STATE OF MICHIGAN
DEPARTMENT OF NATURAL RESOURCES

RR2101 April 2017

Effects of Introduced Steelhead on Resident Brown Trout Population Dynamics in a Small Low-gradient Trout Stream

Andrew J. Nuhfer,
Todd C. Wills,
and
Troy G. Zorn

www.michigan.gov/dnr/

FISHERIES DIVISION
RESEARCH REPORT 2101

Suggested Citation Format

Nuhfer, A. J., T. C. Wills, and T. G. Zorn. 2017. Effects of introduced steelhead on resident Brown Trout population dynamics in a small low-gradient trout stream. Michigan Department of Natural Resources, Fisheries Research Report 2101, Lansing.

For information or assistance on this publication, contact:

MICHIGAN DEPARTMENT OF NATURAL RESOURCES,
Fisheries Division
PO BOX 30446
LANSING, MI 48909
517-373-1280

TTY/TDD: 711 (Michigan Relay Center)

This information is available in alternative formats.

Michigan Department of Natural Resources
Fisheries Research Report 2101, 2017

Effects of Introduced Steelhead on Resident Brown Trout Population Dynamics in a Small Low-gradient Trout Stream

Andrew J. Nuhfer

Michigan Department of Natural Resources, Hunt Creek Fisheries Research Station, 1581 Halberg Road, Lewiston Michigan 49756

Todd C. Wills

Michigan Department of Natural Resources, Lake St. Clair Fisheries Research Station, 33135 South River Road, Harrison Township, Michigan 48045

Troy G. Zorn

Michigan Department of Natural Resources, Marquette Fisheries Research Station, 484 Cherry Creek Road, Marquette, Michigan 49855

Abstract.–We used a before-after-control-impact study design to evaluate the effects of introducing migratory Rainbow Trout (steelhead) *Oncorhynchus mykiss* on the population dynamics of resident Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* from 1995–2008 in a small low-gradient Michigan trout stream. Data on resident trout population density, survival, and growth were collected from a treatment section of Hunt Creek, where adult steelhead were stocked each spring from 1998 through 2003, as well as from two reference stream reaches. We found no differences in population metrics of Brook Trout among treatment and reference sections during years with and without juvenile steelhead. The presence of steelhead had no apparent effect on the density of age-0 Brown Trout, but the mean density of all age-1 and older Brown Trout year classes that interacted with juvenile steelhead of the same age was 382 fish/ha compared to 702 fish/ha for age-1 and older year classes that did not interact with juvenile steelhead of the same age. By contrast, no differences in density of age-1 and older Brown Trout were detected in reference sections between the periods when steelhead were present or absent in the treatment section. Lower annual survival rates for year classes of age-0 Brown Trout that interacted with steelhead in the Hunt Creek treatment section were the primary reason that density of age-1 and older Brown Trout fell to approximately half the levels that existed before steelhead were introduced or after most steelhead had emigrated from the stream; overwinter survival of age-0 Brown Trout that interacted with steelhead was also significantly lower than survival of year classes that did not interact with steelhead. We found no significant differences in the mean length at age of any age class of Brown Trout among the treatment and reference sections that could be attributed to interactions with steelhead. Our examination of habitat use in the treatment section during spawning and rearing revealed that Brown Trout always exhibited a preference for deeper waters and stream segments with more large woody debris (LWD), but Brown Trout were more closely associated with LWD in the presence of steelhead. In 3 of 4 years that we monitored redd superimposition, less than 10% of Brown Trout redds were disturbed by subsequent steelhead spawning, which had no apparent adverse effect on the density of age-0 Brown Trout. Our case study showed that introducing steelhead into small low-gradient trout streams can result in lower densities of resident Brown Trout, largely due to reduced survival of Brown Trout from age 0 to age 1. However, we also showed that upstream passage of steelhead into high-quality trout streams offers tremendous potential to increase production of juvenile steelhead thereby reducing our reliance on hatchery-reared fish to stock the Great Lakes.

Introduction

Michigan contains thousands of miles of streams and rivers that support wild populations of resident Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* (based on Anonymous 1967; Gowing and Alexander 1980). Michigan likewise has thousands of miles of streams that receive spawning runs of migratory Rainbow Trout (or steelhead) *Oncorhynchus mykiss,* Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch* from the Great Lakes, but many of these stream miles lie downstream of barrier dams where summer water temperatures are too high to sustain significant natural reproduction. The majority of colder streams that are suitable for natural reproduction of these adfluvial salmonid species are located upstream of dams that were originally constructed many decades ago and have since deteriorated due to age, poor maintenance, or design. Due to the high cost of maintenance and repair of old and failing dams, opportunities to remove them are increasing over time. Dam removal or upstream fish passage facilities at some dams offer tremendous opportunities to restore connectivity to the Great Lakes. Connectivity advantages include increasing trout and salmon angling opportunities and enhancing the production of smolts for the Great Lakes, augmenting hatchery support for those fisheries. A key concern and impediment to dam removal is that resident (landlocked) trout species might be adversely affected by competition with adfluvial salmonid species from the Great Lakes.

Previous evaluations of interactions between adfluvial salmonid species and resident trout in Michigan streams have yielded ambiguous and sometimes contradictory conclusions. Kruger (1985) hypothesized that growth rates of juvenile Brown Trout were suppressed by competition with abundant steelhead in the Pere Marquette River. He noted that growth of age-2 and older Brown Trout was more rapid and speculated that the increase occurred because most age-2 steelhead smolted in the spring and emigrated from the river. Wagner (1975) found that juvenile Brown Trout, Coho Salmon, and steelhead in the Platte River consumed similar types and numbers of invertebrates. However, he judged that there was not significant competition for food because growth of trout was not affected and because juveniles were believed to be spatially segregated within the stream. Similarly, Ziegler (1988) believed that competition for food between juvenile Brown Trout and steelhead did not occur because she found no differences in food habits among populations that did or did not interact with steelhead, and average daily growth rates for Brown Trout were similar. She did find similarities in habitat use as both species commonly associated with instream structure like large woody debris. Lower abundance of Brown Trout that interacted with steelhead was the only indication that steelhead adversely affected Brown Trout abundance. However, given the large range in abundance for Brown Trout populations in Michigan trout streams, regardless of the presence of steelhead, lower abundance of Brown Trout that interact with steelhead in a given stream is not evidence of adverse effects of interactions between species (Michigan Department of Natural Resources [MDNR], Fisheries Division, unpublished data).

Extensive investigations of microhabitat use and habitat partitioning of various combinations of cohabiting riverine salmonid species have been conducted over the past decades, but their applicability to Michigan is of question given the ecology of salmonid species in the Great Lakes region. For example, evaluations of interactions between steelhead and Brown Trout are relatively rare because these species co-occur primarily in Great Lakes tributaries (Hearn 1987; Kocik and Taylor 1996). Kocik and Taylor (1996) suggested that juvenile steelhead had minimal effects on Brown Trout because juvenile Brown Trout emerged earlier and were larger, generally inhabited deeper and faster water, and did not change their microhabitat use when juvenile steelhead were introduced. In a companion study that Kocik and Taylor (1994) conducted in an artificial stream, steelhead had no adverse effects on Brown Trout survival and growth from June to September. Although studies such as these provide useful insights into the potential for interspecies competition for common resources, they do not resolve the question of whether the survival, growth, and abundance of landlocked salmonids in Great Lakes tributaries is affected by adfluvial salmonids *in situ*; and if so, the severity of and mechanisms underlying the observed change. Therefore, we designed a long-term field study to directly evaluate the effects of introducing steelhead into a stable-flow, low-gradient Great Lakes tributary inhabited by Brown Trout and Brook Trout.

Steelhead are an excellent test species for a case study for several reasons. First, Great Lakes steelhead spend one to three years in their natal stream before emigrating downstream. Therefore, they interact with resident trout species for a longer period of time than other adfluvial species such as Chinook Salmon that typically emigrate downstream as age-0 fish (Dodge and MacCrimmon 1970; Stauffer 1972; Biette et al. 1981; Kwain 1983; Seelbach 1987, 1993). Second, steelhead are stocked extensively into the Great Lakes and have developed naturally-reproducing populations in many tributaries throughout the basin (Biette et al. 1981). Hence, they are the species that is most likely to compete with resident Brook and Brown Trout in Michigan streams if new upstream fish passage is provided. Finally, there is greater public acceptance of agency proposals to provide for upstream passage of steelhead as compared to Chinook Salmon and Coho Salmon because of their iteroparous life history. So, evaluation of their potential effects on resident trout provides information that is particularly relevant to contemporary management needs. Therefore, our objectives were to determine if the introduction of steelhead into Hunt Creek, a landlocked Michigan stream that they did not previously inhabit, would result in any of the following:

1. Change the abundance (density), survival, and growth rates of resident Brook and Brown trout
2. Change the habitat use of Brown Trout
3. Increase the potential for competition for spawning habitat between Brown Trout and steelhead
4. Increase the potential for transmission of diseases or parasites from introduced steelhead to Brown Trout

Methods

Experimental Design and Study Area

We used a before-after-control-impact study design in which steelhead were experimentally-introduced into a 3.4 km treatment section of Hunt Creek inhabited by Brook and Brown trout. We selected two reference sections for comparison; a 0.7 km section of Hunt Creek upstream from an impassible barrier, and a 2.3 km section of nearby Gilchrist Creek (Figure 1). Hunt and Gilchrist creeks, located in northern Oscoda and southern Montmorency counties in Michigan's Lower Peninsula, are relatively low-gradient, groundwater-dominated streams with watersheds that drain extensive glacial sands and gravels deposited approximately 10,000 years ago (Dorr and Eschman 1970). Mean summer low-flow discharge of Hunt Creek and Gilchrist Creek during the study was approximately 0.8 m^3/s and 1.1 m^3/s, respectively. Seasonal flow stability was high in both streams. Thermal conditions for trout were excellent as mean July water temperatures in both streams averaged about 16°C from 1995 through 2008. Both the Hunt Creek treatment and reference sections averaged 6.8 m in width; the average width of the Gilchrist Creek reference section was 7.9 m. Before the introduction of steelhead the only common fish species in Hunt Creek were Brown Trout, Brook Trout, and Mottled Sculpin *Cottus bairdi*; other fish species encountered occasionally were Northern Redbelly Dace *Phoxinus eos,* Creek Chub *Semotilus atromaculatus,* and White Sucker *Catostomus commersonii*. Fish community composition in Gilchrist Creek was similar. Since Brook Trout made up only about 1% of the trout community of Hunt Creek study reach, we consider our study to primarily be an assessment of competition between Brown Trout and steelhead.

We transferred 80 pairs of adult steelhead from the Little Manistee River (Manistee Co., Michigan) to the downstream end of the Hunt Creek treatment section each spring from 1998 to 2003 to simulate fish passage beyond an instream barrier. We selected this number of adults to achieve a spawner density comparable to better quality steelhead rivers draining into northwestern Lake Michigan, such as the Little Manistee River (Seelbach 1993; P. Seelbach, U. S. Geological Survey, personal communication). On the day of transfer, all steelhead were directed into hatchery raceways by a weir, lightly anaesthetized with CO_2, measured and assessed for ripeness, loaded onto a hatchery truck, and transported to Hunt

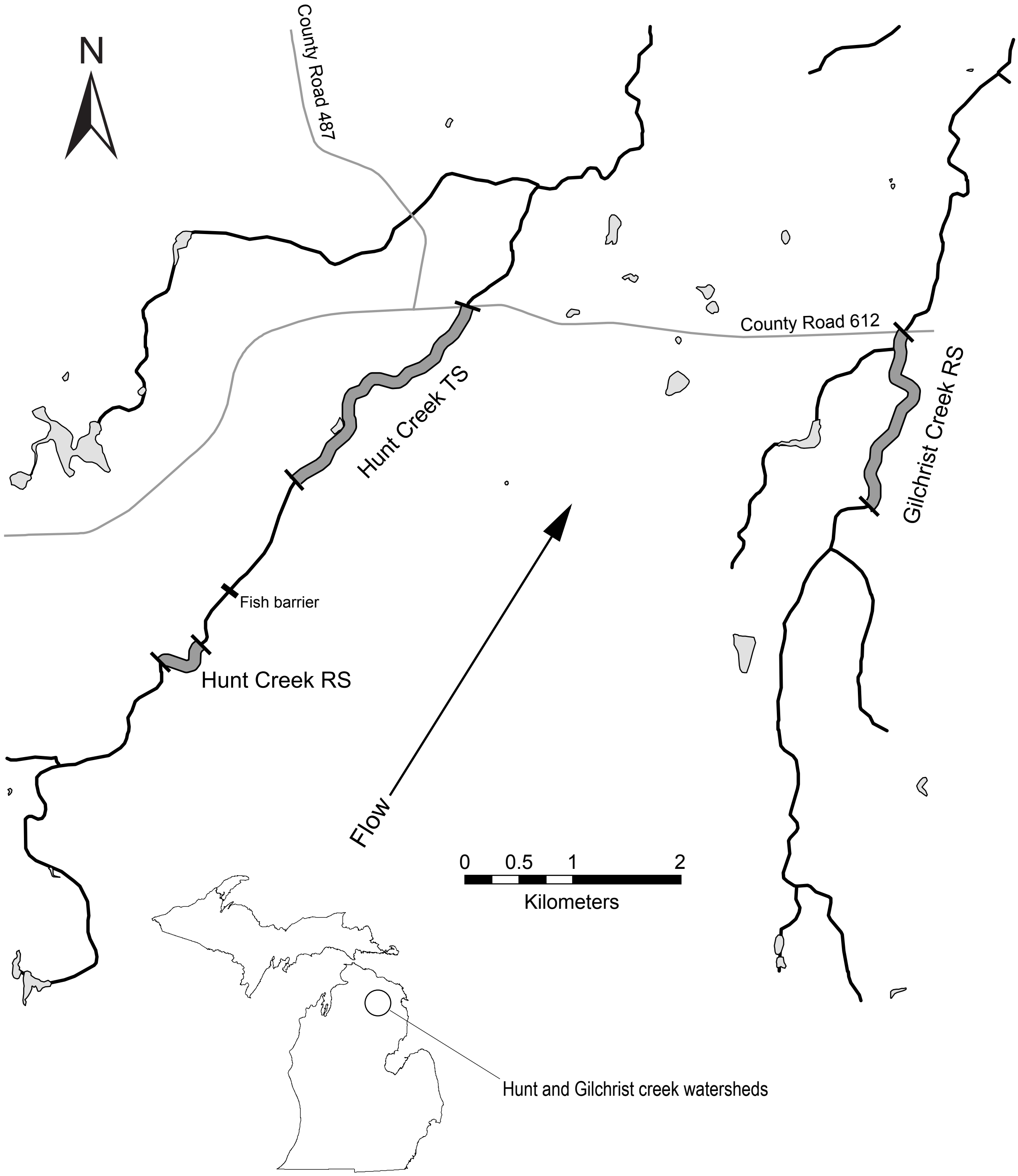

Figure 1.–Map of the study area showing the treatment sections (TS) and reference sections (RS) in Hunt and Gilchrist creeks, Michigan. Hash marks crossing the stream lines indicate the upstream and downstream boundaries of each section, which are shaded in dark grey. An additional 200 m of the TS on Hunt Creek occurred immediately downstream of the fish barrier location shown on the map. The inset shows the location of the Hunt and Gilchrist creek watersheds in Michigan's Lower Peninsula (circled).

Creek (the mean total lengths and weights of adult steelhead averaged over the 6-year stocking period were 72.9 cm and 3.8 kg, respectively). After adult steelhead spawned, they emigrated downstream out of the study area and were not able to return in subsequent years because of a series of dams that block upstream fish passage to the treatment and reference sections in Hunt and Gilchrist creeks.

Population Estimate Methods

Trout populations in Hunt and Gilchrist creeks were estimated in late summer from 1995 to 2008 by two-pass, mark-and-recapture electrofishing with a 2-probe, 240-V DC electrofishing unit towed behind wading electrofishers. Thus, our density, growth, and survival data in the treatment and reference sections spanned 14 years and covered a time period before steelhead introductions (1995–97), a period when juvenile age-0 to age-2 steelhead interacted with resident species (1998–2005), and a period after most steelhead had smolted and emigrated from the stream (2006–2008). The date that we commenced marking runs became progressively earlier throughout the study due to logistical difficulties beyond our control; we began marking runs in late August from 1995 to 2000, mid-August from 2001 to 2003, and at the end of July in 2004–2008. Fish sampling began at the downstream end of each stream reach and proceeded upstream. Recapture collections began on each stream reach immediately after the marking run was complete. All captured salmonids were marked by clipping the dorsal tip of the caudal fin, and data were recorded for separate, contiguous 100-m substations within the treatment and reference sections. Four fixed, 100-m substations located at both the upstream and downstream ends of the Hunt Creek treatment section and the Gilchrist Creek reference section (8 substations/stream) were selected for completion of population estimates during early May 2002 through early May 2008; the population estimates were in turn used to estimate semiannual (i.e., late summer–spring and spring–late summer) survival. Substations were selected for ease of access so as to minimize transport of sampling gear; due to logistical constraints, not all stations were sampled in each year.

We used the Chapman modification of the Petersen mark-recapture formula (Hayes et al. 2007) to compute all population estimates. For our analysis of annual population dynamics (density, growth, and annual survival rates), we pooled late summer population estimate data from 100-m stations within the treatment section and each reference section. We stratified population estimates by 25-mm length groups to account for differences in catchability among fish of different sizes, and then summed these estimates for a total population estimate. During late summer sampling, we collected scale samples as well as total length and weight data from 30 trout of each species per 25-mm length group (if a sufficient number of fish were available) within the treatment and reference sections. During spring sampling, we collected scales, total lengths, and weights from 10 trout of each species per 25-mm length group (if sufficient fish were available) within treatment and reference sections. We used age data from trout scales to apportion population estimates by length groups into estimates by age group for each section and sampling period and computed survival rates from sequential estimates of abundance of age groups. Weighted mean length at age was computed by the methods described by Alexander and Ryckman (1976) and Schneider (2000).

Since individual fish movements can significantly affect estimates of annual survival of stream fishes, we took steps in our analysis to limit the effects of movement on survival estimates. During our study we recorded mark-and-recapture data separately for thirty-four 100-m treatment sections and thirty 100-m reference sections. Our initial analyses of the data clearly showed that estimates of annual survival were more variable and often clearly biased by movement when computations were based on 100-m stations (e.g. estimates of survival greater than 100%). Thus for our analyses of annual survival rates, we pooled data from individual 100-m stations to minimize effects of fish movement on our estimates. We believe that our estimates are a more accurate depiction of the true whole-stream effects of steelhead on resident Brown Trout. The longitudinal distribution of age-0 Brown Trout among 100-m sections of both treatment and reference sections in our study was quite patchy whereas the distribution of yearling and older fish was much more uniform. This suggests that as trout aged and grew there was substantial movement among the short 100-m stations, which would skew estimates of survival for age-0 Brown Trout that were based on short study reaches. Analyses of a statewide database of Brown Trout populations in Michigan's better trout streams collected from stream segments averaging 300 m in length indicates that yearling Brown Trout tend to immigrate into stations with low-density age-0 populations and they either suffer higher mortality or emigrate from stations having high-density age-0 populations (Zorn and Nuhfer 2007, MDNR Fisheries Division, unpublished data).

Habitat Use

We collected data on stream morphology and physical habitat (Table 1) from the treatment section during summer low flow conditions in 1996 so that we could evaluate associations between habitat attributes and salmonid species distributions before and after steelhead introductions. Our methods were a modification of those described in Platts et al. (1983). We established transects every 20 m in the study reaches, and recorded water depth, dominant substrate type, and percent cover in 0.25-m radius circles at 0.5-m intervals along the wetted width of the stream. Percent cover along each transect was partitioned into 5 types; brush, small woody debris, large woody debris, rootwads, or rooted plants. We also recorded undercut banks, stream-shore water depth, and stream bank vegetative stability at each transect (Table 1). We computed gradient (m/km) for each 100-m stream segment from a longitudinal survey of the elevation of the water surface and streambed in the study reach using a level and rod (Harrelson et al. 1994).

Redds

We made annual counts of Brown Trout and steelhead redds in the Hunt Creek treatment section to determine their longitudinal distribution and density, when most spawning occurred, and if steelhead spawning during the spring superimposed their redds upon Brown Trout redds dug the previous fall. Brown Trout redds were counted weekly from 1995 to 2002 starting in the first full week of October and continuing through the middle of November; the final count was usually made at the end of the first week of December. Redd counts were not conducted during the last half of November to avoid conflicts with firearm deer hunters. During redd counts an observer wearing polarized glasses walked upstream along the banks and counted all visible redds. Redds were classified as active if spawning trout were present or if bright polished gravel indicated that it had been recently excavated. The overall maximum length and width of each active redd was measured and recorded so that additional spawning activity at the same site could be identified on subsequent counts. We also measured water depth, velocity, and substrate size in the immediate vicinity of a subsample of redds for both species so that we could compare spawning habitat characteristics. Flagging tape was tied to riparian vegetation at the redd location so that new redds could be distinguished from those counted in previous weeks. We counted and measured steelhead redds each April from 1998 to 2003 using essentially the same methods used for Brown Trout.

We marked a subsample of 130 Brown Trout redd locations over the course of 4 years (1997, 1999, 2000, and 2002) to aid in determining the extent to which spring-spawning steelhead superimposed their redds on Brown Trout redds dug the previous fall. Each fall that we marked Brown Trout redds, we randomly selected different segments of the treatment section (upper, middle, and lower) where we placed markers at redd locations and made diagrams and measurements of each redd. After steelhead spawning ended the following spring, we examined the marked Brown Trout redds and noted if steelhead spawning had occurred at the same location and whether the Brown Trout redd was partially or totally destroyed. We hypothesized that when steelhead superimposed their redds on those of Brown Trout the developing Brown Trout embryos would have been dislodged and most likely killed. To assess whether Brown Trout embryos were still in redds at the time of steelhead spawning, we predicted hatch and

Table 1.–Habitat variables measured or visually estimated along 160 transects (20 per 400-m station) in the 3.4 km Hunt Creek treatment section during 1996. Habitat was measured or estimated within 0.5-m segments along transects perpendicular to stream flow.

Variable	Description
Stream morphology	
Mean stream width (m)	Mean wetted stream width at base flow
Mean stream depth (m)	Mean of all water depth measurements taken along 20 transects
Maximum stream depth (m)	Maximum water depth measured along any transect in each station
Width to depth ratio	Mean stream width divided by mean stream depth
Mean cross sectional area (m^2)	Product of mean stream width and mean depth
Stream gradient (m/km)	Change in vertical elevation of the stream surface per unit of horizontal distance
Undercut bank (cm)	Sum of undercut bank measurements (Platts et al. 1983) made at both ends of 20 transects per station
Mean shore depth (cm)	Mean of shore depth measurements (Platts et al. 1983) made at both ends of 20 transects per station
Variance of depth measurements	The variance of all water depth measurements made in a station
Stream bank vegetative stability rating	Ratings from 1 (poor) through 4 (excellent); See Platts et al. 1983.
Cover percentages	Values for cover types (defined below) were determined by summing the percentages of each 0.5 m transect segment in a station composed of partially or completely submerged cover capable of providing shelter for trout
Large woody debris (% LWD)	Logs > 25 cm in diameter and ≥ 2 m long
Small woody debris (% SWD)	Wood 10–24 cm in diameter and ≥ 2 m long
Rootwads (% RW)	Bases of trees and root structure
Brush (% Brush)	Accumulations of brush of sufficient density to provide overhead cover for fall fingerling or larger trout
Rooted plants (% RP)	Plant beds dense enough to provide overhead cover for fall fingerling or larger trout
Aggregate woody cover (% Wood)	Sum of values for percent LWD, SWD, and RW
Substrate percentages	Percentages of each substrate type in a station
Detritus/organics	Deposits of fine flocculent organic particles or coarser organics such as leaves or needles
Silt or clay	Particle diameter < 0.04 mm
Sand	Particle diameters 0.125–2 mm
Gravel	Particle diameters 2–64 mm
Cobble	Particle diameters 65–250 mm
Boulder	Particle diameters > 250 mm

emergence dates for Hunt Creek Brown Trout using hourly water temperature data collected in Hunt Creek and temperature-based models developed to predict days to 50% hatch and swim-up of Brown Trout fry (Crisp 1981, 1988).

Disease Testing

We collected Brown Trout and steelhead downstream of the lower boundary of the treatment section of Hunt Creek from 1996–2004 and had them examined for an array of fish parasites, as well as for various bacterial and viral diseases, before and after the introduction of steelhead. We also collected Brown Trout downstream of the Gilchrist Creek reference section in 1995, 2000, and 2006 for disease testing (additional disease testing data were collected in Gilchrist Creek in 1990 and 1994 as part of a separate effort). For both species (Brown Trout and steelhead), we tested fish that were at least age-1 and less than 250 mm, because these trout were considered more likely to harbor parasites or disease than age-0 fish, and yet they were very abundant in the population. So, removal of 30–60 fish per year for testing was unlikely to significantly affect populations in the nearby study reaches. Whirling disease *Myxosoma cerebralis* was the primary parasite of concern because it was known to be present in the Little Manistee River, which was the source of adult steelhead used for the study. Bacteriological and parasite testing conducted prior to 2003 was done at the MDNR Fish Health Laboratory while viral screening was done by the U. S. Fish and Wildlife Service (USFWS), Fish Health Lab in La Crosse, Wisconsin. Beginning in 2003 fish health inspections were performed at the Aquatic Animal Health Laboratory at Michigan State University in East Lansing, Michigan. These later health screenings included use of more sophisticated testing procedures including culture on selective media, quantitative ELISA, molecular assays, and PCR assays.

Statistical Methods

Density, survival, and growth–We used analysis of variance (ANOVA) to determine if Brown Trout and Brook Trout density, survival, and growth were significantly different between the treatment and reference sections in Hunt and Gilchrist creeks, with and without the presence of steelhead. Brown Trout and Brook Trout year classes that did not interact with steelhead of the same age were compared to year classes that did interact with steelhead of the same age, causing the calendar years for comparisons to differ for each age class studied (appendices A to F). For example, the age-0 Brown Trout and steelhead interacted in 1998–2003, but interspecific interactions of age-1 fish occurred in 1999–2004. Because resident trout populations in the Hunt Creek treatment section and Gilchrist Creek reference section were composed of only about 1% Brook Trout we did not evaluate interactions among the three species. We treated stream section (treatment or reference) and time period (with or without steelhead) as main effects. Given their substantial influence on trout population dynamics in Michigan rivers, we used spawner density (for age-0) and year class strength (for age-1 and older) resident trout as covariates for analysis of resident trout density, and year class strength as a covariate for analysis of resident trout survival and growth (Zorn and Nuhfer 2007). When appropriate, the data were $\log_{10}$ transformed to meet the necessary distributional assumptions for ANOVA.

We focused our initial analyses on identifying significant stream section × time period interactions that are indicative of variability in the density, survival, or growth of resident Brown Trout and Brook Trout among stream sections with or without the presence of steelhead. Once we identified significant interactions with ANOVA, we focused on comparisons of each main effect (stream section or time period) within levels of the other to determine before-after differences between and within treatment and reference sections. We used Bonferroni-adjusted P-values for all multiple comparisons, which included the following: 1) between time periods (with or without steelhead) within stream sections; and

2) between stream sections (treatment vs. reference) within time periods. We set the rejection criterion α at 0.05 for all comparisons.

Habitat

Dependent variables for Brown Trout and steelhead density were computed for eight contiguous 400-m subsections of the treatment reach from mark-and-recapture data collected in September 1996 and 2000. We developed simple least squares and multiple linear regression (MLR) models to explain variation in the density (kg/400m) of Brown Trout or steelhead among 400-m subsections of Hunt Creek based on the habitat data we collected (Table 1). We used Brown Trout density data collected in 1996 to assess relationships between habitat and Brown Trout density during a period when no steelhead were present. We evaluated relationships between both Brown Trout and steelhead density in 2000 and the habitat variables measured in 1996 to determine if the relations between habitat features and Brown Trout density changed after steelhead were introduced to the treatment section (the year 2000 was the first year of the study when three year classes of juvenile steelhead interacted with Brown Trout, i.e. ages 0 through age 2). Since Hunt Creek exhibits high interannual stability in summer low-flow conditions, we did not remeasure habitat variables for the year 2000 fish-habitat modeling exercise.

We used Pearson correlations of dependent and predictor variables to guide variable selection into our MLR models but we also considered whether an entered variable was hypothesized to have causal relations with the response variable. Usually, only a few independent variables were significantly correlated with the dependent variable, but sometimes several variables of a given type (e.g. mean depth and width-to-depth ratio) were correlated. When more than one collinear independent variable was significantly correlated with a dependent variable, we present only the one that explained the highest amount of variation. 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. We evaluated the relative influence of independent variables on the dependent variable by comparing their standardized regression coefficients. All variables included were significant ($P \leq 0.05$).

Redds

We compared habitat features at Brown Trout and steelhead redd locations using a one-way ANOVA (water velocity, depth, and redd size were treated as dependent variables; species was treated as the main effect) and evaluated substrate frequency of use data with a Chi-square test. When appropriate, the data were transformed to meet the necessary distributional assumptions for ANOVA. We set the rejection criterion α at 0.05 for all comparisons. All data were analyzed with IBM SPSS statistics version 18.0 (IBM, Inc. 2009).

Results

Abundance

We generated 14 August trout population estimates for the Hunt Creek treatment section as well as the Hunt and Gilchrist Creek reference sections from 1995–2008 ($N = 42$). Across all years the total density of Brown Trout ranged from 1,271–2,650 fish/ha in the treatment section, 1,965–5,130 fish/ha in the Gilchrist Creek reference section, and 510–2,409 fish/ha in the Hunt Creek reference section. Age-0 fish were the most abundant age class in the Hunt Creek treatment section and the Gilchrist Creek reference section, typically comprising 53–78% of total density in both stream sections. The abundance of age-0 Brown Trout in the Hunt Creek reference section was more variable, comprising 32–88% of total Brown Trout density (Appendix A). Brook Trout occurred in relatively low abundance in both the Hunt Creek treatment section and Gilchrist Creek reference section, with densities ranging from 17–167 fish/ha and 3–63 fish/ha. Since it is accessible to fish emigrating from an upstream salmonid population comprised almost entirely of Brook Trout, the density of Brook Trout in the Hunt Creek reference section was much higher, ranging from 966–5,121 fish/ha (Appendix B).

Juvenile steelhead populations in the Hunt Creek treatment section produced by adults stocked from 1998 to 2003 were much higher than juvenile Brown Trout or Brook Trout populations (Appendix C). Mean density of age-0 steelhead from the 1998–2003 year classes in the Hunt Creek treatment section averaged 2,889 fish/ha (74% of age-0 trout) compared to 980 fish/ha for Brown Trout (25% of age-0 trout), and 38 fish/ha for Brook Trout (1% of age-0 trout). Species percent composition of age-1 juveniles produced from the 1998–2003 year classes was 63% steelhead, 36% Brown Trout and 2% Brook Trout. Most steelhead smolted and emigrated during the spring at age 2, but by late summer they still comprised 26% of all age-2 trout while Brown and Brook Trout accounted for 73% and 1%, respectively.

Although the density of age-0 Brown Trout did vary significantly by stream section, with approximately twice as many age-0 Brown Trout in Gilchrist Creek as in Hunt Creek during periods with and without steelhead, the presence of steelhead had no apparent effect on age-0 Brown Trout abundance in Hunt Creek as compared to the Gilchrist Creek reference section (Table 2). However, the density of age-1 and older Brown Trout varied significantly among stream sections with and without the presence of steelhead as indicated by a significant stream section × time period interaction (Table 3). In Hunt Creek, the density of age-1 and older Brown Trout that interacted with steelhead as age-0s was significantly less than that of year classes that did not interact with steelhead of the same age (Table 4). Mean density of all age-1 and older Brown Trout year classes that interacted with steelhead was 382 fish/ha as compared to 702 fish/ha for Brown Trout that did not interact with steelhead (Table 2). By contrast, no differences in the density of age-1 and older Brown Trout were detected in the Hunt or Gilchrist Creek reference sections between the periods when steelhead were present or absent in the Hunt Creek treatment section (Table 4). Age-1 and older Brown Trout populations in the Gilchrist Creek reference section were quite stable over the 14 years that late summer populations were estimated, while the population of similar age classes was relatively more variable in the Hunt Creek reference section. The coefficients of variation for mean abundance of age-0 through age-3 Brown Trout in Gilchrist Creek ranged from 0.21 to 0.32. Coefficients of variation for mean abundance of age-0 through age-3 Brown Trout in the Hunt Creek reference section were approximately two times higher than in Gilchrist Creek.

When compared among stream sections, the density of age-1 and older Brown Trout in the Hunt Creek treatment section that interacted with steelhead was significantly lower compared to Brown Trout abundance in Gilchrist Creek during the same years (Figure 2, Table 4). For example, the mean density of age-3 Brown Trout in Hunt Creek during the period without steelhead was almost exactly the same as in Gilchrist Creek (treatment section:reference section ratio of 1.0, Table 2). In comparison, during the period with steelhead, there were only half as many age-3 Brown Trout in Hunt Creek compared to Gilchrist Creek (treatment section:reference section ratio of 0.5, Figure 2).

We found no differences in the mean density of age-0 or age-1 and older Brook Trout that could be attributed to interactions with steelhead. However, the density of both age groups of Brook Trout did vary significantly by stream section (Table 3). The density of Brook Trout was low in both the Hunt Creek treatment section and the Gilchrist Creek reference section throughout the study; Brook Trout in the Hunt Creek treatment section comprised only about 3% of total Brown Trout and Brook Trout numbers compared to about 1% in the Gilchrist Creek reference section (Table 2). In contrast, the density of Brook Trout was much higher in the Hunt Creek reference section (Appendix B). The density of age-1 and older Brook Trout across all stream sections varied significantly by time period (Table 3); point estimates of age-1 and older Brook Trout density were higher during the period without steelhead (Appendix B).

Table 2.–Age-specific densities (number per hectare) of Brown Trout, Brook Trout, and steelhead in treatment and reference sections (TS and RS) when the same age classes of trout and steelhead co-occurred compared to reference periods when identical age classes of steelhead and trout did not co-occur. Mean and standard error (SE) of the mean values are shown. Y = steelhead present in Hunt Creek treatment section.

				Density at age					
Location	Steelhead	Species	Metric	0	1	2	3	4	5+
Hunt TS		Brown	Mean	1,252	428	166	82	21	5
		Brown	SE	133	20	10	8	1	1
	Y	Brown	Mean	980	226	90	47	14	5
	Y	Brown	SE	23	31	8	4	3	2
		Brook	Mean	33	27	4	0		
		Brook	SE	14	6	1	0		
	Y	Brook	Mean	38	11	1	0		
	Y	Brook	SE	9	1	0	0		
		Steelhead	Mean	14	9	3	1		
		Steelhead	SE	12	7	1	1		
	Y	Steelhead	Mean	2,889	396	32	3		
	Y	Steelhead	SE	389	45	15	3		
Gilchrist RS		Brown	Mean	2,564	656	204	85	18	4
		Brown	SE	232	49	29	10	2	1
	Y	Brown	Mean	1,892	556	202	95	26	4
	Y	Brown	SE	212	43	17	9	7	1
		Brook	Mean	10	15	4	0		
		Brook	SE	4	5	1	0		
	Y	Brook	Mean	12	13	1	0		
	Y	Brook	SE	4	4	0	0		
Hunt RS		Brown	Mean	905	253	142	92	33	12
		Brown	SE	198	41	15	9	7	4
	Y	Brown	Mean	860	179	73	37	22	9
	Y	Brown	SE	227	31	23	9	7	3
		Brook	Mean	1,735	380	23	1		
		Brook	SE	360	140	6	1		
	Y	Brook	Mean	2,062	220	22	0		
	Y	Brook	SE	364	45	7	0		

Table 3.–*P*-values from analysis of variance modeling the effects of stream section (treatment or reference) and time period (with or without steelhead) on Brown Trout and Brook Trout density in Hunt and Gilchrist creeks, Michigan (N = 42 population estimates). YAO = yearling and older; NS = not significant.

Species	Metric	Source of variation	*F*	*df*	*P*
Brown Trout	Age 0 density	Spawner density	–	–	NS
		Stream section	15.74	2, 36	<0.001
		Time period	–	–	NS
		Stream section × time period	–	–	NS
	YAO density	Year class strength	17.171	1, 22	<0.001
		Stream section	6.729	2, 22	0.005
		Time period	6.578	1, 22	0.018
		Stream section × time period	3.772	2, 22	0.039
Brook Trout	Age 0 density	Spawner density	–	–	NS
		Stream section	66.44	2, 35	<0.001
		Time period	–	–	NS
		Stream section × time period	–	–	NS
	YAO density	Year class strength	–	–	NS
		Stream section	18.457	2, 28	<0.001
		Time period	6.809	1, 28	0.014
		Stream section × time period	–	–	NS

Table 4.–Bonferroni-adjusted *P*-values from multiple comparison tests evaluating mean differences in Brown Trout density and survival 1) within the treatment and reference sections during time periods with and without steelhead, and 2) between the treatment and reference sections (TS and RS) during time periods with or without steelhead in Hunt and Gilchrist creeks, MI. *P*-values reflect comparisons of locations or periods from tables 3 and 6 where significant stream section × time period interactions were observed. NS = not significant.

Metric	Section	Time period	*t*	*df*	*P*
YAO density	Hunt TS	With vs. Without	-3.44	22	0.007
	Hunt RS		–	–	NS
	Gilchrist RS		–	–	NS
	Hunt TS vs. Gilchrist RS	With	-3.81	22	0.004
	Hunt TS vs. Hunt RS		–	–	NS
	Hunt TS vs. Gilchrist RS	Without	–	–	NS
	Hunt TS vs. Hunt RS		–	–	NS
Age 0–1 survival (annual)	Hunt TS	With vs. Without	-5.27	21	<0.001
	Gilchrist RS		–	–	NS
	Hunt TS vs. Gilchrist RS	With	-4.62	21	<0.001
	Hunt TS vs. Gilchrist RS	Without	–	–	NS
Age 0–1 survival (late summer–spring)	Hunt TS	With vs. Without	-2.88	93	0.010
	Gilchrist RS		–	–	NS
	Hunt TS vs. Gilchrist RS	With	-2.30	93	0.048
	Hunt TS vs. Gilchrist RS	Without	–	–	NS

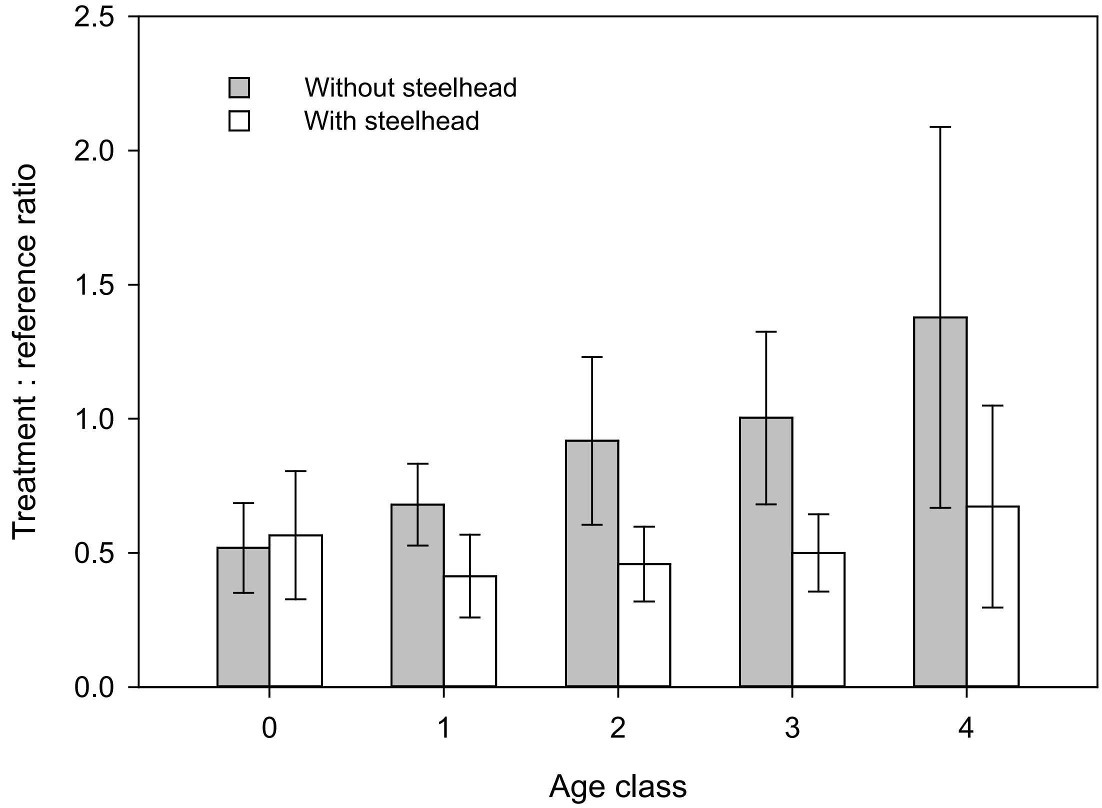

Figure 2.–Mean ratios of late summer density of Brown Trout age classes in the Hunt Creek treatment section compared to the Gilchrist Creek reference section for periods without or with steelhead. A ratio of 1.0 indicates no difference between the two sections; a ratio greater than 1.0 indicates a higher density in the treatment section while a ratio less than 1.0 indicates a higher density in the reference section. Vertical bars depict the 95% confidence limits for the mean ratios.

Annual Survival

Since our analysis of age-1 and older Brown Trout density revealed significant differences among stream sections with and without the presence of steelhead, we analyzed annual survival data by individual age classes to better understand the mechanistic process behind the observed changes. We found a significant stream section × time period interaction for age 0–1 survival, indicating variability in survival to age 1 among treatment and reference sections for periods with and without steelhead. Mean annual survival of age-0 Brown Trout in Hunt Creek was significantly lower when age-0 steelhead were present (Table 4). Mean annual survival of age-0 Brown Trout was 23% during 1998 to 2003 (when age-0 steelhead were present) compared to 37% during years when no age-0 steelhead were present (Table 5). This difference in mean survival among periods represents an average reduction in survival of 38% for age-0 Brown Trout that interacted with steelhead. By contrast, no differences in mean annual survival of age-0 Brown Trout among periods with or without steelhead were detected in the Gilchrist Creek reference section (Tables 5 and 6).

Table 5.–Annual survival of Brown Trout and Brook Trout age classes in treatment and reference sections (TS and RS) when the same age classes of steelhead co-occurred compared to reference periods when identical age classes of steelhead and trout did not co-occur. Mean and standard error (SE) of the mean values are shown. Y = steelhead present in Hunt Creek treatment section.

				Percent survival from previous year to age			
Location	Steelhead	Species	Metric	1	2	3	4
Hunt TS		Brown	Mean	37	37	48	27
		Brown	SE	2	2	5	3
	Y	Brown	Mean	23	42	53	30
	Y	Brown	SE	3	4	4	4
		Brook	Mean	158	16	4	
		Brook	SE	44	5	3	
	Y	Brook	Mean	34	14	0	
	Y	Brook	SE	6	1	0	
Gilchrist RS		Brown	Mean	26	29	39	26
		Brown	SE	3	3	5	5
	Y	Brown	Mean	31	36	48	26
	Y	Brown	SE	3	1	5	4
		Brook	Mean	218	22	0	
		Brook	SE	51	7	0	
	Y	Brook	Mean	253	10	0	
	Y	Brook	SE	112	5	0	
Hunt RS		Brown	Mean	39	65	70	37
		Brown	SE	10	12	8	7
	Y	Brown	Mean	28	45	59	98
	Y	Brown	SE	8	13	13	56
		Brook	Mean	21	8	27	
		Brook	SE	6	4	27	
	Y	Brook	Mean	12	11	0	
	Y	Brook	SE	3	4	0	

Table 6.–Semi-annual survival of Brown Trout age classes in treatment and reference sections (TS and RS) when the same age classes of steelhead co-occurred compared to reference periods when identical age classes of steelhead and trout did not co-occur. Mean and standard error (SE) of the mean values are shown. S = spring; F = fall; Y = steelhead present in Hunt Creek treatment area.

			Percent survival			
Location	Steelhead	Metric	F (age 0) to S (age 1)	S (age 1) to F (age 1)	F (age 1) to S (age 2)	S (age 2) to F (age 2)
Hunt TS		Mean	70	72	54	81
		SE	9	5	5	9
	Y	Mean	43	69	49	83
	Y	SE	5	9	8	11
Gilchrist RS		Mean	39	88	36	94
		SE	6	9	4	9
	Y	Mean	33	82	42	101
	Y	SE	4	12	7	11

In the Hunt Creek treatment section, survival of age-1 through age-3 Brown Trout that interacted with steelhead was similar to year class groups that did not interact with steelhead of the same ages (Table 5). Likewise, we found no differences in mean survival among periods with or without steelhead for older age classes of Brown Trout in the Gilchrist Creek reference section (Table 4). Our initial analyses of population estimate data revealed substantial Brown Trout immigration to the Hunt Creek reference section, as indicated by annual survival estimates >100% for some age classes (Table 5, Appendix D). Therefore, we excluded the Hunt Creek reference section from further Brown Trout survival analyses and focused on differences within and between the Hunt Creek treatment section and Gilchrist Creek reference section. Mean annual survival of age-0 Brown Trout that did not interact with steelhead in the Hunt Creek treatment section was 1.5 times higher than in the Gilchrist Creek reference section during the same period (treatment section:reference section ratio of 1.5, Figure 3). However, the survival of age-0 Brown Trout in the Hunt Creek treatment section was significantly lower than the Gilchrist Creek reference section during the 6 years that age-0 steelhead were present (treatment section:reference section ratio of 0.75; Figure 3, Table 4). There were no significant differences in annual survival for older age classes of Brown Trout in Hunt Creek as compared to Gilchrist Creek (Table 7).

An inverse relationship between density of age-0 trout and annual survival to age 1 was evident in both the Hunt Creek treatment section and the Gilchrist Creek reference section (Figure 4). Survival of Brown Trout to age 1 declined exponentially with increased density of age-0 trout in Hunt Creek (Brown Trout and steelhead combined) and age-0 Brown Trout in Gilchrist Creek (Figure 5; $F = 25.5$; $df = 1, 24$; R2 = 0.52; $P < 0.001$; $R^2 = 0.52$).

Estimates of survival of age-0 Brook Trout in both the Hunt Creek treatment section and the Gilchrist Creek reference section in some years were obviously skewed upward by immigration of age-1 fish into the study sections between years. Survival estimates of age-0 Brook Trout ranged from 20–365% in Hunt Creek and from 53–610% in Gilchrist Creek (Appendix E). We concluded that these highly-variable and biased survival estimates for Brook Trout were not suitable for a meaningful evaluation of potential effects of interactions with steelhead on Brook Trout survival rates.

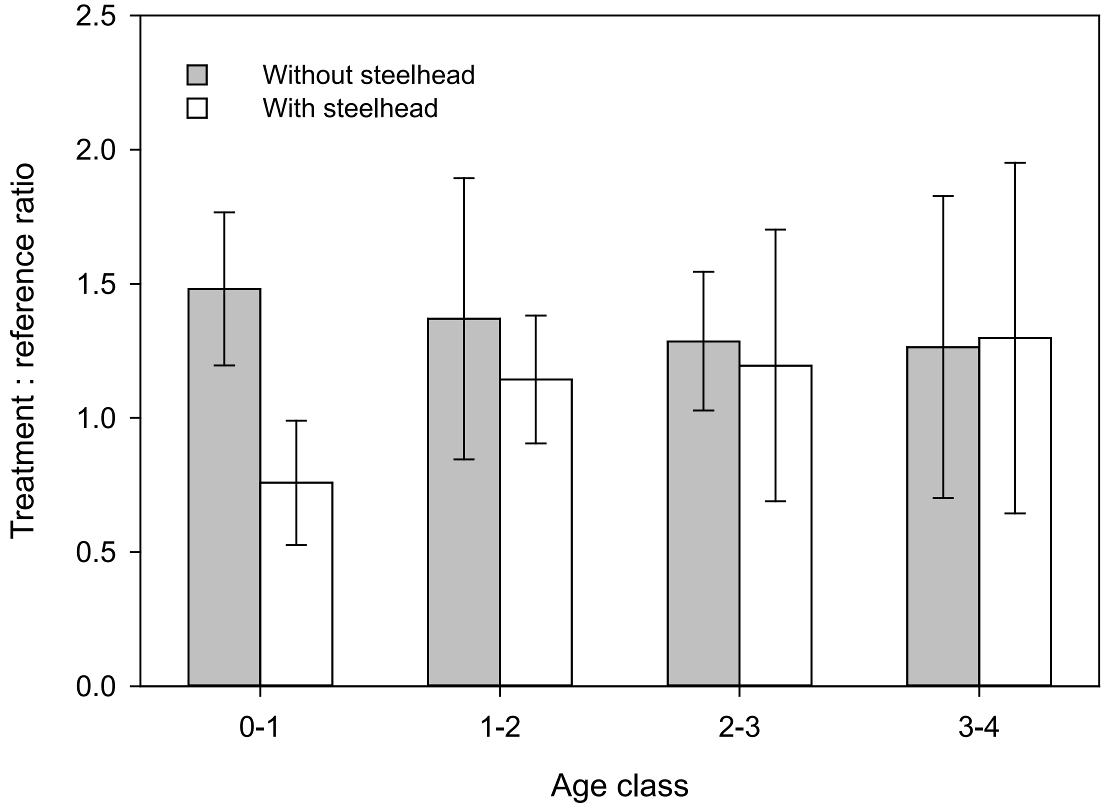

Figure 3.–Mean ratios of annual survival of Brown Trout by age in the Hunt Creek treatment section compared to the Gilchrist Creek reference section for periods without or with steelhead. Vertical bars depict the 95% confidence limits for the mean ratios.

Table 7.–*P*-values from analysis of variance modeling the effects of stream section (treatment or reference) and time period (with or without steelhead) on Brown Trout and Brook Trout survival in Hunt and Gilchrist creeks, Michigan. *N* refers to the total number of population estimates used in the analysis. LS = late summer; S = spring.

Species Metric	Age	Source of variation	*F*	*df*	*P*
Brown Trout	0–1	Year class strength	7.70	1, 21	0.011
Annual survival		Stream section	–	–	NS
N=42		Time period	9.72	1, 21	0.005
		Stream section × time period	10.09	1, 21	0.005
	1–2, 2–3,	Year class strength	–	–	NS
	3–4, 4–5	Stream section	–	–	NS
		Time period	–	–	NS
		Stream section × time period	–	–	NS
Semi-annual survival	0(LS)–1(S)	Year class strength	50.00	1, 93	<0.001
N=98		Stream section	–	–	NS
		Time period	–	–	NS
		Stream section × time period	3.85	1, 93	0.05
	1(S)–1(LS),	Year class strength	–	–	NS
		Stream section	5.53	1, 93	0.021
		Time period	–	–	NS
		Stream section × time period	–	–	NS
	1(LS)–2(S),	Year class strength	–	–	NS
	2(S)–2(LS)	Stream section	–	–	NS
		Time period	–	–	NS
		Stream section × time period	–	–	NS
Brook Trout	1–2, 2–3	Year class strength	–	–	NS
Annual survival		Stream section	–	–	NS
N=42		Time period	–	–	NS
		Stream section × time period	–	–	NS

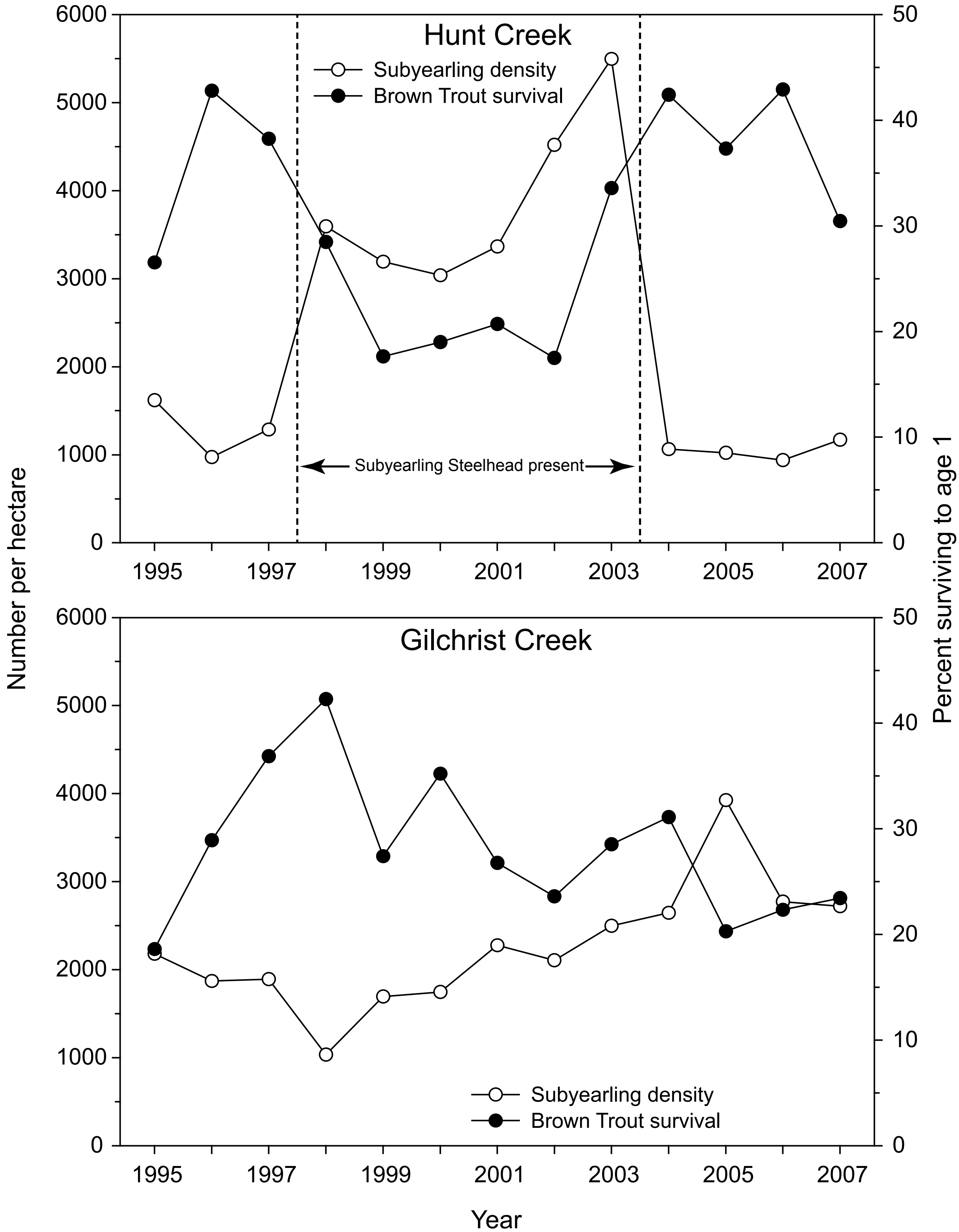

Figure 4.–Density of age-0 Brown Trout and steelhead in the Hunt Creek treatment section, and the percent of age-0 Brown Trout surviving to age 1 (top panel). Bottom panel shows density of age-0 Brown Trout in the Gilchrist Creek reference section, and the percent of them surviving to age 1.

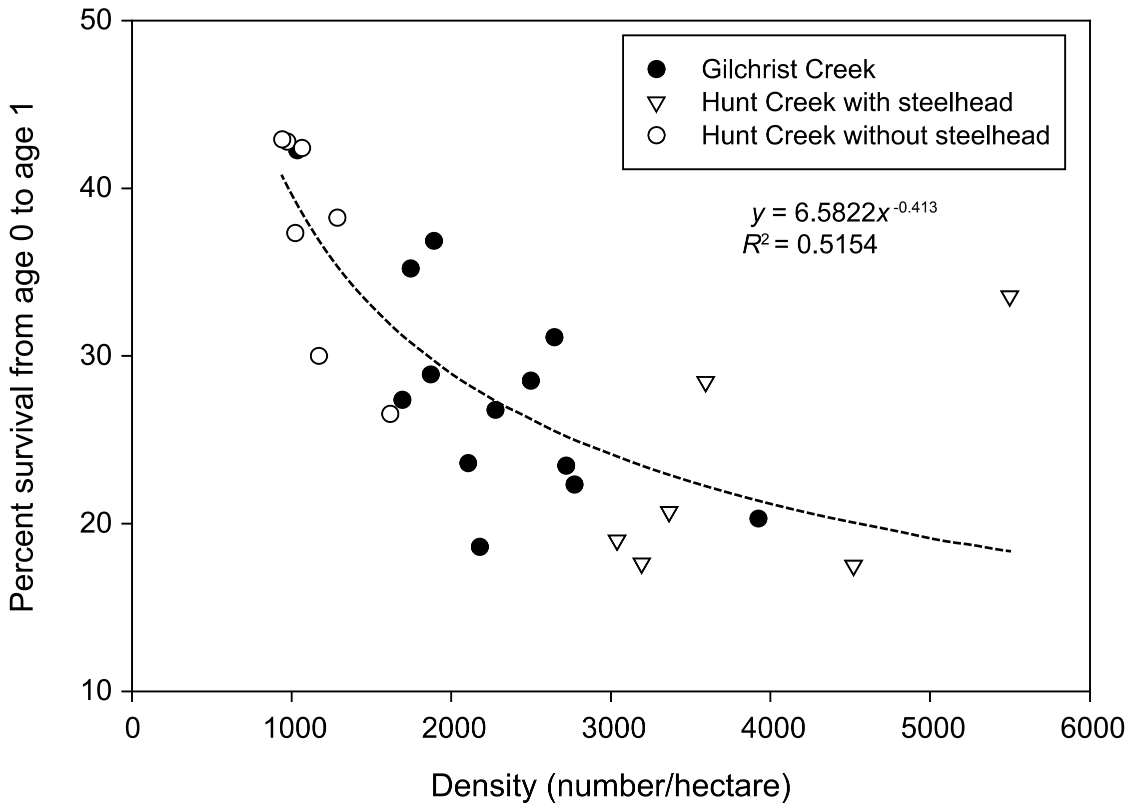

Figure 5.–Brown Trout survival from age 0 to age 1 versus density of age-0 Brown Trout in Gilchrist Creek during 1995–2007. Survival from age 0 to age 1 for Brown Trout in the treatment section of Hunt Creek is distinctly identified for years with and without age-0 steelhead. The power function line fit to all the data (Percent survival to age 1 = 6.582 × Age-0 Brown Trout and steelhead density $^{-0.413}$) explained 52% of variation in survival to age 0.

Semiannual Survival

We estimated semiannual survival (both spring to late summer and late summer to spring) in each of the eight 100-m index stations in the upper and lower reaches of the Hunt Creek treatment and Gilchrist Creek reference sections (N = 98 estimates over the study period). Since the stream section × time period interaction for Brown Trout survival from age 0 (late summer) to age 1 (spring) was within rounding error of being significant (P = 0.053; Table 7), we chose to further explore the variability in age-0 Brown Trout overwinter survival by examining differences within and between stream sections during periods of steelhead presence and absence. Late summer to spring survival of age-0 Brown Trout that interacted with steelhead was significantly lower than survival of year classes within the Hunt Creek treatment section that did not interact with steelhead (Tables 3 and 6). It was significantly lower when compared to the Gilchrist Creek reference section (Figure 5, Table 4). In Hunt Creek, an average of 43% of age-0 Brown Trout that interacted with steelhead survived from late summer to the next spring compared to 70% for year classes that did not interact with steelhead (Table 6). By contrast, a similar change in mean survival of age-0 Brown Trout from the same year classes did not occur in the Gilchrist Creek reference section (Figure 5, Table 4). No significant differences in semiannual survival rates were found between groups of age-1 or age-2 Brown Trout in Hunt Creek regardless of the presence of steelhead (Table 7). We did not assess semiannual survival for older age classes of Brown Trout, because most steelhead smolted and emigrated from the stream when they were 2 years old.

Growth

We found no significant differences in the mean length at age for any age class of Brown Trout between the treatment and reference sections that could be attributed to interactions with steelhead; that is, all tests for interactions between section and time period were not significant (Tables 8 and 9). The mean length of Brown Trout over the course of the 14-year study was significantly different between the Hunt Creek treatment section and the reference sections on Gilchrist Creek and Hunt Creek (Table 9). Point estimates of mean length for all age groups of Brown Trout in Gilchrist Creek were consistently smaller than fish of the same age in either the Hunt Creek treatment or reference sections (Appendix F).

Habitat Use

Brown Trout in the treatment section of Hunt Creek exhibited a preference for deeper waters and stream segments with more large woody debris (LWD) cover regardless of whether or not steelhead were present. However, LWD played a more prominent role in explaining variation in Brown Trout density after a juvenile steelhead population was established. In the absence of steelhead, two-thirds of the variation in total biomass and biomass of yearling and older Brown Trout among 400-m sections of the Hunt Creek was accounted for by mean depth and percent LWD; mean depth alone explained over 60% of the variation in total biomass of Brown Trout and biomass of age-1 and older Brown Trout (Table 10). When steelhead were present nearly 80% of the variation in total biomass or biomass of age-1 and older steelhead and Brown Trout combined among 400-m stations was explained by percent LWD; adding mean water depth to these models increased adjusted R^2 values by about 5% (Table 11).

Table 8.–Mean and standard error (SE) of Brown Trout length-at-age in treatment and reference sections (TS and RS) when the same age classes of steelhead co-occurred compared to reference periods when identical age classes of steelhead and Brown Trout did not co-occur. Y = steelhead present in Hunt Creek treatment area.

			Length (mm) at age				
Location	Steelhead	Metric	0	1	2	3	4
Hunt TS		Mean	83	166	224	271	342
		SE	2	2	3	1	5
	Y	Mean	86	168	234	294	341
	Y	SE	2	2	2	3	4
Gilchrist RS		Mean	74	147	206	265	332
		SE	2	2	3	3	6
	Y	Mean	81	155	218	269	318
	Y	SE	3	3	3	5	4
Hunt RS		Mean	74	158	225	284	341
		SE	3	2	5	5	6
	Y	Mean	81	163	237	295	334
	Y	SE	3	3	6	9	6

Table 9.–*P*-values from analysis of variance modeling the effects of stream section (treatment or reference) and time period (with or without steelhead) on Brown Trout mean length-at-age in Hunt and Gilchrist creeks, MI ($N = 42$ population estimates).

Metric	Source of variation	*F*	*df*	*P*
Age 0 mean length-at-age	Year class strength	14.22	1, 35	0.001
	Stream section	8.48	2, 35	0.001
	Time period	–	–	NS
	Stream section × time period	–	–	NS
Age 1 mean length-at-age	Year class strength	6.59	1, 35	0.015
	Stream section	14.24	2, 35	<0.001
	Time period	–	–	NS
	Stream section × time period	–	–	NS
Age 2 mean length-at-age	Year class strength	8.13	1, 35	0.007
	Stream section	3.46	2, 35	0.042
	Time period	4.65	1, 35	0.038
	Stream section × time period	–	–	NS
Age 3 mean length-at-age	Year class strength	17.92	1, 35	<0.001
	Stream section	6.25	2, 35	0.005
	Time period	–	–	NS
	Stream section × time period	–	–	NS
Age 4 mean length-at-age	Year class strength	–	–	NS
	Stream section	4.72	2, 35	0.015
	Time period	–	–	NS
	Stream section × time period	–	–	NS
Age 5 mean length-at-age	Year class strength	–	–	NS
	Stream section	–	–	NS
	Time period	11.98	1, 35	0.002
	Stream section × time period	–	–	NS

Table 10.–Regression models developed for biomass of Brown Trout (kg/400 m) in the absence of steelhead in 400-m subsections of the 3.4 km Hunt Creek treatment section during September 1996. Habitat variables were measured in June–July 1996. All regression models and standardized coefficients shown were significant ($P \leq 0.05$).

Dependent variable	Total *df*	Adj R^2	*F*	Independent variables	Unstandardized coefficients *B*	Unstandardized coefficients Std. Error	Standardized coefficients Beta
Brown Trout total biomass	7	0.62	12.184	Mean depth	344.62	98.73	0.82
Brown Trout total biomass	7	0.66	7.665	Mean depth	276.73	106.85	0.66
				% LWD	4.03	3.08	0.33
Biomass of Brown Trout >300 mm	7	0.52	8.685	Mean depth	142.94	48.50	0.77
Biomass of Brown Trout >300 mm	7	0.61	6.494	Mean depth	105.56	50.15	0.57
				% LWD	2.22	1.45	0.41
Biomass of age-1 and older Brown Trout	7	0.61	11.739	Mean depth	338.74	98.87	0.81
Biomass of age-1 and older Brown Trout	7	0.67	8.165	Mean depth	264.09	103.17	0.63
				% LWD	4.43	2.98	0.37
Biomass of age-0 Brown Trout	7	0.53	8.864	% sand + % detritus	0.05	0.02	0.77

Table 11.–Regression models developed for Brown Trout (BNT) and steelhead (STT) biomass (kg/400 m) in 400-m subsections of the 3.4 km Hunt Creek treatment section during September 2000. Habitat variables were measured in June–July 1996. All regression models and standardized coefficients shown were significant ($P \leq 0.05$).

Dependent variable	Total *df*	Adj R^2	*F*	Independent variables	Unstandardized coefficients *B*	Unstandardized coefficients Std. Error	Standardized coefficients Beta
Total biomass BNT + STT	7	0.79	27.531	% LWD	8.34	1.59	0.91
Total biomass BNT + STT	7	0.84	19.801	% LWD	7.01	1.58	0.76
				Mean depth	94.34	54.64	0.30
Biomass age-1 and older BNT + STT	7	0.78	26.343	% LWD	8.02	1.56	0.90
Biomass age-1 and older BNT + STT	7	0.52	8.704	Width:Depth ratio	-2.64	0.90	-0.77
Biomass age-1 and older BNT + STT	7	0.84	19.397	% LWD	6.70	1.54	0.75
				Mean depth	94.09	53.23	0.30
Total biomass BNT	7	0.78	26.095	% LWD	8.10	1.59	0.90
Biomass age-1 and older BNT	7	0.76	23.233	% LWD	7.64	1.58	0.89
Biomass of BNT > 300 mm	7	0.42	6.103	Mean shore depth	1.06	0.43	0.71
Biomass of BNT > 300 mm	7	0.59	6.063	Mean shore depth	0.85	0.38	0.57
				% LWD	1.27	0.68	0.47
Biomass age-1 and older STT	7	0.44	6.557	Mean cross section	2.90	1.13	0.72
Biomass age-1 and older STT	7	0.43	6.381	Mean depth	24.87	9.85	0.72

Distributional patterns of age-0 Brown Trout in Hunt Creek were difficult to explain. The percentage of sand and detritus combined was the only habitat feature found to be significantly related to biomass of age-0 Brown Trout in the absence of steelhead (Table 10). We found no significant regression relations between habitat variables and age-0 steelhead or Brown Trout biomass in 400-m stations when steelhead were present. We found no significant relationship between the number of age-0 Brown Trout in 400-m stream sections and the number of Brown Trout redds present in the sections during the previous year regardless of the presence of steelhead.

The only significant regression relations between the biomass of age-1 and older steelhead and our habitat variables were the related variables of mean depth and mean stream cross section. Either of these variables alone explained about 44% of variation in density of older steelhead (Table 11).

Redds

Over 90% of Brown Trout spawning activity observed in Hunt Creek occurred during the last half of October and the first half of November each year. Few active Brown Trout redds were counted during the first week of October or December. The highest number of redds counted (active and inactive redds combined) occurred near the end of October in 4 out of 5 years that weekly redd counts were made. From 1995 through 2002, the highest annual density of active and inactive Brown Trout redds counted per day in the Hunt Creek treatment section ranged from 2.1 to 5.4 redds per 100 m, and averaged 3.5 redds per 100 m.

Most adult steelhead in Hunt Creek spawned within a week or two after they were stocked although some steelhead began excavating redds within a day of being transferred. Stocking dates ranged from March 22 to April 1 between 1998 and 2003; the numbers of active redds counted peaked within two weeks after planting. In most years the number of steelhead redds counted two weeks after stocking was higher than the number of female steelhead stocked, indicating that some females deposited eggs in more than one redd. From 1998 through 2003 the highest densities of steelhead redds counted per day ranged from 1.2 to 2.4 per 100 m and averaged 1.8 per 100 m.

Steelhead consistently dug the majority of their redds within 1 km of the site where adults were stocked each year from 1998 to 2003 whereas Brown Trout redds were more uniformly distributed throughout the study reach of Hunt Creek. Nearly 60% of the steelhead redds counted in the thirty-two 100-m stations upstream of the stocking site during the study were found in the first nine 100-m stations immediately upstream compared to only 37% of Brown Trout redds (Figure 6). Steelhead also spawned intensively in a 200-m reach of Hunt Creek immediately downstream of the stocking site. Steelhead redds were rarely found further downstream, but were commonly found as far as 4.4 km upstream from the stocking site where upstream movement of spawners was blocked by an impassible barrier (Figure 1).

Steelhead selected redd site locations with higher mean water velocities and depths than Brown Trout, but there was broad overlap in the range of depths and velocities where redds for the two species were located (Table 12). Estimates for mean velocity and depth immediately upstream of redd pits of steelhead were significantly greater than for Brown Trout. Mean water depth on top of the tailspill was 2 cm deeper for Brown Trout than for steelhead, but broad overlap occurred between habitats used by the species.

Differences in the size of gravel substrate used for redd construction by steelhead and Brown Trout was the most notable difference in spawning habitat use between the species. Nearly half of Brown Trout spawned over small gravel substrate (0.6–2.5 cm diameter) while the other half spawned over gravel larger than 2.5 cm in diameter. By contrast, over 90% of steelhead spawned over gravel larger than 2.5 cm (Table 12). On average, steelhead redds were about twice as long and wide as Brown Trout redds. Multiple pairs of both species commonly engaged in colonial spawning. Thus, the upper end of the range in lengths and widths of redds measured represent colonial redds.

The extent of superimposition of steelhead redds on Brown Trout redds varied by river section. On average, steelhead superimposed their redds upon 14% of Brown Trout redds excavated the previous fall (Table 13). In 3 of 4 years, less than 10% of Brown Trout redds were disturbed by subsequent steelhead spawning. However, in one year (2000) 55% of marked Brown Trout redds were disturbed by steelhead; all were located within 0.9 km immediately upstream of the site where steelhead were stocked and where they were most likely to spawn (Figure 6). In most cases, Brown Trout redds that were disturbed were completely obliterated.

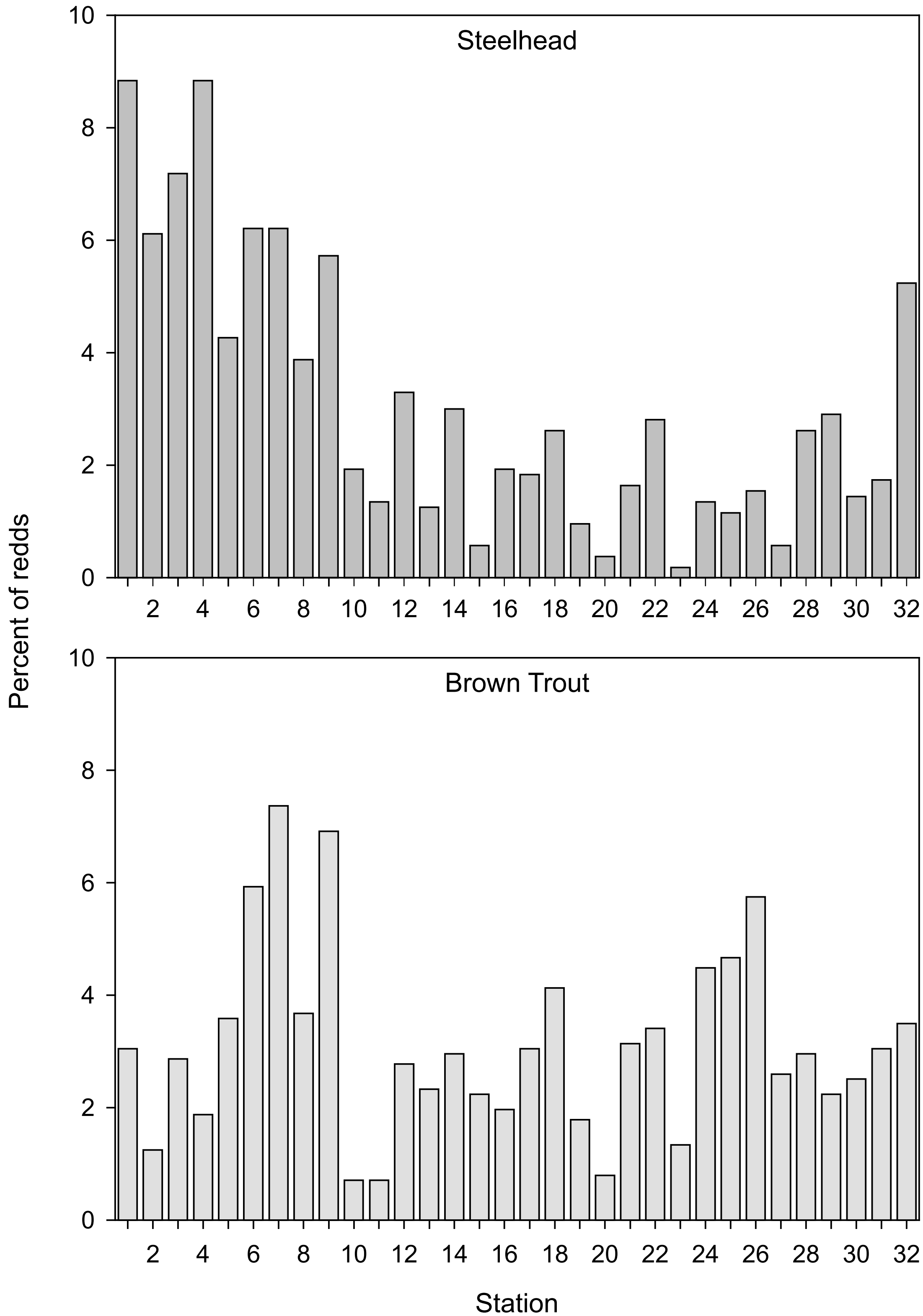

Figure 6.–Average distribution of steelhead (top panel) and Brown Trout (bottom panel) redds among 100-m stations in the Hunt Creek treatment section. Brown Trout redds were counted each fall from 1995 to 2002 and steelhead redds were counted each spring from 1998 to 2003.

Table 12.–*P*-values from one-way analysis of variance comparing habitat features of Brown Trout and steelhead redds in the treatment section of Hunt Creek (substrate frequency of use was compared using a Chi-square test). NS = not significant.

	Brown Trout				Steelhead				
Habitat feature	Mean	SE	Range	*N*	Mean	SE	Range	*N*	*P*
Water velocity (m/s) at 0.6 × depth: 30 cm upstream of redd pit	0.64	0.01	0.20–1.01	140	0.68	0.01	0.30–1.20	186	≤0.05
Water velocity (m/s) at 0.6 × depth: on top of tailspill	0.81	0.03	0.57–1.08	23	0.80	0.02	0.60–0.99	31	NS
Water depth (m): 30 cm upstream of redd pit	0.27	0.01	0.13–0.49	101	0.34	0.01	0.19–0.62	91	≤0.05
Water depth (m): On top of tailspill	0.26	0.01	0.06–0.70	231	0.24	0.01	0.11–0.55	234	≤0.05
Redd length m	1.87	0.10	0.66–4.37	61	3.66	0.13	0.76–6.93	91	≤0.05
Redd width m	0.81	0.05	0.18–1.96	61	1.78	0.07	0.64–3.68	91	≤0.05
% of redds in gravel 0.6–2.5 cm	45	–	–	165	8	–	–	165	≤0.05
% of redds in gravel >2.5 cm	55	–	–	165	92	–	–	165	<0.05

Table 13.–Frequency and percentage of marked Brown Trout redds in the treatment section of Hunt Creek dug up by steelhead that spawned the following spring.

	Number of Brown Trout redds		Percent of Brown Trout
Year	marked	dug up by steelhead	redds affected
1997	30	2	6.7
1999	40	3	7.5
2000	18 [a]	10	55.5
2002	30	2	6.7
All years	118	17	14.4

[a] We marked thirty Brown Trout redds, but a beaver dam built after Brown Trout spawned blocked steelhead access to an upstream segment where twelve marked redds were located. The remaining redds were located within 0.9 km immediately upstream of the site where steelhead were stocked and were most likely to spawn.

We estimated that Brown Trout would have been incubating in redds for all years in which steelhead spawned in Hunt Creek, because of overlap in steelhead spawning and predicted incubation periods of Brown Trout. Steelhead stocking dates ranged from March 22 to April 1, and numbers of active redds peaked within 2 weeks of planting. Predicted Brown Trout hatch dates ranged from January 30 to March 26 from 1996 to 2008 with a median of March 4; predicted fry emergence dates ranged from April 16 to May 18 with a median of April 27. We used November 1 as the starting date in models predicting hatch and swim-up since Brown Trout redd counts were usually highest during the last week of October.

Parasites and Diseases

Introduction of steelhead coincided with initial instances of whirling disease and bacterial kidney disease in Hunt Creek Brown Trout, but no viral diseases were detected over the course of the study. Whirling disease spores were not detected in Brown Trout from either Hunt or Gilchrist creeks prior to steelhead introductions (Tables 14 and 15). A single spore was found in a pooled sample of 5 Brown Trout collected from Hunt Creek several months after steelhead were first stocked in 1998; low levels of whirling disease spores were found in all Hunt Creek Brown Trout samples tested from 2000 to 2004 and in all steelhead samples examined between 2001 and 2004. Whirling disease spores were found in 7 of 30 Brown Trout collected from Gilchrist Creek in 2005, but were not detected in the last sample collected in 2006. Brown Trout found to harbor whirling disease spores in both Hunt and Gilchrist creeks exhibited either no damage or negligible tissue damage. Minor cranial deformity was observed in one steelhead from Hunt Creek that tested positive for whirling disease, but in general there was little or no tissue damage observed in infected steelhead.

The bacterium causing bacterial kidney disease (BKD), *Renibacterium salmoninarum*, was found in all samples of Brown Trout and steelhead examined from 2003–04 in Hunt Creek and 2005–06 in Gilchrist Creek (Tables 14 and 15), although it was not found in samples tested in prior years. Nearly 90% of Brown Trout tested from Hunt Creek in 2004 were infected with *R. salmoninarum*; 63% and 82% of Brown Trout collected from Gilchrist Creek in 2005 and 2006 were infected. Fish that were infected with high concentrations of *R. salmoninarum* typically displayed the widespread granuloma characteristic of BKD. Steelhead from Hunt Creek that tested positive for *R. salmoninarum* were lightly infected and did not exhibit signs of tissue damage.

Discussion

Abundance

Our most striking finding was that age-1 and older Brown Trout that interacted with steelhead in the Hunt Creek treatment section as juveniles were only about half as abundant as year classes that did not interact with juvenile steelhead. No differences in density of age-1 and older Brown Trout were found in either of our reference sections for these time periods. We did not find this result reported elsewhere and we could find no similar long-term, before-and-after studies of interactions between these two species. Prior to our study it has been logistically difficult to make before-and-after comparisons of the effects juvenile steelhead on Brown Trout due to a lack of pre-steelhead abundance data. Juveniles have co-existed in undammed coldwater tributaries of Michigan for over a century, because both Brown Trout and steelhead were introduced into the Great Lakes region in the late 1800s. Using an alternative approach, Peck (2001) analyzed a time series of population data and concluded that increased contemporary abundance of steelhead in a tributary to Lake Superior had reduced densities of resident Brook Trout and Brown Trout.

Table 14.–Incidence of the whirling disease parasite as well as bacterial and viral diseases in Brown Trout and steelhead collected from the treatment section of Hunt Creek. Data are presented as incidence/sample size. In 1998 and 2000–02 positive whirling disease test results are given only as (+) because tests were run on 5-fish pooled samples. B = Brown Trout, Y = steelhead.

		Year								
Parasite or disease	spp.	1996	1997	1998	1999	2000	2001	2002	2003	2004
Whirling disease	B	0/55	0/49	+	0/60	+	+	+	1/60	11/56
Myxosoma cerebralis	Y				0/30		+	+	2/60	5/34
Bacterial diseases										
Bacterial kidney disease	B	0/60	0/60	0/60	0/60	0/60	0/58	0/40	7/60	49/56
Renibacterium salmoninarum	Y						0/60	0/60	3/60	0/34
Bacterial furunculosis	B	0/30	0/30	0/30	0/29	0/30	0/30	0/30	0/60	0/56
Aeromonas salmonicida	Y						0/30	0/30	0/60	0/34
Enteric redmouth	B	0/30	0/30	0/30	0/29	0/30	0/30	0/30	0/60	0/56
Yersinia ruckeri	Y						0/30	0/30	0/60	0/34
Flavobacterium sp.	B								0/60	0/56
	Y								0/60	0/34
Vagococcus sp.	B								0/60	0/56
	Y								0/60	0/34
Carnobacterium sp.	B								0/60	0/56
	Y								0/60	0/34
Aeromonas hydrophila	B									0/56
	Y									15/34
Viral diseases										
Viral hemorrhagic	B	0/60	0/60	0/60	0/60	0/60	0/58	0/40	0/60	0/56
septicemia	Y				0/30		0/60	0/60	0/60	0/34
Infectious hematopoietic	B								0/60	0/56
necrosis	Y								0/60	0/34
Infectious pancreatic	B	0/60	0/60	0/60	0/60	0/60	0/58	0/40	0/60	0/56
necrosis	Y				0/30		0/60	0/60	0/60	0/34

Table 15.–Incidence of the whirling disease parasite as well as bacterial and viral diseases in Brown Trout from the reference section of Gilchrist Creek. Data are presented as incidence/sample size.

Parasite or disease	Year				
	1990	1994	1995	2005	2006
Whirling disease *Myxosoma cerebralis*		0/30	0/37	7/30	0/60
Bacterial diseases					
Bacterial kidney disease *Renibacterium salmoninarum*	0/60	0/60	0/60	19/30	49/60
Bacterial furunculosis *Aeromonas salmonicida*	0/30	0/30	0/30	0/30	0/60
Enteric redmouth *Yersinia ruckeri*	0/30	0/30	0/30	0/30	0/60
Flavobacterium sp.				0/30	0/60
Vagococcus sp.				0/30	0/60
Carnobacterium sp.				0/30	23/60
Aeromonas hydrophila					18/60
Viral diseases					
Viral hemorrhagic septicemia				0/30	0/60
Infectious hematopoietic necrosis				0/30	0/60
Infectious pancreatic necrosis				0/30	0/60

Our findings differ from those of Kocik and Taylor (1996), who suggested that steelhead have little effect on resident Brown Trout in low-gradient rivers because age-0 Brown Trout are larger and use different microhabitats. Their hypothesis that size differences and habitat segregation among sympatric age-0 fish limited adverse effects on Brown Trout was bolstered by their conclusion that juvenile steelhead had no discernible effect on abundance or survival of juvenile Brown Trout in Gilchrist Creek (Kocik and Taylor 1995). However, Kocik and Taylor (1995) sampled Brown Trout and steelhead in only three 100-m study reaches, whereas our abundance and annual survival estimates were derived from a treatment section that was 11 times larger (3.4 km). Thus, even short-distance movements of trout between annual sampling events may have skewed their results. Another important difference between our work and that of Kocik and Taylor (1995) is the source of steelhead: they introduced steelhead as fry, whereas our steelhead originated from natural reproduction by translocated adult spawners. Given the potential for a mismatch between stocking time and temperature or streamflow (and the resulting negative effect on recruitment) when introducing steelhead fry, along with the suggestion that steelhead fry produced from the natural spawning of stocked adults are more fit than stocked fry from another source (see Berejikian et al. 2005), it is likely that the high young-of-the year steelhead densities observed in our study relative to the Kocik and Taylor (1995) study are more representative of natural conditions. Trout movement, the much smaller size of their sampling universe, and the difference in the source of steelhead are plausible reasons for the conflict between our findings and Kocik and Taylor's (1995) findings; however, our results actually affirm their conceptual model, which suggests that if competitive interactions occur at a stage when steelhead have a numerical advantage over Brown Trout, then steelhead can indeed have a negative effect on the Brown Trout population. Interestingly, Kocik and Taylor's (1995) experimental stream reach on Gilchrist Creek was within the much longer reach that we used as a reference zone for our study.

Our finding that juvenile steelhead had no measurable effect on resident Brook Trout abundance should be viewed with caution. Brook Trout comprised only a few percent of the total trout community in both the Hunt Creek treatment section and the Gilchrist Creek reference section. We also found substantial immigration of yearling Brook Trout into both treatment and reference sections from outside the reaches we sampled as indicated by survival estimates higher than 100% (Appendix E). We believe that yearling Brook Trout immigrated into our treatment section from upstream where both age-0 and yearling Brook Trout were very abundant (Appendix B). Thus, at least a portion of the age-1 and older Brook Trout we sampled in the treatment section did not interact with steelhead as age-0s and are therefore were not truly indicative of the sympatric abundance level that might be found in a closed population. Peck (2001) suggested that competition between age-0 Brook Trout and juvenile steelhead reduced survival rates for Brook Trout resulting in lower abundance of older Brook Trout in several Michigan streams that flow into Lake Superior, but our data were not suitable for testing this hypothesis.

Survival

Our finding that lower annual survival rates for sympatric year classes of age-0 Brown Trout in the Hunt Creek treatment section were the primary reason that density of older and larger Brown Trout fell to approximately half the levels that existed before steelhead were introduced (or after most steelhead had emigrated from the stream) is similar to that of Peck (2001). He reported that survival of Brook Trout and Brown Trout from age 0 to age 1 declined over time as a result of increased steelhead populations in a Lake Superior tributary even though abundance of resident age-0 fish did not change. Our conclusions on reduced survival of age-0 Brown Trout when they were sympatric with steelhead differs with the findings from earlier Gilchrist Creek studies (Kocik and Taylor 1995, 1996) which sampled much smaller areas of stream over a considerably shorter time period.

Annual survival of age-0 Brown Trout in the treatment section of Hunt Creek was not obviously affected by variation in Brown Trout year class density over the 14-year study. Late summer density of age-0 Brown Trout was very stable over this period, averaging 1,136 fish/ha with a coefficient of variation of 0.27 (Table 2). However, in years when adult steelhead spawned, the total density of steelhead and Brown Trout age-0s combined averaged 3,869 fish/ha and survival of age-0 Brown Trout was consistently lower for these sympatric year classes (Figure 4). We could not quantify the relative magnitude of intra- and inter-species density effects on survival of age-0 Brown Trout in Hunt Creek. Intraspecies competition effects on survival of age-0 Brown Trout were clearly evident in the Gilchrist reference section where nearly half the variation in annual survival of age-0 Brown Trout (adjusted $R^2 = 0.44$) was explained by year class density. However, in Hunt Creek there was no significant relation between age-0 Brown Trout density and survival (adjusted $R^2 = -0.08$, $P = 0.78$). We hypothesize that much higher densities of age-0 Brown Trout in Gilchrist Creek (mean of 2,276 fish/ha 1995–2008) as compared to Hunt Creek (mean of 1,136 fish/ha 1995–2008) may account for our findings. A compilation of Brown Trout population data for 17 Michigan rivers by Zorn and Nuhfer (2007) also suggested survival of age-0 Brown Trout was density dependent.

A common tenet of competition theory among salmonine fishes is that larger individuals have a competitive advantage (Hearn 1987). In Hunt Creek, the mean length of age-0 Brown Trout in late summer was 17 mm greater than that of age-0 steelhead (83 mm vs. 66 mm), but age-0 steelhead were nearly three times more abundant than age-0 Brown Trout when the two species co-occurred (Table 2). Although steelhead did not appear to influence Brown Trout survival as much as equivalent numbers of Brown Trout, their sheer numbers evidently did reduce survival of age-0 Brown Trout in

Hunt Creek (Figure 5). Increased metabolic costs of defending territories are a plausible mechanism to explain why mortality of the larger age-0 Brown Trout increased when they were sympatric with steelhead. Elliott (1994) observed that attack rates by juvenile Brown Trout in defense of territories increased as a function of both fish size and density of trout without territories. He suggested that costs of territorial defense provided a reasonable explanation for mortality of larger age-0 fish in a cohort at high densities while mortality of smaller age-0 fish increased due to lack of food. Our conclusion that juvenile steelhead reduced survival of age-0 Brown Trout (or triggered emigration) is bolstered by the fact that we found no differences in annual survival among periods in our reference section. This conclusion is also consistent with our finding that 70% of allopatric age-0 Brown Trout survived from fall to the next spring as compared to 43% survival of age-0 Brown Trout that were sympatric with juvenile steelhead (Table 6).

We found no evidence that steelhead affected survival of older age classes of trout. We postulate that a combination of mortality and emigration reduced abundance of yearling and older steelhead such that habitat availability or competition for other resources was less limiting for older Brown Trout. This finding was not surprising given that during years steelhead were present in the Hunt Creek treatment section mean densities of age-1 and older Brown Trout and steelhead combined (813 fish/ha) were only about 14% higher than densities of age-1 and older Brown Trout (702 fish/ha) in the absence of steelhead. Median density of age-1 and older salmonid species in Michigan's better wild trout streams is around 760 fish/ha so total densities of Brown Trout and steelhead combined in Hunt Creek were not particularly high (MDNR Fisheries Division, unpublished data). Density-dependent processes are more likely to be found in high-density Brown Trout populations and at early life stages (Elliott 1994; Zorn and Nuhfer 2007).

In contrast to the survival results for age-0 Brown Trout, we found no significant relation between densities of age-0 steelhead and their survival over the next year. On average, 86% of age-0 steelhead had died or emigrated from our treatment section by age-1 (fall). Although we did not make population estimates outside our study section of Hunt Creek, sampling to obtain steelhead for disease testing conducted downstream from the study section demonstrated that yearling steelhead were relatively abundant all the way to the stream mouth, a distance of 6.6 km downstream from the site where adult steelhead were stocked. Substantial downstream movement of presmolt age-0 and yearling steelhead has been observed by other investigators in Michigan streams and in Pacific Coast streams (Chapman and Bjornn 1969; Bjornn 1971; Stauffer 1972; Seelbach 1993). The magnitude of this emigration appears to be related to habitat quality in natal streams. Downstream movement of presmolt steelhead during fall and winter is more likely to occur when there is little coarse substrate available as cover for juveniles (Chapman and Bjornn 1969; Bjornn 1971). Habitat for salmonine species is often considered to be more limiting during winter than during other times of the year (Hunt 1969; Cunjak and Power 1986; Harwood et al 2002; Mitro and Zale 2002). Coarse substrate ($\geq$ 33 mm) was rare in Hunt Creek and moreover, available coarse substrates were often embedded with sand and did not provide high-quality cover for small fish. Adjustments in juvenile steelhead density to available habitat through mortality and emigration during their first year may have contributed to the relatively uniform density of age-1 steelhead we observed over time in Hunt Creek (Appendix C).

Growth

Co-occurrence with steelhead had no significant effect on mean lengths at age of Brown Trout. Year class density of Brown Trout and stream section (treatment or reference) were the only sources of variation consistently related to mean length-at-age. Our findings were similar to several other Michigan investigations that found little or no effect of competition on Brown Trout growth parameters. Kocik and Taylor (1995) found some evidence that age-0 Brown Trout were larger and had faster average summer growth rates in Gilchrist Creek when steelhead were present, but by age 1 negative effects of steelhead on age-1 Brown Trout size or instantaneous growth rates were not apparent. Similarly, Ziegler (1988) found no significant differences in daily growth rates between Brown Trout populations with or without steelhead. Kruger (1985) speculated that competition with juvenile steelhead in the Pere Marquette River reduced growth rates of younger age groups of Brown Trout, because they were smaller than the average for Michigan trout streams until age 2 but grew faster than average after same-age steelhead smolted and emigrated to Lake Michigan. Today however, mean lengths of age-1 through age-5 Brown Trout in the Pere Marquette River are all substantially larger than average for Michigan in spite of the fact that estimates of juvenile steelhead abundance in the river at the MDNR population index station are higher than anywhere else in the state (MDNR Fisheries Division, unpublished data). Thus, the more recent and exhaustive Michigan data suggests that Brown Trout length at age is not negatively affected by co-occurring age classes of steelhead.

The findings from our current study are most concordant with those of Elliott (1994) who asserted that average growth of stream Brown Trout is usually unrelated to density because populations are largely regulated through density-dependent mortality and emigration. Our observation of higher mortality of age-0 Brown Trout in the presence of steelhead also supports the hypothesis that the primary population adjustments we observed were due to higher mortality when total age-0 salmonid densities were high. If average growth of Brown Trout was indeed lower under conditions of sympatry, then the change was masked by sampling location and year as suggested by Jenkins et al. (1999).

Habitat Use

Our finding that variation in density of both allopatric and sympatric age-1 and older Brown Trout among 400-m sections of the Hunt Creek treatment section was best explained by combinations of mean water depth and percent LWD was consistent with other investigations of Brown Trout habitat preference for sites with cover (e.g. Fausch and White 1981; Kennedy and Strange 1982; Fausch et al. 1988; Heggenes 1988; Flebbe and Dolloff 1995; Dieterman et al. 2006). Our observation that percent LWD explained somewhat more of the variation in age-1 and older Brown Trout density when steelhead were present (as compared to allopatric density), could indicate that Brown Trout became even more cover oriented as total trout densities increased. Cunjak and Power (1986) reported higher associations of trout with cover when available cover was limited. In Hunt Creek, we detected no changes in growth (mean length at age) or annual survival rates of age-1 and older Brown Trout, which suggests that cover for older fish was no more limiting when steelhead were present. We did find that survival of age-0 Brown Trout was lower in the presence of steelhead, so perhaps density related adjustments to available cover took place at an earlier age. We hypothesize that numbers of age-1 steelhead were sufficiently reduced through mortality or downstream emigration such that habitat suitability for older Brown Trout was not significantly changed by the presence of steelhead. Variation in density of age-1 and older steelhead alone was best explained by mean depth or cross section, but the combined density of age-1 and older Brown Trout and steelhead was best explained by percent LWD.

Overall, our evaluation of mesohabitat effects on steelhead and Brown Trout distribution among stream sections was consistent with observations from other Michigan studies in low gradient streams where similar microhabitats were used by both species (Zeigler 1988; Kocik and Taylor 1996). In the absence of steelhead, the only mesohabitat feature that explained significant variation in density of age-0 Brown Trout among 400-m stations was percent sand and detritus. This probably occurred because sand and detritus substrates are associated with lower water velocity areas that are preferred habitat for younger fish (Kocik and Taylor 1996; Raleigh et al. 1984, 1986). We did not find an association between age-0 Brown Trout and the number of redds per station as was reported for a Pennsylvania (Beard and Carline 1991) and Michigan (Benson 1953) trout stream. The conflict in results may be a result of the larger distance between sampling stations in the other studies. Although there was large variation in the numbers of redds per station in Hunt Creek (Figure 6), relatively small scale movement of juveniles away from areas where redds were concentrated to stations with more suitable rearing habitat apparently occurred. Surprisingly, we found no significant relationships between densities of co-occurring age-0 Brown Trout and steelhead (either individually or collectively) and the mesohabitat features we measured. We speculate that this might have occurred because the overall higher density of sympatric age-0 fish resulted in higher percentages of fish occupying suboptimal habitats. The significantly lower survival of sympatric age-0 Brown Trout that we documented in this study also suggested that some aspect of habitat may have been less suitable (or limiting) when the same age classes of steelhead were present.

Spawning Interactions

Steelhead spawning activity had limited effects on Brown Trout reproduction in Hunt Creek during our study. This is in sharp contrast to a New Zealand study where superimposition of Rainbow Trout redds upon Brown Trout redds in a stream with limited suitable spawning habitat resulted in a 95% reduction in Brown Trout spawning success (Hayes 1987). By contrast, in three of the four years when we made observations of redd superimposition, less than 10% of Brown Trout redds in Hunt Creek were disturbed by steelhead spawning. Similar densities of age-0 Brown Trout during periods of steelhead presence and absence in Hunt Creek, and the lack of interaction between period and section (treatment or reference), offer further evidence for our conclusion that steelhead spawning had little or no impact on Brown Trout spawning success.

We evaluated redd superimposition as a form of interference competition because of the observation that multiple adfluvial salmonid species that spawn in Lake Michigan tributaries often successively use the same spawning riffles. The relatively low level of redd superimposition in Hunt Creek may have occurred because suitable spawning habitat was widely available; approximately 50% of the substrate in our treatment section was gravel. Interference competition for spawning sites also might have been more intense if adult steelhead had been introduced into the study reach earlier in the year. In our study, we stocked adult steelhead near the end of March so they had less time to distribute themselves over suitable spawning habitats as compared to fish from natural spawning runs that sometimes ascend rivers to spawning areas many months prior to spawning. Naturalized steelhead in Michigan have been observed spawning as early as February although the peak of steelhead spawning activity at the latitude we conducted our study is typically in late March and early April (M. Tonello, MDNR, personal communication). The concentration of steelhead spawning within the first kilometer of Hunt Creek upstream from the steelhead stocking site may have actually caused more disruption of previously constructed steelhead redds as compared to Brown Trout redds. Intraspecies disruption of spawning beds via redd superimposition has been previously reported for large runs of other pacific salmon species (Wickett 1958, McNeil 1964, Kocik et al. 1991). Given the similarities in the range of water depths and velocities at redd sites for both Brown Trout and steelhead in our study (Table 12) and the broad range of suitable spawning habitat for the two species (Raleigh 1984, 1986), significant disruption of Brown Trout redds by spawning steelhead could occur in streams where little gravel substrate is available. In our study, we noted this when redds were marked in the lower reach of the Hunt Creek treatment section where most steelhead spawning typically occurred.

Parasites and Disease

The discovery of *Myxobolus cerebralis* spores in Hunt Creek Brown Trout the first year that adult steelhead were transferred into the creek from a whirling disease positive river suggests that the range of the parasite within Michigan could be expanded through increases in fish passage. We can not be certain that steelhead were the source of *M. cerebralis* since alternate vectors of infection such as transfer of myxospores from angler waders (Gates et al. 2008) or transport of spores from other infected sites by avian piscivores could also have occurred (Koel et al. 2010). As of 2003, *Myxobolus cerebralis* spores have been detected in about 8% of 455 samples of trout from Michigan streams and rivers (with and without Great Lakes access) including some from watersheds close to the Thunder Bay River watershed that includes Hunt Creek (MDNR Fisheries Division, unpublished data). Regardless of how whirling disease was transmitted to Hunt Creek, it apparently had no adverse effects on juvenile steelhead or Brown Trout populations given that age-0 Brown Trout populations remained stable over the course of the study while the density of age-0 steelhead was highest for the last year classes produced in 2002 and 2003, well after *M. cerebralis* was detected in both species. Levels of infection were regarded as relatively low in all trout examined and evidence of minor tissue damage attributable to the disease was observed in only a few individual steelhead. Brown Trout are known to be far less susceptible to effects of whirling disease than Rainbow Trout (steelhead) and have thrived in some western rivers in spite of high exposures to *M. cerebralis* (O'Grodnick 1979; Thompson et al. 1999). The apparent lack of ill effects on steelhead in our study was a further indication that whirling disease infection intensity was low. The obligate intermediate oligochaete host (*Tubifex tubifex*) for whirling disease is typically most abundant in stream reaches with siltation or nutrient enrichment (Zendt and Bergersen 2000; Hiner and Moffitt 2002). Most northern Michigan trout streams, including Hunt Creek, flow through relatively pristine watersheds where point sources of organic enrichment or nutrients are uncommon. Moreover, the background levels of nutrients such as phosphorus in contemporary Michigan trout streams are generally very low due to the geology of the region (Dorr and Eschman 1970; Cwalinski et al. 2006; Zorn and Nuhfer 2007). Kaeser et al. (2006) postulated that a relative lack of organic enrichment in Pennsylvania trout streams is the reason wild trout population declines have not been observed in the region since whirling disease was first documented there in 1956. Some of the highest densities of juvenile steelhead recently sampled in Michigan were found in streams where *M. cerebralis* has been detected in trout (MDNR Fisheries Division, unpublished data), which is a further indication that the disease has had little impact on Michigan trout populations.

Bacterial kidney disease was the only other "disease of concern" detected in fish from our study streams but there is no reason to believe it originated from stocked steelhead. The causative agent of BKD, *Renibacterium salmoninarum* was first detected in Brown Trout and steelhead from Hunt Creek examined in 2003. We suspect that the bacterium was present in resident Brown Trout before that time but was not detected because less sophisticated detection methods were used prior to 2003. Bacterial kidney disease is apparently widespread throughout the state. A survey of feral salmonid fish populations conducted by MDNR and the USFWS from 2000–2003 detected *R. salmoninarum* in 51 of 67 watersheds within the Great Lakes (Faisal et al. 2012). The few steelhead found to harbor *R. salmoninarum* were not heavily infected and displayed no evidence of tissue damage. By contrast, some samples of Brown Trout from both our treatment and reference sections were heavily infected with *R. salmoninarum* and exhibited the typical granulomatous lesions characteristic of BKD. We had no way to differentiate between mortality of Brown Trout that might have been caused by BKD as opposed to other causes. Since the disease was present in both our treatment and reference sections we speculate that any effects BKD had on mortality should have been similar among sites.

Management Implications

Fish passage decisions should include consideration of both the costs and benefits of restoring biological connections between rivers and the Great Lakes. The overarching objective of this long-term research project was to obtain quantitative measures of the potential effects of competition between steelhead and resident Brown Trout that might occur as a result of future decisions to pass adfluvial salmonids upstream of existing fish barriers. Our case study clearly showed that interactions among juvenile steelhead and Brown Trout reduced survival of young Brown Trout and lowered abundance of older and larger Brown Trout in Hunt Creek. It is challenging to estimate how these findings apply to individual streams within the diverse suite of trout streams found in Michigan. Since the average density of age-0 Brown Trout in Hunt Creek during this study was 1,136 fish/ha as compared to a median density of 655 fish/ha at 35 fixed index sites in high-quality trout streams sampled for Fisheries Division's Streams Status and Trends Program from 2002 to 2004 (MDNR Fisheries Division, unpublished data), we believe that our findings best represent the effects of interactions among salmonid species in smaller trout streams where densities of age-0 trout are relatively high. During years that adult steelhead spawned in Hunt Creek, late-summer density of all age-0 salmonids averaged about 4,000 fish/ha, resulting in lower survival rates for juvenile Brown Trout. We believe that lowered survival of juvenile Brown Trout due to interactions with juvenile steelhead is less likely to occur in streams where densities of age-0 Brown Trout are lower. In addition, some larger streams have the capacity to produce and sustain some of the highest densities of large resident Brown Trout found in Michigan despite the presence of dense populations of juvenile steelhead (e.g., the Pere Marquette and Little Manistee rivers, MDNR Fisheries Division, unpublished data). Our field study demonstrated that steelhead with access to high-quality tributary streams have the reproductive capacity to generate very large numbers of juveniles that could reduce our reliance on hatchery-reared fish to support sports fisheries in the Great Lakes and tributary streams. Given that it currently costs MDNR Fisheries Division an average of $1.41 per steelhead stocked (MDNR Fisheries Division, unpublished data), opportunities to restore self-sustaining runs of steelhead on Michigan streams by removing dams or installing fish passage should be given serious consideration.

Acknowledgments

Many personnel of the Fisheries Division and university students provided assistance with this study. Special thanks to fisheries research technician T. J. Adams who coordinated field sampling, assisted with data summarization, and aged thousands of trout scales. We also thank the many biologists and technicians from the Northern Lake Huron and Central Lake Michigan management units and the Alpena and Charlevoix fisheries research stations who assisted with electrofishing. Financial support for this study came from the Federal Aid in Sport Fish Restoration Fund and the MDNR Fish and Game fund.

References

Alexander, G. R., and J. R. Ryckman. 1976. Trout production and catch under normal and special angling regulations in the North Branch of the Au Sable River, Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1840, Ann Arbor.

Anonymous. 1967. Michigan stream classification 1967 system. Michigan Department of Natural Resources Fisheries Division. Lansing.

Beard, T. D. Jr., and R. F. Carline. 1991. Influence of spawning and other stream habitat features on spatial variability of wild Brown Trout. Transactions of the American Fisheries Society 120:711-722.

Benson, N. G. 1953. The importance of ground water to trout populations in the Pigeon River, Michigan. Transactions of the North American Wildlife Conference 18:268-281.

Berejikian, B., D. Van Doornik, A. LaRae, S. Tezak, and J. Lee. 2005. The effects of exercise on behavior and reproductive success of captively reared steelhead. Transactions of the American Fisheries Society 134:1236–1252.

Biette, R. M., D. P. Dodge, R. L. Hassinger, and T. M. Stauffer. 1981. Life history and timing of migrations and spawning behavior of Rainbow Trout (Salmo gairdneri) populations of the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 38:1759-1771.

Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100:423-438

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams with special reference to food and feeding. H. R. MacMillan Lectures in Fisheries, Symposium on salmon and trout in streams. University of British Columbia Pp. 153-176.

Crisp, D. T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology 11:361-368.

Crisp, D. T. 1988. Prediction, from temperature, of eying, hatching, and swim-up times for salmonid embryos. Freshwater Biology 19:41-48.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident Brook Trout (Salvelinus fontinalis) and Brown Trout (Salmo trutta). Canadian Journal of Fisheries and Aquatic Sciences 43:1970-1981.

Cwalinski, T. A., N. A. Godby, Jr., and A. J. Nuhfer. 2006. Thunder Bay River Assessment. Michigan Department of Natural Resources, Fisheries Special Report 37, Ann Arbor.

Dieterman, E. J., W. C. Thorn, C. S. Anderson, and J. L. Weiss. 2006. Summer habitat associations of large Brown Trout in southeast Minnesota streams. Minnesota Department of Natural Resources Investigational Report 539, St. Paul.

Dodge, D. P., and H. R. MacCrimmon. 1970. Vital statistics of a population of Great Lakes Rainbow Trout (Salmo gairdneri) characterized by an extended spawning season. Journal of the Fisheries Research Board of Canada 27:613-618.

Dorr, J. S., Jr., and D. F. Eschman. 1970. Geology of Michigan. The University of Michigan Press, Ann Arbor.

Elliott, J. M. 1994. Quantitative ecology and the Brown Trout. Oxford University Press. New York.

Faisal, M., C. A. Schulz, T. P. Loch, R. K. Kim, J. Hnath, and G. Whelan. 2012. Current status of fish health and disease issues in the Laurentian Great Lakes: 2005–2010. Pages 259–302 *in* W. W. Taylor, A. J. Lynch, and N. J. Leonard, editors. Great Lakes Fisheries Policy and Management: A binational perspective. Michigan State University Press, East Lansing.

Fausch, K. D., and R. J. White. 1981. Competition between Brook Trout (Salvelinus fontinalis) and Brown Trout (Salmo trutta) in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables 1950-85. U.S. Forest Service General Technical Report PNW-GTR-213.

Flebbe, P. A., and C. A. Dolloff. 1995. Trout use of woody debris and habitat in Appalachian wilderness streams of North Carolina. North American Journal of Fisheries Management 15:579-590.

Gates, K. K., C. S. Guy, A. V. Zale, and T. B. Horton. 2008. Adherence of myxospores to waders: Implications for disease dissemination. North American Journal of Fisheries Management 28:1453-1458.

Gowing, H., and G. R. Alexander. 1980. Population dynamics of trout in some streams of the northern Lower Peninsula of Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1877, Ann Arbor.

Harrelson, C. C., Rawlins, C. L., and J. P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field techniques. U. S. Department of Agriculture, Forest Service, General Technical Report RM-245. Rocky Mountain Forest and Range Experiment Station, Fort Collins.

Harwood, A. J., N. B. Metcalfe, S. W. Griffiths, and J. D. Armstrong. 2002. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 59:1515-1523.

Hayes, J. W. 1987. Competition for spawning space between Brown (*Salmo trutta*) and Rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences 44:40-47.

Hayes, D. B., J. R. Bence, T. J. Kwak, and B. E. Thompson. 2007. Abundance, biomass and production. Pages 327-374 in Guy, C., and M. Brown (editors) Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda.

Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: A review. Fisheries 12:24-31

Heggenes, J. 1988. Physical habitat selection by Brown Trout (Salmo trutta) in riverine systems. Nordic Journal of Freshwater Research 64:74-90.

Hiner, M., and C. M. Moffitt. 2002. Modeling Myxobolus cerebralis infections in trout: Associations with habitat variables. Pages 167-179 in J. L. Bartholomew and J. C. Wilson, editors. Whirling disease: reviews and current topics. American Fisheries Society Symposium 29, Bethesda, Maryland.

Hunt, R. L. 1969. Overwinter survival of wild fingerling Brook Trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board of Canada 26:1473-1483.

IBM Inc. 2009. SPSS statistics version 18.0.

Jenkins, T. M. Jr., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of Brown Trout in streams. Ecology 80:941-956.

Kaeser, A. J., C. Rasmussen, and W. E. Sharpe. 2006. An examination of environmental factors associated with Myxobolus cerebralis infection of wild trout in Pennsylvania. Journal of Aquatic Animal Health 18:90-100.

Kennedy, G. J. A., and C. D. Strange. 1982. The distribution of salmonids in upland streams in relation to depth and gradient. Journal of Fish Biology 20:579-591.

Kocik, J. F., and W. W. Taylor. 1994. Summer survival and growth of Brown Trout with and without steelhead under equal total salmonid densities in an artificial stream. Transactions of the American Fisheries Society 123:931-938.

Kocik, J. F., and W. W. Taylor. 1995. Effect of juvenile steelhead (Oncorhynchus mykiss) of age-0 and age-1 Brown Trout (Salmo trutta) survival and growth in a sympatric nursery stream. Canadian Journal of Fisheries and Aquatic Sciences 52:105-114.

Kocik, J. F., and W. W. Taylor. 1996. Effect of juvenile steelhead on juvenile Brown Trout habitat use in a low-gradient Great Lakes tributary. Transactions of the American Fisheries Society 125:244-252.

Kocik, J. F., W. W. Taylor, and W. C. Wagner. 1991. Abundance, size, and recruitment of pink salmon (Oncorhynchus gorbuscha) in selected Michigan tributaries of the Upper Great Lakes, 1984-1988. Journal of Great Lakes Research 17:203-213.

Koel, T. M., B. L. Kerans, S. C. Barras, K. C. Hanson, and J. S. Wood. 2010. Avian piscivores as vectors for Myxobolus cerebralis in the Greater Yellowstone ecosystem. Transactions of the American Fisheries Society 139:976-988.

Kruger, K. M. 1985. Pere Marquette River angler survey and Brown Trout evaluation. Master’s thesis. Michigan State University, East Lansing.

Kwain, W. 1983. 1983. Downstream migration, population size and feeding of juvenile Rainbow Trout. Journal of Great Lakes Research 9:52-59.

McNeil, W. J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. Journal of the Fisheries Research Board of Canada 21:1385-1396.

Mitro, M. G., and A. V. Zale. 2002. Seasonal survival, movement, and habitat use of age-0 Rainbow Trout in the Henrys Fork of the Snake River, Idaho. Transactions of the American Fisheries Society 131:271-286.

O’Grodnick, J. J. 1979. Susceptibility of various salmonids to whirling disease (Myxosoma cerebralis). Transactions of the American Fisheries Society 108:187-190.

Peck, J. W. 2001. Population dynamics of juvenile steelhead and coho salmon in Michigan’s Lake Superior tributaries, 1982-97. Michigan Department of Natural Resources Fisheries Research Report 2057, Ann Arbor.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U. S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-138, Ogden, Utah.

Raleigh, R. F., T. Hickman, R. C. Solomon, and P. C. Nelson. 1984. Habitat suitability information: Rainbow Trout. U.S. Fisheries and Wildlife Service FWS/OBS-82/10.60.

Raleigh, R. F., L. D. Zuckerman, and P. C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: Brown Trout, revised. U.S. Fish and Wildlife Service Biol. Rep. 82(10.124).

Schneider, J. C. 2000. Weighted average length and weighted age composition. Chapter 15 in J. C. Schneider, editor. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.

Seelbach, P. W. 1987. Effect of winter severity on steelhead smolt yield in Michigan: An example of the importance of environmental factors in determining smolt yield. American Fisheries Society Symposium 1:441-450.

Seelbach, P. W. 1993. Population biology of steelhead in a stable-flow, low-gradient tributary of Lake Michigan. Transactions of the American Fisheries Society 122:179-198.

Stauffer, T. M. 1972. Age, growth, and downstream migration of juvenile Rainbow Trout in a Lake Michigan tributary. Transactions of the American Fisheries Society 101:18-28.

Thompson, K. G., R. B. Nehring, D. C. Bowden, and T. Wygant. 1999. Field exposure of seven species or subspecies of salmonids to Myxobolus cerebralis in the Colorado River, Middle Park, Colorado. Journal of Aquatic animal Health 11:312-329.

Wagner, W. C. 1975. Food habits of coexisting juvenile coho salmon, Brown Trout, and Rainbow Trout in the Platte River, 1967 and 1972. Michigan Department of Natural Resources, Fisheries Research Report 1831, Ann Arbor.

Wickett, W. P. 1958. Review of certain environmental factors affecting the production of pink and chum salmon. Journal of the Fisheries Research Board of Canada 15:1103-1123.

Zeigler, R. L. 1988. Stream resource utilization of sympatric and allopatric juvenile Brown (*Salmo trutta*) and steelhead (*Salmo gairdneri*). Master's thesis. Michigan State University, East Lansing.

Zendt, J. S., and E. P. Bergersen. 2000. Distribution and abundance of the aquatic oligochaete host Tubifex tubifex for the salmonid whirling disease parasite Myxobolus cerebralis in the Upper Colorado River basin. North American Journal of Fisheries Management 20:502-512.

Zorn, T. G., and A. J. Nuhfer. 2007. Influences on Brown Trout and Brook Trout population dynamics in a Michigan River. Transactions of the American Fisheries Society 136:691-705.

Troy G. Zorn, Reviewer
Tracy L. Kolb, Editor
Alan D. Sutton, Graphics and Desktop Publisher
Ellen S. Grove, Desktop Publisher

Approved by Gary E. Whelan

Appendix A.–August–September density of Brown Trout (number per hectare) in the treatment and reference sections of Hunt and Gilchrist creeks, Michigan. Sections are arranged in ascending order by their total length. Shading represents Brown Trout year classes that did not interact with steelhead of the same age in the Hunt Creek treatment section where adult steelhead spawned each spring from 1998 through 2003. Mean abundance for year class groups that did not interact with steelhead was compared to those that interacted with steelhead (unshaded) in both the treatment and reference sections.

	Age					
Year	0	1	2	3	4	5+
	Hunt Creek treatment section (3.4 km)					
1995	1,618	511	199	133	21	10
1996	973	429	165	71	17	7
1997	1,286	416	147	66	16	2
1998	1,050	492	121	94	19	4
1999	950	299	164	71	28	1
2000	939	168	100	69	25	4
2001	1,023	178	65	50	20	6
2002	906	212	94	36	19	4
2003	1,011	158	76	37	11	8
2004	1,062	339	86	54	7	9
2005	1,023	451	118	42	9	6
2006	937	382	200	63	16	0
2007	1,108	402	142	69	24	0
2008	2,011	337	190	86	22	4
	Gilchrist Creek reference section (2.3 km)					
1995	2,179	733	280	116	14	1
1996	1,870	405	175	60	17	6
1997	1,891	540	131	45	17	5
1998	1,035	697	135	64	25	9
1999	1,694	437	201	83	8	4
2000	1,746	464	141	72	17	0
2001	2,275	615	185	86	17	3
2002	2,105	609	237	73	18	1
2003	2,497	497	218	88	9	0
2004	2,645	712	180	76	24	1
2005	3,925	823	250	116	14	2
2006	2,771	796	334	128	43	6
2007	2,720	619	265	123	48	7
2008	2,512	638	111	114	27	8

Appendix A.–Continued.

Year	Age 0	1	2	3	4	5+
	Hunt Creek reference section (0.7 km)					
1995	384	307	179	98	21	20
1996	250	71	108	138	33	30
1997	1,049	126	89	69	36	8
1998	1,452	433	97	94	44	15
1999	557	262	178	75	24	13
2000	537	154	96	56	15	0
2001	882	77	27	39	18	0
2002	161	228	73	22	19	7
2003	1,571	109	43	43	10	15
2004	831	243	28	11	43	4
2005	358	236	172	30	39	19
2006	1,130	334	195	77	2	10
2007	1,399	283	123	116	18	6
2008	1,842	231	167	92	75	2

Appendix B.–August–September density of Brook Trout (number per hectare) in the treatment and reference sections of Hunt and Gilchrist creeks, Michigan. Sections are arranged in ascending order by their total length. Shading represents Brook Trout year classes that did not interact with steelhead of the same age in the Hunt Creek treatment section where adult steelhead spawned each spring from 1998 through 2003. Mean abundance for year class groups that did not interact with steelhead was compared to those that interacted with steelhead (unshaded) in both the treatment and reference sections.

	Age			
Year	0	1	2	3
	Hunt Creek treatment section (3.4 km)			
1995	24	10	1	1
1996	83	53	4	0
1997	106	53	8	0.4
1998	69	37	10	0
1999	54	11	2	2
2000	43	16	2	0
2001	22	9	2	0
2002	20	8	1	0
2003	19	9	1	0
2004	6	10	1	0
2005	29	21	1	0
2006	3	21	1	0
2007	11	7	3	0
2008	4	15	1	0
	Gilchrist Creek reference section (2.3 km)			
1995	15	30	6	0
1996	23	32	5	0
1997	32	27	4	0
1998	26	17	6	0
1999	20	30	8	0
2000	2	11	2	0
2001	8	13	1	0
2002	11	6	2	0
2003	2	7	0	0
2004	1	10	2	0
2005	1	2	0	0
2006	4	2	0	0
2007	3	9	1	0
2008	1	4	1	0

Appendix B.–Continued.

Year	Age 0	1	2	3
	Hunt Creek reference section (0.7 km)			
1995	2,855	404	46	0
1996	2,318	208	14	0
1997	3,463	374	8	0
1998	3,763	1319	39	0
1999	1,910	187	28	0
2000	2,162	119	9	0
2001	1,540	242	0	0
2002	1,240	427	45	0
2003	1,755	147	12	0
2004	830	199	30	0
2005	692	237	37	0
2006	1,111	295	7	0
2007	1,366	108	3	0
2008	1,243	98	36	6

Appendix C.–August–September density of steelhead (number per hectare) in a 3.4-km treatment section of Hunt Creek, Michigan where adult steelhead spawned each spring from 1998 through 2003. A few steelhead that did not smolt and emigrate reproduced at low levels after 2003 (shaded cells).

	Age			
Year	0	1	2	3
1998	2,545	0	0	0
1999	2,243	343	0	0
2000	2,100	248	6	0
2001	2,343	360	3	0
2002	3,614	484	7	0
2003	4,487	381	47	0
2004	2	561	27	0
2005	0	0	99	0
2006	3	0	2	20
2007	62	11	6	4
2008	4	34	6	2

Appendix D.–Annual percent survival of Brown Trout in the treatment and reference sections of Hunt and Gilchrist creeks, Michigan. Sections are arranged in ascending order by their total length. Shading represents Brown Trout year classes that did not interact with steelhead of the same age in the Hunt Creek treatment section where adult steelhead spawned each spring from 1998 through 2003. Mean abundance for year class groups that did not interact with steelhead was compared to those that interacted with steelhead (unshaded) in both the treatment and reference sections.

Year	Age 0–1	1–2	2–3	3–4
	Hunt Creek treatment section (3.4 km)			
1995	27	32	35	13
1996	43	34	40	23
1997	38	29	64	29
1998	28	33	59	30
1999	18	33	42	35
2000	19	39	51	28
2001	21	53	56	38
2002	17	36	39	30
2003	34	54	71	20
2004	42	35	49	17
2005	37	44	53	37
2006	43	37	35	38
2007	30	47	61	32
	Gilchrist Creek reference section (2.3 km)			
1995	19	24	21	15
1996	29	32	26	29
1997	37	25	49	55
1998	42	29	62	13
1999	27	32	36	21
2000	35	40	61	24
2001	27	39	39	21
2002	24	36	37	13
2003	29	36	35	27
2004	31	35	64	19
2005	20	41	51	37
2006	22	33	37	37
2007	23	18	43	22

Appendix D.–Continued.

Year	Age 0–1	1–2	2–3	3–4
	Hunt Creek reference section (0.7 km)			
1995	19	35	77	34
1996	51	124	64	26
1997	41	76	106	64
1998	18	41	78	25
1999	26	40	34	14
2000	14	18	37	30
2001	26	95	83	47
2002	68	19	59	43
2003	16	26	25	100
2004	28	71	107	368
2005	93	83	45	7
2006	25	37	59	23
2007	17	59	75	65

Appendix E.–Annual percent survival of Brook Trout in the treatment and reference sections of Hunt and Gilchrist creeks, Michigan. Sections are arranged in ascending order by their total length. Shading represents Brook Trout year classes that did not interact with steelhead of the same age in the Hunt Creek treatment section where adult steelhead spawned each spring from 1998 through 2003. Mean abundance for year class groups that did not interact with steelhead was compared to those that interacted with steelhead (unshaded) in both the treatment and reference sections.

	Age		
Year	0–1	1–2	2–3
	Hunt Creek treatment section (3.4 km)		
1995	216	46	0
1996	64	15	10
1997	35	19	0
1998	16	6	17
1999	30	15	0
2000	20	13	0
2001	36	15	0
2002	44	16	0
2003	55	14	0
2004	365	12	0
2005	71	6	0
2006	219	12	0
2007	133	11	0
	Gilchrist Creek reference section (2.3 km)		
1995	210	18	0
1996	120	13	0
1997	53	22	0
1998	115	45	0
1999	58	7	0
2000	610	5	0
2001	77	12	0
2002	60	0	0
2003	600	33	0
2004	400	0	0
2005	400	0	0
2006	213	50	0
2007	133	6	0

Appendix E.–Continued.

Year	Age 0–1	1–2	2–3
	Hunt Creek reference section (0.7 km)		
1995	7	3	0
1996	16	4	0
1997	38	10	0
1998	5	2	0
1999	6	5	0
2000	11	0	0
2001	28	19	0
2002	12	3	0
2003	11	21	0
2004	29	19	0
2005	43	3	0
2006	10	1	0
2007	7	33	188

Appendix F.–Weighted mean length at age (mm) of Brown Trout in the treatment and reference sections of Hunt and Gilchrist creeks, Michigan. Sections are arranged in ascending order by their total length. Fish were sampled during September from 1995 to 2001, and during August from 2002 to 2007. Shading represents Brown Trout year classes that did not interact with steelhead of the same age in the Hunt Creek treatment section where adult steelhead spawned each spring from 1998 through 2003. Mean abundance for year class groups that did not interact with steelhead was compared to those that interacted with steelhead (unshaded) in both the treatment and reference sections.

	Age				
Year	0	1	2	3	4
	Hunt Creek treatment section (3.4 km)				
1995	90	163	209	266	359
1996	90	164	214	270	333
1997	88	171	230	272	367
1998	91	173	224	273	325
1999	85	174	230	279	338
2000	91	168	230	274	338
2001	85	173	237	289	339
2002	83	170	234	298	346
2003	79	163	236	302	333
2004	81	162	242	303	352
2005	76	158	227	285	341
2006	82	163	225	287	351
2007	80	170	229	267	325
2008	78	166	231	269	337
	Gilchrist Creek reference section (2.3 km)				
1995	81	153	198	264	339
1996	78	148	197	267	331
1997	80	150	214	273	334
1998	85	148	213	264	324
1999	86	166	217	278	357
2000	85	159	224	269	340
2001	80	152	218	266	338
2002	78	152	223	288	315
2003	69	149	217	277	329
2004	73	153	221	272	332
2005	65	138	204	260	313
2006	72	139	196	252	314
2007	72	148	204	250	305
2008	67	151	206	258	296

Appendix F.–Continued.

Year	Age 0	1	2	3	4
	Hunt Creek reference section (0.7 km)				
1995	87	158	214	274	341
1996	78	157	198	259	309
1997	81	170	242	287	345
1998	78	157	232	305	362
1999	85	151	227	294	346
2000	88	160	224	289	361
2001	86	166	227	296	340
2002	80	164	236	288	324
2003	69	171	245	301	351
2004	74	163	261	333	338
2005	64	154	226	272	348
2006	77	157	224	281	318
2007	66	159	231	281	324
2008	65	153	228	282	327