.6	1.8	0.10	0.01	0.10	11.7	11	7	3
Slagle Creek	Lower	325	2,736.2	2.2	8.5	0.29	1.09	0.61	13.5	73	22	6
	Middle	325	2,601.7	0.7	8.0	0.33	0.94	0.49	13.3	71	9	7
	Upper	165	830.4	1.2	4.9	0.23	0.21	0.31	10.8	41	6	7
Woodpecker Creek	Lower	132	645.0	0.9	4.3	0.16	0.15	0.34	12.4	64	52	7
	Middle	120	463.7	3.4	3.7	0.13	0.15	0.37	13.1	71	35	4
	Upper	120	351.3	0.5	2.9	0.16	0.08	0.18	13.9	33	4	6