STATE OF MICHIGAN
DEPARTMENT OF NATURAL RESOURCES

Number 2060
December 9, 2002

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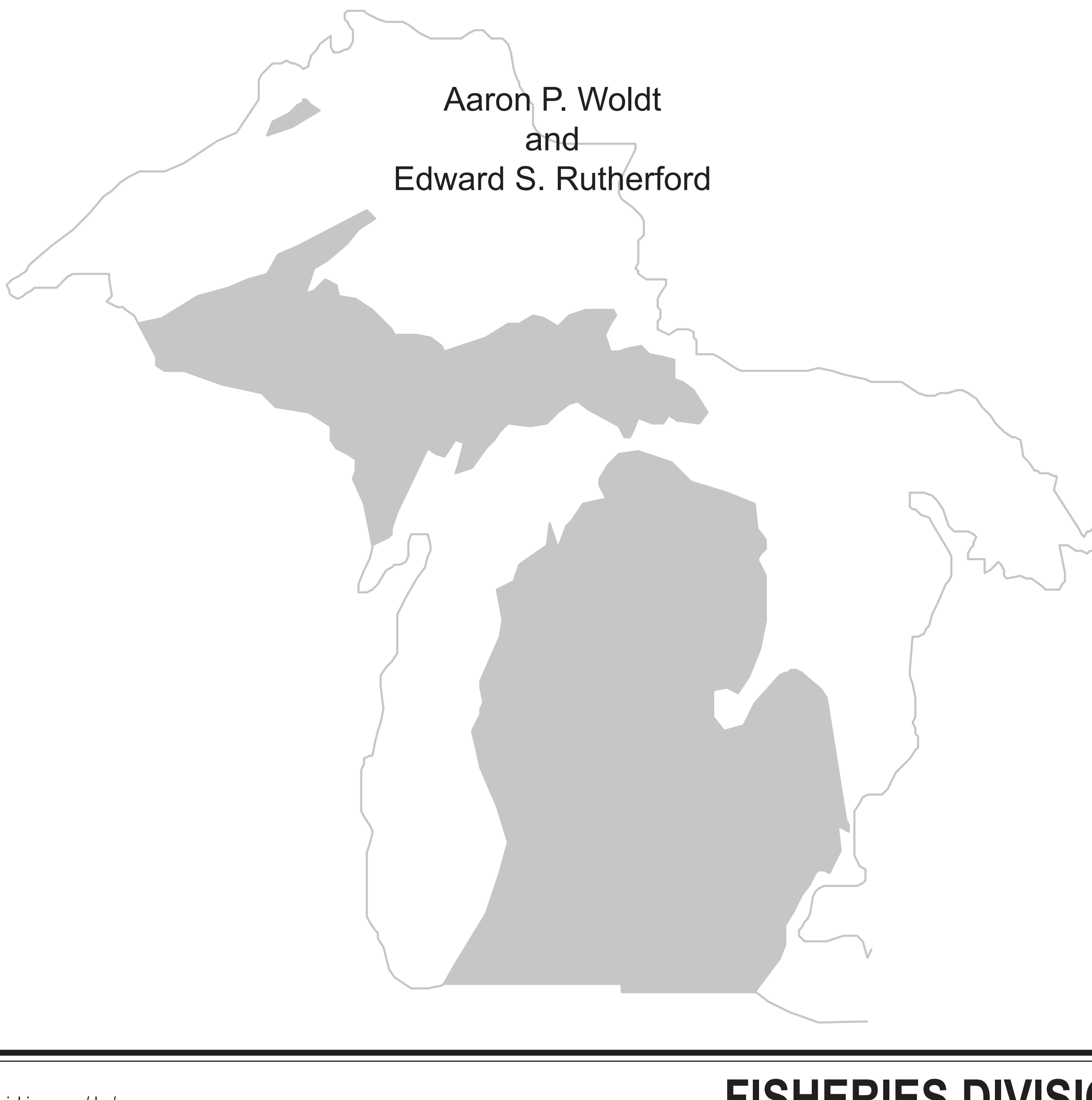

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MICHIGAN DEPARTMENT OF NATURAL RESOURCES
FISHERIES DIVISION

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Printed under authority of Michigan Department of Natural Resources
Total number of copies printed 200 — Total cost $509.88 — Cost per copy $2.55

Michigan Department of Natural Resources
Fisheries Research Report 2060, 2002

Production of Juvenile Steelhead in two Central Lake Michigan Tributaries

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Abstract.–Steelhead *Oncorhynchus mykiss* are a large and economically important part of the Lake Michigan sport fishery. Approximately 30-50% of steelhead taken in Michigan's sport harvest are produced in stable, cold-water tributaries in the northwestern part of the Lower Peninsula. In most of these tributaries, hydropower dams limit anadromous salmonid production by denying spawners access to upstream habitat and by altering quality of habitat in downstream river sections. Recent (1989) changes in water flow from peaking to run-of-river over Tippy Dam may have increased steelhead abundance and production in the Manistee River. The objectives of this study were to estimate abundance, growth and survival rates, and production of juvenile steelhead below Tippy Dam and to compare these values with those for parr in the adjacent Little Manistee River, a free-flowing river that historically has supported a healthy population of young steelhead. We estimated steelhead parr abundance and survival in the Manistee River using mark-recapture and multiple pass-depletion methods, and estimated steelhead parr abundance in the Little Manistee River using multiple pass-depletion methods. We collected parr in August, September, and October 1997, and March 1998 in the Manistee and Little Manistee rivers using DC electrofishing. We estimated growth and production from changes in length and weight over time.

Young-of-the-year (YOY) steelhead were abundant (3,029,604 ± 589,803) in the Manistee River in July 1997, but numbers quickly declined in late July due to stressful high temperatures (mean = 20.3°C) which caused very low survival (%S = 1.7) in July. Although parr abundance in July in the Little Manistee River was much lower (307,259 ± 66,248) than in the Manistee River, daily temperatures averaged 17.0°C and were closer to optimum for parr growth and survival, and parr survival (%S = 87.6) was higher. As a result, production of steelhead parr was higher in the Little Manistee River (1.89 g/m^2) than in the Manistee River (1.54 g/m^2) during the July 1997-March 1998 sampling period, and significantly more age-2 pre-smolts were found in the Little Manistee River (30,865 ± 13,297) than in the Manistee River (1,369 ± 492) in March 1998. Growth rates of steelhead parr did not differ conclusively between the Manistee and Little Manistee rivers. The results of this study indicate that thermal stress caused by the surface-release flow regime of Tippy Dam may cause low survival and production of juvenile steelhead below Tippy Dam. On average, daily temperatures in July below Tippy Dam were warmer (mean = 20.3°C) and fluctuated over a significantly smaller range (daily fluctuation = 0.8 ± 0.6°C) than those in the Little Manistee River (mean = 17.0°C, daily fluctuation = 3.5 ± 1.7°C). Higher daily temperatures and smaller daily fluctuations produced a larger number of accumulated degree days (629) in the Manistee River than in the Little Manistee River (527).

Introduction

The steelhead *Oncorhynchus mykiss* fishery is a large and economically important part of Michigan's sport fishery. This fishery is maintained primarily through stocking, but naturally-reproducing populations exist in many northern tributaries of Lake Michigan, Lake Superior, and Lake Huron. The extent of natural steelhead production in these rivers has not been quantified. In many rivers where steelhead reproduce, operation of hydropower dams may adversely affect quality of habitat for, and production of juvenile steelhead in river sections downstream of dams. Habitat quality is important for juvenile steelhead, as they inhabit their natal stream for long periods (1-3 years) of time.

Steelhead were first introduced into the Lake Michigan watershed in 1880 (Latta 1974; Mrozinski 1995), and since have been stocked annually (with the exception of 1891 and 1892) in a variety of Great Lakes tributaries (Mrozinski 1995). In 1996, the state of Michigan stocked approximately 614,000 steelhead into Lake Michigan tributaries, and Wisconsin, Indiana, and Illinois added 1,179,000 more (Holey 1997). As a result, spring, summer, and fall spawning runs of adult steelhead occur in many tributaries to Lake Michigan, and these runs support large and economically important river, lake, and pier fisheries. In 1985, approximately 17,000 steelhead (11% of salmonid river catch) were harvested in the Manistee River (Rakoczy and Lockwood 1988), and in 1992, approximately 43,555 steelhead (29% of salmonid lake catch) were harvested in Lake Michigan from boats and piers (Rakoczy and Svoboda 1994). From October 1982 to September 1983, anglers (stream, boat, and pier) spent 3.1 million dollars in Manistee County alone (Keller et al. 1990). The majority of this sum was paid by non-residents attracted by the boat fishery and angling opportunities during large spawning runs of steelhead and other salmonids on the Manistee and Little Manistee rivers (Keller et al. 1990).

Since their introduction, steelhead in Michigan waters have experienced two major population declines (Keller et al. 1990). The first was brought on by construction of hydropower dams on large spawning streams like the Manistee, Muskegon, and Au Sable rivers, and the second occurred due to predation by sea lamprey (Keller et al. 1990). Hydropower dams fragment river habitat and deny migratory fish access to spawning habitat above dams. As a result, natural reproduction of migratory salmonids is reduced. Hydropower dams also affect the quality of water they release by altering patterns of river discharge, trapping sediments, blocking downstream drift of aquatic invertebrates, and altering temperature of released water (Petts 1984). The direction of temperature change is controlled by the location of the outflow mechanism and the degree of reservoir stratification. Generally, surface-release reservoirs in summer discharge warmer-than-ambient water, and lower-level-release reservoirs discharge colder-than-ambient water (Petts 1984). Tippy Dam reservoir stratifies strongly and exhibits temperature differences from top to bottom of nearly 15°C (Michigan Department of Natural Resources, Fisheries Division, unpublished data). This high degree of stratification potentially can limit production of fishes below the dam.

Tippy Dam historically was operated under a surface-release, peaking-flow regime. Under peaking, water is held in the reservoir and released twice daily in large pulses. This method of dam operation negatively impacts many aquatic organisms below the dam. The large water pulses can displace habitat (i.e. large woody debris) for aquatic animals, scour riverbanks and bottom, uproot riparian vegetation, and physically displace larval fishes. Physical displacement and high mortality rates of larval fish have been documented in many other rivers with peaking regimes (Cushman 1985; Bain et al. 1988; Scheidegger and Bain 1995). Below Tippy Dam, low flow periods between pulses concentrated fishes in pools, stranded other fishes, and exposed salmonid spawning redds to the air (T.J. Rozich, Michigan Department of Natural Resources, personal communication). As a result, natural salmonid production was probably low in the Manistee River under this flow regime.

Quality of natal habitat is important for success of juvenile steelhead. In Ontario, Bowlby and Roff (1986) found that groundwater, biomass of benthic invertebrates, and percent pool area positively affected juvenile trout biomass, while high summer temperature negatively affected trout biomass. In Minnesota, Close and Anderson (1997) found that young-of-the-year (YOY) steelhead survival increased with increasing substrate diameter and decreased with increasing levels of river discharge. Newcomb (1998) found a significant negative correlation between YOY steelhead density and maximum summer temperature on the Betsie River, a Lake Michigan tributary near the Manistee and Little Manistee rivers. Steelhead spend 1-3 years in their natal stream before migrating to the lake (Seelbach 1993). The majority of wild steelhead spend 2 years in their natal stream, but steelhead will migrate as YOY or yearlings due to habitat limitations (Leider et al. 1986; Loch et al. 1988). The fate of these young migrants is unknown, but their relatively small size could lead to high levels of predation during migration. Ward et al. (1989) and Seelbach et al. (1994) observed higher survival and return rates for larger smolts.

In early 1989, Consumers Power Company (CPCo), the operator of Tippy Dam, voluntarily began operating the dam under a run-of-river (ROR) flow regime. In 1993, CPCo was re-licensed by the Federal Energy Regulatory Commission (FERC). As part of that agreement, CPCo was required to operate Tippy Dam under a ROR flow regime, which would create more stable flows below the dam, decrease habitat displacement, bank erosion, and bottom scour, and eliminate de-watering of salmonid redds. ROR flows, coupled with a $600,000 bank stabilization project on Suicide Bend, were expected to improve fish nursery habitat and increase spawning success of salmonids below the dam.

Since 1989, production of steelhead and chinook salmon *Oncorhynchus tshawytscha* parr below Tippy Dam seemingly has been high, but the survival and fate of these naturally produced juveniles are largely unknown. Hundreds of thousands of salmonid parr are now seen at stream margins in the first 3-3.5 km of river below Tippy Dam each May and June. The majority of naturally produced steelhead parr disappear in early July around the time of peak river temperature and are not seen in large numbers again. Groups of YOY steelhead are found only in plumes of cool groundwater at this time. Fisherman report catching very few one or two year old steelhead on the Manistee River, and the adult sport catch is heavily comprised (approximately 50-70%) of hatchery fish (Michigan Department of Natural Resources, Fisheries Division, unpublished data).

Determining the fate of juvenile steelhead in the Manistee River has important management implications for the State of Michigan. In order to properly maintain the steelhead resource and avoid over-stocking or under-stocking, managers must have an estimate of wild steelhead production. If steelhead production is affected by operation of hydropower dams, efforts can be made in the future to address this issue. Almost all large Michigan rivers are impounded by hydropower dams, but these dams are regularly re-licensed. Re-licensing gives managers the opportunity to address and mitigate wildlife concerns at dams all around the state.

Goal and Objectives

The goal of this project was to assess stock structure of juvenile steelhead below Tippy Dam on the Manistee River and to compare this structure with that of the Little Manistee River, a nearby, free-flowing river that supports a healthy population of young steelhead. This goal incorporated three objectives: 1) to document and compare changes in abundances, growth and survival rates, and productions of juvenile steelhead in both the Manistee and Little Manistee rivers; 2) to assess habitat quality in the Manistee and Little Manistee rivers and explain variation in juvenile steelhead stocks based on habitat parameters; and 3) to provide management personnel with recommendations to improve survival and production of Manistee River steelhead.

Methods

Study Area

Manistee River–The mainstem Manistee River originates in southeastern Antrim County and flows southwest approximately 371 km into Manistee Lake and subsequently into Lake Michigan (Figure 1a). The river drains a 4,557 km^2 watershed that contains 54% forested (coniferous, deciduous, and wetland) land (Rozich 1998). Approximately 3% of the watershed is in urban and suburban land use, and 39% of the watershed is in agricultural land use as pasture, fruit orchards, or Christmas tree plantations (Rozich 1998). Surficial geology along the mainstem is primarily outwash plain composed of deep, well drained, sandy deposits. As a result, about 90% of the annual discharge in the Manistee River is groundwater (Berry 1992). This large percentage of groundwater makes the discharge of the Manistee River extremely stable.

Two large hydropower dams operated by CPCo on the mainstem Manistee River form complete barriers to upstream movement of fishes, and limit survival of downstream migrants passing through the dams' turbines. Hodenpyl Dam is located approximately 30 km upstream of Tippy Dam, which is approximately 60 km from Lake Michigan and is the upstream limit of anadromous fish species. The stretch of river below Tippy Dam is dominated by anadromous salmonids in spring, summer, and winter, although populations of yellow perch *Perca flavescens*, walleye *Stizostedion vitreum*, smallmouth bass *Micropterus dolomieu*, northern pike *Esox lucius*, redhorse suckers *Moxostoma spp.*, white suckers *Catastomous commersoni*, resident brown trout *Salmo trutta*, and lake sturgeon *Acipenser fulvescens* persist. Each year, the area below Tippy Dam is stocked with approximately 90,000 steelhead smolts, 100,000 coho salmon *Oncorhynchus kisutch* smolts, and 30,000 juvenile brown trout (MDNR 1997). About 125,000 chinook salmon smolts are planted in the Manistee River near the mouth (MDNR 1997). There also is wild production of steelhead, chinook salmon, and brown trout below Tippy Dam in the mainstem river and several coldwater tributaries. The 3.5 km stretch of river immediately below Tippy Dam is very heavily fished in spring, summer, and fall for steelhead, and in fall for chinook salmon.

Tippy Dam marked the upstream boundary of the study area in the Manistee River (Figure 2). The study area was divided into four strata based on habitat analysis conducted by Ichthyological Associates (1991) and Rutherford et al. (1997). Stratum 1 stretched from Tippy Dam to 1.5 km below the dam and consisted largely of shallow depth (<1 m) areas with gravel runs. Stratum 2 extended from 1.5 to 3.5 km below the dam and was characterized by medium-depth (1-2 m) gravel runs with sparsely-spaced, shallow-gravel runs. Stratum 3 stretched from 3.5 to 5.3 km below the dam and consisted of both shallow and deep (2-3 m) runs composed of a gravel/sand mix. Stratum 4 extended from 5.3 to 8.3 km below the dam at High Bridge. This stratum consisted primarily of deep (2-3 m), sandy runs. The average river width in the study area was 56 m (Rozich 1998).

Little Manistee River–The Little Manistee River originates in mideastern Lake County and flows northwest approximately 110 km into Manistee Lake and subsequently into Lake Michigan (Figure 1b). The river drains a 590 km^2 watershed that is comprised mainly of forested land (Seelbach 1993), as much of the river runs through the Manistee National Forest. The river has an average width of 13 m and average depth of <1 m with pools up to 2 m in depth (Seelbach 1993). Soils in the area, much like those in the Manistee River watershed, are composed primarily of very porous, glacial outwash sand. As a result, much of the discharge in the Little Manistee River is groundwater, and the Little Manistee River is also an extremely stable-flow, cold river (Richards 1990; Seelbach 1993).

The Little Manistee River is a relatively unimpounded river system. There are no hydropower dams on this river, but there is a small dam near the headwaters in the town of Luther which prevents migrating fish from entering the upper 6 km of river. The Michigan DNR also operates a weir that is located approximately 5 km east of the town of Stronach. This weir serves as an egg-collecting facility for the state's hatchery program. Steelhead eggs are collected in spring, and chinook salmon eggs are collected in fall. During these time periods (approximately one month in both spring and fall), impassable steel grates are placed in the river to block upstream migration of fish. During the rest of the year, the grates are raised out of the water to allow normal fish movement up and down the river.

The fish community in the Little Manistee River is a characteristic coldwater community dominated by wild salmonids. The river supports naturally reproducing populations of brown trout, brook trout *Salvelinus fontinalis*, chinook salmon, coho salmon, and steelhead (Seelbach 1986; Seelbach 1993; Rutherford et al. 1997). Each spring the MDNR stocks approximately 750,000 chinook salmon smolts in the Little Manistee (MDNR 1997). Almost all returning adult chinook salmon are harvested at the weir during fall egg take, but some adults get through before the weir grates are lowered or jump the weir grates and successfully spawn upstream of the weir. All returning adult steelhead are passed over the weir, and some are stripped of eggs or milt during the egg-take procedure. Much of the Little Manistee River between the weir and Luther Dam is heavily fished in spring for steelhead and in fall for steelhead and chinook salmon. The river also supports a substantial brown trout fishery and a smaller brook trout fishery during trout season.

The dam near Luther was the upstream boundary of the study area, and the MDNR weir was the downstream boundary. The study area was divided into 5 strata (Figure 1b) based on riverine substrate (sand or gravel) determined by Seelbach (1986).

Pine Creek and Bear Creek–Pine Creek and Bear Creek are cold, groundwater-fed tributaries that flow into the Manistee River. Pine Creek enters the mainstem Manistee River from the south approximately 14 km below Tippy Dam. Pine Creek supports a wild population of brown trout (Rozich 1998) and also contains stretches of spawning gravel (near Huff Road) that produce chinook salmon, coho salmon, and steelhead smolts. Bear Creek flows into the Manistee River from the north approximately 21 km below Tippy Dam. The upper reaches of Bear Creek and its tributaries (Second and Third creeks) have wild populations of brook and brown trout, and produce chinook salmon, coho salmon, and steelhead smolts. Much of lower Bear Creek is fished heavily in fall for chinook salmon and in spring and fall for steelhead (Rozich 1998).

Estimation of Abundance and Density

General–Steelhead parr abundance in the Manistee River was estimated using mark-recapture and pass-depletion methods, and parr abundance in the Little Manistee River was estimated using pass-depletion methods. Samples for the mark-recapture estimates in the Manistee River were collected and marked over 8 days in July 1997. Pass-depletion sampling was conducted on the Manistee River in August 1997, September 1997, and March 1998. Pass-depletion sampling was conducted on the Little Manistee River in July 1997, October 1997, and March 1998. Relative density of steelhead also was estimated for Pine and Bear creeks in August 1997 and October 1997.

Parr Marking–Based on previous investigations of steelhead parr abundance and survival in Michigan streams (Taube 1975; Stauffer 1977; Carl 1983; Seelbach 1986), we calculated that it was necessary to mark approximately 50,000 steelhead in July in order to have a reasonable probability of finding marked fish in the area below Tippy Dam in fall. In July 1997, an estimated 49,966 YOY steelhead were collected with a 40-foot minnow seine in shoreline areas in the first 1.5 km downstream of Tippy Dam. Fry were placed in a covered horse trough and supplied with dissolved oxygen until sufficient numbers were collected to make marking efficient. Each day, 50-100 steelhead fry were sampled for total length and weight. Weights were used to generate an average weight per steelhead fry. Then, buckets of fry were weighed using a hanging spring scale. Total steelhead weight was divided by average weight per steelhead to estimate the total number of steelhead marked per day. Steelhead then were poured into a dip net in small batches (10-15 fish), marked with a pressure-sprayed fluorescent pigment (Pribble 1976), and released back into the river. Fish were released at 6 discrete sites within 2 km of the dam, and different pigment colors were used at each site.

Parr Recapture–All steelhead parr (or a 50% subsample when samples sizes >1,000) collected during depletion runs on the Manistee River, and sampling runs in Pine and Bear creeks, were examined for marks. Fish were anesthetized in a dilute solution of tricaine methane sulfonate, placed on a tray, and examined for marks on each side under a black light. The total number of fish examined and the total number of marks found was recorded.

Wherever possible, the marked:unmarked ratio for the Manistee River samples was used in a Petersen Ratio to estimate the total number of steelhead parr present below Tippy Dam.

Mark-Recapture Estimates–A Petersen Ratio (Everhart and Youngs 1981) was used to calculate mark-recapture estimates of steelhead parr abundance. Parr abundance was calculated using the following equation:

$$N = \frac{M * C}{R}$$

where N is the population estimate, M is the number of parr marked and released, C is the number of parr examined for marks, and R is the number of parr marked and recaptured.

The variance of this estimator was calculated using the following formula (Everhart and Youngs 1981):

$$V(N) = N^2 * \frac{(N - M) * (N - C)}{M * C * (N - 1)}$$

where V(N) is the variance of the estimator, and N, M, and C represent the same variables as above.

The Petersen estimate assumes full mark retention, equal survival for both marked and unmarked fish, no immigration or emigration during the study, and random mixing of marked and unmarked individuals. These assumptions were tested with the following experiments.

Mark Retention, Marked Fish Survival, and Marking Efficiency–In October 1996, mark retention and survival of marked fish were quantified by marking 3 batches of 100 fish (TL = 5-7 cm) at MDNR's Wolf Lake State Fish Hatchery near Kalamazoo, Michigan. Two control batches of 100 fish each were handled similarly to marked fish but were not marked. Each batch of fish was housed in individual round tanks (approximately 1.0 m^3) with a flow-through water supply and kept until 21 January 1997. All fish were fed daily to satiation with standard trout pellets, and mortalities were removed daily by hatchery personnel. All sprayed fish were checked for marks on 12 December 1996 and 21 January 1997. Marked fish had very low average mortality ($\bar{z}$ = 3.3%), and all deaths occurred within 24 hours of marking. No fish died in the control tanks. Of the marked fish, an average of 63.1% had retained their marks in December 1996, and 62.6% had retained marks in January 1997. All sprayed fish were assumed to be marked in October, but since fish were not checked for marks immediately after spraying, it is unclear if the percentages above reflect marking efficiency or mark retention. The percentages likely represented low marking efficiency and high (100%) mark retention, as studies by Pauley and Troutt (1988), Nielson (1990), and Seelbach (1993) demonstrated high mark retention for this technique when the mark is properly applied. Marking efficiency can be increased by marking smaller batches of fish, and this was done in the following experiments.

In July 1997, marking efficiency and survival of wild marked fish were quantified twice by marking 3 batches of approximately 70 fish (TL = 3-5 cm) for each trial and retaining them in covered, oxygenated tanks (approximately 0.15 m^3) for 2 hours. In the first trial, no current was generated in the tanks. In the second trial, tanks were continuously stirred to provide current and simulate flow of river water. At both times a control group of approximately 75 fish was handled but not marked and held in a similar tank. After two hours, all fish were examined for marks and mortalities were counted. Live fish were released back into the river. In both trials of this experiment, all sprayed fish had pigment marks, so marking efficiency was 100%. Marked fish mortality averaged 40.8% in Run #1 and 29.1% in Run #2, and control fish mortality averaged < 1.5%. The higher rate of mortality in marked fish in this field experiment relative to the Wolf Lake experiment is likely due to the smaller size of fish marked in the field experiment.

Emigration and immigration were assumed negligible because no marked fish were ever found in Pine or Bear creeks, nor were marked fish found great distances (>600 m) from the marking sites. Mixing of marked individuals probably occurred, because some parr (n = 10) were found 100 to 500 m from their marking site 1-3 months after marking.

In 1997, 49,966 YOY steelhead were collected and marked in the Manistee River.

Based on a marking efficiency of 100.0%, mark retention of 100.0%, and an average mortality of 29.1%, an estimated 35,426 steelhead parr survived, retained marks, and were available for recapture. The lower, field-measured mortality rate was used for the 1997 fish, because flow in the experimental tanks more closely matched conditions encountered by marked fish in the river and in the hatchery tanks where mortality was lower.

Depletion Estimates–The two-pass depletion method of Seber and LeCren (1967) was used to calculate juvenile steelhead abundances for each site, for each age class, and in each sampling period in both the Manistee and Little Manistee rivers. Steelhead abundances were calculated using the following equation (Everhart and Youngs 1981):

$$N = \frac{C_1^2}{C_1 - C_2}$$

where N is steelhead abundance, C_1 is the number of steelhead parr captured in pass #1, and C_2 is the number of steelhead parr captured in pass #2.

Variances of this estimator were calculated using the following formula (Everhart and Youngs 1981):

$$V(N) = \frac{C_1^2 * C_2^2 * (C_1 + C_2)}{(C_1 - C_2)^4}$$

where V(N) is the variance of the estimator, and N, C_1, and C_2 represent the same variables as above.

The Seber and LeCren technique assumes that effort is constant between passes, the population being sampled is closed (no immigration or emigration), and that the chance of capture is equal for all fish and constant from sample to sample. Sampling effort was kept constant by shocking the same area in each pass and by using the same equipment for the duration of the experiment. Immigration and emigration were limited by allowing as little time as possible between passes. The transect areas were not blocked off with nets, however, owing to the size of the river being sampled.

Steelhead parr were sampled in the mainstem Manistee River in August 1997, September 1997, and March 1998 using DC electrofishing. Fish were collected in each time period at 36 shoreline sites (only 35 sites in March due to high water) which were selected using a stratified random design and allocated across the 4 habitat strata. Each shoreline site extended 3 m from shore, and had an area of approximately 300 m^2. Shoreline samples were apportioned among strata using Neyman allocation (Scheaffer et al. 1996), and the same 36 sites were shocked in each sampling period. There were 16 sites in stratum 1, 13 in stratum 2, 6 in stratum 3, and 1 in stratum 4. Two electrofishing passes were made through each shoreline site, and all steelhead were collected and held in buckets on shore. In August 1997, the mid-river area between Tippy Dam and High Bridge Road was sampled using MDNR's DC boomshocker. The boomshockers sampled as close to shoreline areas as was possible. All parr in each pass were counted and assigned an age (See Methods—Age and Growth).

Steelhead parr were sampled in the Little Manistee River in July and October 1997, and March 1998 using DC electrofishing. Steelhead were collected in each time period at 14 sites spread across the five habitat strata. Each site had an area of approximately 300 m^2. Sites were apportioned among strata based on substrate type and matched those determined by Seelbach (1986). The same 14 sites were shocked in each sampling period. There was one site in stratum 1, two in stratum 2, four in stratum 3, four in stratum 4, and three in stratum 5. Two electrofishing passes were made through each site, and all steelhead were collected and held in buckets on shore. All parr in each pass were counted and assigned an age (See Methods—Age and Growth).

The site abundances of juvenile steelhead were used to estimate the total number of juvenile steelhead at each time period in each river using stratified random sampling (Scheaffer et al. 1996). Densities were calculated for each age class, at each time period, and in each river by dividing the stratified random sampling abundance estimates by river area. The Manistee River study site had a total area of 47.2 ha, and the Little Manistee River study site had a total area of 109.0 ha.

Relative densities of steelhead parr in Bear Creek and Pine Creek were estimated for August 1997 and October 1997 using DC electrofishing. Fish were collected in each time period at 3 sites in each system. Each site had an area of approximately 300 m^2. The same three sites were shocked in both sampling periods. Only one electrofishing pass was made through each site. All parr in each pass were counted and assigned an age (See Methods—Age and Growth). Densities were calculated for each station, for each age group, and in each sampling period.

Age and Growth

Age and growth of steelhead parr in all study areas were estimated from changes in mean length and weight at age. At each site, the total length and wet weight of a random subsample of parr were measured. Scales were taken (above the lateral line and below the center of the dorsal fin) from all parr with a length greater than 8 cm. A subsample of collected scales was pressed onto acetate slides, viewed at a magnification of 40X on a microprojector, and read for age (Jearld 1983). An age-length key was constructed for each river or creek in each sampling period (Stevenson and Campana 1992) and used to sort fish into age classes.

Where possible, average lengths, weights, conditions, absolute growth rates, relative growth rates, and instantaneous growth rates were calculated for parr in each age class, for each time period, and in each river or creek. Growth rates were not calculated for parr collected in creeks. Condition was calculated for individual fish using the Fulton Index of Condition (Anderson and Gutreuter 1983):

$$C = \frac{W}{L^3} * 10^5$$

where C is condition, W is wet weight in g, and L is total length in mm. Fish condition in the Manistee and Little Manistee rivers also was assessed by plotting $\log_e$-transformed, length-weight relations for juvenile steelhead at all sampling periods (Pitcher and Hart 1996). Plots were fit with a linear least-squares regression model, and model slopes were compared with ANCOVA.

Absolute growth rates were calculated using the following equation (Pitcher and Hart 1996):

$$g_a = \frac{W_{t+1} - W_t}{t}$$

where g_a is absolute growth, W_{t+1} is average weight at time t+1, W_t is average weight at time t, and t is number of days between times t and t+1.

Relative growth rates were calculated using the following equation (Pitcher and Hart 1996):

$$g_r = \frac{g_a}{W_t}$$

where g_r is relative growth rate, g_a is absolute growth, and W_t is average weight at time t.

Instantaneous growth rates were calculated using the following equation (Cone and Krueger 1988):

$$G = LN(W_{t+1}) - LN(W_t)$$

where G is instantaneous growth, W_{t+1} is average weight at time t+1, and W_t is average weight at time t. Instantaneous growth rates were converted to instantaneous daily growth rates (G_d) by dividing G by the number of days between time t and time t+1.

Survival

Juvenile steelhead survival in the Manistee and Little Manistee rivers was estimated from the change in abundance over time. Where possible, percent survival, daily instantaneous loss rate, and percent of population dying per day were calculated for each age class, for each time period, and in each river. Percent survival was calculated using the following formula:

$$\%S = \left(\frac{N_{t+1}}{N_t}\right) * 100\%$$

where %S is percent survival, N_{t+1} is abundance of parr at time t+1, and N_t is abundance of parr at time t.

Daily instantaneous loss rates were calculated using the following formula (Everhart and Youngs 1981):

$$Z = \frac{-LN(\frac{N_{t+1}}{N_t})}{t}$$

where Z is instantaneous loss rate, N_{t+1} is abundance of parr at time t+1, N_t is abundance of parr at time t, and t is the time interval in days between time t+1 and time t.

Percent of population dying per day was calculated using the following equation:

$$\%D = (1 - e^{-Zt}) * 100\%$$

where %D is percent dying per day, Z is instantaneous loss rate, and t is one day.

Instantaneous mortality rates also were estimated from the slope of $\log_e$-transformed abundance versus time. A Pareto model (Lo 1985) was used to fit abundances of YOY from the Manistee River, and a linear-least squares model (Everhart and Youngs 1981) was used to fit YOY abundance data from the Little Manistee River. A Pareto model assumes that survival increases with increasing fish size, and the linear model assumes an exponential decline in fish abundance.

Production

Juvenile steelhead production in the Manistee and Little Manistee rivers from July 1997 to March 1998 was estimated using Allen's (1971) method. Log_e-transformed steelhead density (y-axis) was regressed against average wet weight of individuals (x-axis), and production (area under these curves) was calculated using the following formula (Pitcher and Hart 1996):

$$P = \int_{w_0}^{w_t} D_i dw$$

where P is production, w_0 is average weight at time 0, w_t is average weight at time t, D_i is density at time i, and dw is the derivative of average weight.

This method is less problematic than Ricker's (1946) method of production estimation, because it makes no assumptions about the way population numbers decrease over time or the way fish grow over time (Pitcher and Hart 1996). The Ricker method can only be used if Z and G are constant for the population of interest over the time period of interest. However, there is no way to estimate variance around the production estimate with the Allen technique.

Habitat Analysis

River Temperature–From May 1996 to June 1998, instream water temperature was continuously monitored at six sites in the mainstem Manistee River, two sites in the Little Manistee River, two sites in Pine Creek, and four sites in Bear Creek. Temperature was monitored using submersible data recorders (HOBO and STOWAWAY) that measured water temperature approximately every hour. Temperature information was downloaded from each recorder about every four months using a laptop computer, and then the recorders were re-deployed. In most cases, mean daily temperatures, mean daily fluctuations (fluctuation = daily maximum temperature – daily minimum temperature), maximum temperatures, and accumulated degree days were calculated at sites of interest.

Microhabitat Data–In August 1997, microhabitat data were collected at each of the 36 sample sites on the Manistee River. A 1-m^2 quadrat was randomly placed at the beginning, middle, and end of each site. The following parameters were measured inside the quadrat: temperature (°C—digital thermometer), conductivity (µS—Hach conductivity meter), pH (Hach pH meter), depth (m), flow at 0.4.depth (m/s—Swoffer 2100 flow meter), substrate composition (visual estimation), percent bottom cover of vegetation (visual estimation), percent bottom cover of woody debris (visual estimation), and percent shaded area (visual estimation). In June 1998, microhabitat data were collected in a similar fashion at each of the 14 Little Manistee River sample sites.

The microhabitat data were analyzed using both a Principal Components Analysis (PCA) and Multiple Linear Regression (MLR). All habitat data were put in the PCA, and those principal components that explained the most variation in the habitat variables were used to generate MLR models (one for each sampling period) to predict YOY steelhead abundance from habitat variables. The raw data also were used to build MLR models that predicted YOY steelhead abundance from habitat variables. In the raw data models, only parameters that were significantly correlated to YOY steelhead abundance were included. Co-linear habitat variables also were excluded from MLR models. Stepwise regression, both forward and backward, was used to help select the best models. A regression model was constructed for each sampling period in both the Manistee and Little Manistee rivers.

Statistical Analyses

In general, parametric tests were used because samples were normally distributed and had equal variances. ANCOVAS were used to compare regression slopes and intercepts in length-weight regressions. Confidence intervals (95%) were calculated around most point estimates. All statistical tests were performed and all regression models were fit using SYSTAT 7.0. Results were considered statistically significant at $\alpha = 0.05$ or if the 95% confidence intervals did not overlap.

Results

General

During pass-depletion electrofishing, a total of 40 fish species were caught in the Manistee River, 17 in the Little Manistee River, 17 in Bear Creek, and 19 in Pine Creek (Table 1). Species considered common were found at > 50% of sites in a system, and those considered rare were found at < 10% of sites in a system. The Manistee River had a more diverse fish community and supported many more commonly occurring coolwater and warmwater fish species than the other study systems.

Abundance and Density

Manistee River–YOY steelhead abundance in the Manistee River dropped drastically from 3,029,604 ± 589,803 in July 1997 to 1,692 ± 519 in March 1998 (Table 2), and YOY steelhead density dropped from 64,187 ± 12,496/ha in July 1997 to 36 ± 11/ha in March 1998 (Table 3). The largest losses occurred over the July 15 to August 12 interval. The August 12 mark-recapture (108,795 ± 50,374) and pass-depletion estimates (51,490 ± 13,389) for YOY steelhead were not significantly different (Table 2). Because of smaller variance, we assumed the August pass-depletion estimate was more accurate, and we used this estimate in subsequent calculations for Manistee River YOY steelhead. Abundance and density of each cohort dropped significantly over each sampling interval, with the exception of the significant increase in abundance (59 ± 36 to 1,369 ± 492) and density (1 ± 1/ha to 29 ± 10/ha) of the age-1 cohort between September 1997 and March 1998 (Tables 2 and 3).

Abundance of steelhead parr differed among strata in the Manistee River. On average, 60% of steelhead parr in the Manistee River were found in Stratum 1, 24% were found in Stratum 2, 15% were found in Stratum 3, and 1% were found in Stratum 4.

Little Manistee River–Steelhead parr abundance and density remained relatively constant in the Little Manistee River from July 1997 to March 1998 (Tables 2 and 3). Abundance and density of each cohort dropped over the entire sampling period, but never by a significant amount between consecutive sampling intervals. A 50% drop (though not significant due to large confidence intervals) in abundance (61,572 ± 29,576 to 30,865 ± 13,297) and density (565 ± 271/ha to 283 ± 122/ha) for the age-1 cohort occurred between October 1997 and March 1998 (Tables 2 and 3).

In July 1997, YOY steelhead density was significantly higher in the Manistee River (64,187 ± 12,496/ha) than in the Little Manistee River (2,819 ± 608/ha) (Figure 3). Due to higher loss rates in the Manistee River, however, the Little Manistee River had a significantly higher density of YOY steelhead by August 1997. The Little Manistee River had a significantly higher density of YOY steelhead for the remainder of the study.

Abundance of steelhead parr differed among strata in the Little Manistee River. On average, 13% of steelhead parr in the Little Manistee River were found in Stratum 1, 28% were found in Stratum 2, 28% were found in Stratum 3, 23% were found in Stratum 4, and 8% were found in Stratum 5.

Pine and Bear creeks–Due to the small number of sites sampled (three in each tributary), the relative density estimates of steelhead parr in Pine and Bear creeks had large confidence intervals (Table 3). As a result of these large confidence intervals, any trends in density that may exist may not be readily observable. However, both Pine (1,344 ± 4,313/ha) and Bear creeks (1,411 ± 1,405/ha) had fall YOY steelhead densities that were fourfold higher than those in the Manistee River (338 ± 117/ha) (Table 3). The fall YOY relative densities in these creeks were on the same order of magnitude as those in the Little Manistee River (2,471 ± 704/ha) (Table 3).

Age and Growth

Manistee and Little Manistee rivers–Average body length and weight of YOY and age-1 steelhead were significantly higher in the Little Manistee River than in the Manistee River in all sampling periods except March 1998, when YOY steelhead in the Manistee River were significantly longer and heavier than YOY steelhead in the Little Manistee River (Figures 4 and 5, Appendix Table 1). Not enough age-2 fish were sampled to compare average lengths and weights between the two rivers.

Average body condition of YOY and age-1 steelhead was significantly higher in the Manistee River than in the Little Manistee River in October 1997 and March 1998 (Figures 6 and 7). Not enough age-2 fish were sampled to compare condition between the two rivers.

Slopes of $\log_e$ transformed length-weight regressions did not differ significantly between the Manistee (slope = 2.9048) and Little Manistee rivers (slope = 2.9021) (Figure 8). This suggests similar patterns in growth over the lifespan of juvenile steelhead in each system. However, the intercept of the Manistee River regression (intercept = -4.362) was statistically larger than the intercept of the Little Manistee River (intercept = -4.425), (Figure 8).

YOY steelhead from the Manistee River appeared to have higher absolute, relative, and instantaneous daily growth rates in both the September/October and March sampling periods than YOY steelhead from the Little Manistee River (Table 4). Not enough age-1 and age-2 fish were collected in the Manistee River to calculate rates for these cohorts. These growth differences may or may not have been statistically significant, since it was not possible to quantify the variance around these estimates.

Pine Creek and Bear Creek–Average body length and weight of YOY steelhead were significantly higher in Bear Creek than in Pine Creek in both August/September and October 1997 (Table 5). Average body condition of YOY steelhead was significantly higher in Pine Creek than in Bear Creek in both August/September and October 1997 (Table 5). Average body length and weight of age-1 steelhead were significantly higher in Bear Creek than in Pine Creek in September 1997, and average body condition of age-1 steelhead was significantly higher in Pine Creek than in Bear Creek in October 1997 (Table 5). Summer sampling dates for the creeks did not coincide well enough with summer sampling dates on the Manistee and Little Manistee rivers to make comparisons between the rivers and creeks meaningful. However, average body length and weight of YOY steelhead were significantly higher in Bear Creek than in either the Manistee or Little Manistee rivers in fall (October) (Figure 4 and Table 5), and average body length and weight of age-1 steelhead were significantly higher in Bear and Pine creeks than in the Manistee and Little Manistee rivers in fall (Figure 5 and Table 5). Not enough age-2 fish were sampled to compare lengths between the rivers and creeks. Average body condition of YOY steelhead was significantly higher in Pine Creek than in the Little Manistee River in fall (Figure 6), and average body condition of age-1 steelhead was significantly higher in both Pine and Bear Creeks than in the Little Manistee River (Figure 7). Not enough age-2 fish were sampled to compare condition between the rivers and creeks.

Survival

Manistee River–Percent survival (%S), instantaneous daily loss rate (Z), and percent of population lost per day varied greatly from July 1997 to March 1998 (Table 6). The lowest survival (1.7%) for YOY steelhead occurred during the July 15 to August 12 interval. In fall and winter, parr survival increased to 10.6 and 30.9%, respectively.

A Pareto model, which assumes fish survival increases with increasing body size, fit the YOY steelhead abundance data well (Figure 9). The instantaneous mortality rate varies in this model; it is highest at the start (0.146/day) and becomes smaller over time (0.028 to 0.013). Not enough age-1 and age-2 steelhead were captured, likely due to low survival in the YOY stage, to allow calculation of survival and loss rates for these cohorts.

Little Manistee River–Survival of YOY and age-1 steelhead was much higher (50.1 to 99.7%) and the daily loss rates were much lower (0.00005 to 0.005/day) in the Little Manistee River than in the Manistee River (Table 6). Most survival and loss rates differed by an order of magnitude between the two systems. Of note was the relatively low survival rate (50.1%) for age-1 steelhead during the October to March interval (Table 6). Not enough age-2 steelhead were captured to allow calculation of survival and loss rates for this cohort.

A linear-least squares model fit the Little Manistee YOY steelhead abundance data well (Figure 10). Both the model and the interval calculations (Table 6) yielded a constant daily Z of 0.002 for YOY steelhead from the Little Manistee River from July 1997 to March 1998.

Production

Manistee River–The Manistee River yielded 1.54 g/m^2 of juvenile steelhead production from July 1997 to March 1998 (Figure 11). Due to low survival during the YOY stage, there was very little production of age-1 and age-2 fish in this system. In fact, not enough age-1 and age-2 fish were captured to calculate a production estimate for these cohorts. The great majority of YOY production came from newly-hatched parr, and little production was added from subsequent fish growth due to low YOY survival.

Little Manistee River–The Little Manistee River yielded 1.89 g/m^2 of juvenile steelhead production from July 1997 to March 1998. Most (1.14 g/m^2) of this total was from YOY production (Figure 12), and the remainder (0.75 g/m^2) was from age-1 fish. In this system, fish survived longer and were able to contribute to the production of the system over a longer period of time. As a result, the Little Manistee River produced a higher biomass of steelhead per unit area than the Manistee River.

Habitat Analysis

Microhabitat Data–The PCA followed by regression approach did not generate models that predicted YOY steelhead abundance from habitat parameters well. In all six PCA models (one for each sampling period in both the Manistee and Little Manistee rivers), 77-95% of the variation in the measured habitat parameters was explained by the first three principal components. Substrate parameters (i.e. % gravel, % sand, and % cobble) loaded most heavily on the principal components, but all habitat variables loaded to some degree on each principal component. Regressing the YOY abundance onto the habitat-based principal components did not yield models that predicted YOY abundance well from the habitat variables. The adjusted R^2 values for the regressions ranged from 0.06 to 0.19. Therefore, multiple linear regressions of average raw habitat data were used to build models that better predicted YOY abundance from the habitat parameters.

The habitat models that best predicted (highest adjusted R^2 and model $p < 0.05$) YOY steelhead abundance in each system are summarized in Table 7. Significant habitat parameters varied over time and between river systems. In the Manistee River, temperature predicted 22% of variance in YOY steelhead abundance in August 1997, % boulder in substrate predicted 30% of variance in YOY steelhead abundance in September 1997, and % boulder (54%) and temperature (6%) predicted 60% of variance in YOY steelhead abundance in March 1998 (Table 7). In the Little Manistee River, % gravel in substrate predicted 37% of variance in YOY steelhead abundance in July 1997, pH (27%) and depth (15%) predicted 42% of variance in YOY steelhead abundance in September 1997, and % vegetation (37%) and pH (19%) predicted 56% of variance in YOY steelhead abundance in March 1998 (Table 7).

River Temperature–The July 1997 daily-average temperature regime at Tippy Dam ranged from 19.3 to 21.2°C (Figure 13), and the July monthly mean was 20.3°C (Table 8). In contrast, the daily-average temperature regime at 6-Mile Bridge in the Little Manistee River ranged from 14.8 to 19.7°C (Figure 13), and the July monthly mean was 17.0°C (Table 8).

Daily temperatures also had little daily fluctuation below Tippy Dam (Table 8). On average, daily temperature fluctuation averaged only 0.8 ± 0.6°C below Tippy Dam in July 1997 (Table 8). Sites in the Manistee River above Tippy Dam at Cameron Bridge (mean = 13.3°C, fluctuation = 4.5 ± 2.6°C) and West Sharon Road (mean = 17.9°C, fluctuation = 3.6 ± 2.1°C) had lower mean daily temperatures and significantly higher mean daily fluctuations (Table 8). Daily fluctuation did not differ significantly among the four sites below Tippy Dam. Daily temperature fluctuations at 6-Mile Bridge in the Little Manistee River (3.5 ± 1.7°C) and at Leffew Road in Bear Creek (5.4 ± 3.0°C) were significantly higher than the temperature fluctuation below Tippy Dam (Figure 8). Mean daily temperatures at these sites (17.0°C and 17.6°C respectively) were lower than the daily mean below Tippy Dam (20.3°C) (Table 8).

Owing to the high mean daily temperature and low daily fluctuation below Tippy Dam in July 1997, a higher number of degree days accumulated below Tippy Dam (629) than at Cameron Bridge (413), West Sharon Road (554), 6-Mile Bridge in the Little Manistee River (527), and Leffew Road in Bear Creek (544) (Table 8).

Discussion

The contrast between YOY steelhead survival and production in the Manistee and Little Manistee rivers indicates that habitat conditions in the area below Tippy Dam, while excellent for reproduction, are unsuitable for parr. These conditions, especially consistently high July temperatures, may cause a population bottleneck for steelhead production in the mainstem Manistee River (Tables 2 and 8). The bottleneck in parr production appeared to occur mainly through increased mortality rather than decreased growth. Large summer losses of YOY steelhead were not seen in the colder Little Manistee River (Tables 2 and 8), and growth parameters did not differ conclusively between the Manistee and Little Manistee rivers (see Growth section below). Our hypothesis of temperature limitation on steelhead parr production is supported by recent work in the nearby Betsie River, where summer loss rates of YOY steelhead in the thermally stressed mainstem (summer mean = 19.7°C) were higher than loss rates in cooler, tributary streams (summer mean = 14.6°C) (Newcomb 1998). Thus, it appears that warm summer temperatures can lower the survival and production of steelhead in thermally stressed rivers, and this process is likely occurring below Tippy Dam on the Manistee River.

Growth

Growth of steelhead parr differed between the study rivers, but not consistently so. In general, average length and weight of YOY and age-1 steelhead were significantly higher in the Little Manistee River than in the Manistee River (Figures 4 and 5, Appendix Table 1), but body condition of YOY and age-1 steelhead was significantly higher in the Manistee River than in the Little Manistee River (Figures 6 and 7). Slopes of length-weight regressions did not differ significantly between the Manistee and Little Manistee rivers, but the Manistee River regression intercept was significantly larger than the Little Manistee River regression intercept, suggesting that Manistee River YOY steelhead had a higher weight at hatching than Little Manistee River steelhead (Figure 8). Despite this initial difference, Little Manistee River YOY steelhead were significantly longer and heavier by summer and fall than Manistee River YOY steelhead (Figures 4 and 5, Appendix Table 1). The fall size difference could have been the result of faster growth rates in the Little Manistee River due to a more optimal temperature regime, but the growth rate calculations did not support this assertion. Absolute, relative, and instantaneous daily growth rates of YOY steelhead were highest in the warmer Manistee River (Table 4). Also, the average fall length of YOY steelhead below Tippy Dam (7.2 ± 0.08) was comparable to average lengths of YOY steelhead reported in 9 other Great Lakes streams (5.0-8.0 cm) (Seelbach 1993). Thus, it is unclear what effect, if any, the operation of Tippy Dam may have had on YOY steelhead growth.

The lack of a clear difference in parr growth between rivers was surprising considering the differences in river temperatures. It is possible that the fish sampled below Tippy Dam were exceptional fish able to deal with the stressful high temperatures below the dam. Perhaps many of the steelhead lost below Tippy Dam starved or were stunted due to the warm temperature regime and were then eaten by size-selective predators. If this were the case, these fish would be removed from the population sample and any effect of temperature on the growth of juvenile steelhead would be masked.

It is also possible that density of available prey was higher in the Manistee River than in the Little Manistee River, allowing fast growth despite higher metabolic costs. Macroinvertebrate densities available to steelhead parr in either river are unknown. However, increased foraging may lead to increased predation, since steelhead would need to spend more time actively feeding and less time in hiding.

Abundance and Survival

Juvenile steelhead abundances declined rapidly below Tippy Dam from July 1997 to March 1998 (Table 2). The greatest declines were seen in YOY steelhead during the July 15 to August 12 interval. Mean river temperature below Tippy Dam reached its highest point during this interval and likely induced thermal stress in YOY steelhead (Figure 13). There was a significant increase in abundance and density of the age-1 cohort between September 1997 and March 1998 below Tippy Dam (Table 2). This likely represented overwinter migration of age-1 steelhead from Pine and Bear creeks into the main river channel during winter of 1997, but the increase could also be due to sampling error. Overwinter movement of steelhead parr from tributary to mainstem streams due to space limitations has been previously documented by Bjornn (1971) in the Lehmi River, Idaho and by Leider et al. (1986) in the Kalama River, Washington.

YOY steelhead abundance was much more stable in the Little Manistee River than in the Manistee River, and did not decline dramatically during summer (Table 2). The October 1997 abundance estimates for YOY and age-1 steelhead did not differ significantly from those of fall 1981, 1982, and 1983 in the Little Manistee River (Seelbach 1993). A 50% drop in population for the age-1 cohort occurred between October 1997 and March 1998 in the Little Manistee River. This high rate of pre-smolt mortality was previously documented by Seelbach (1987) and shown to range from 13-90% depending on winter severity in Michigan streams.

Fall 1997 density estimates of YOY steelhead in the Manistee River were an order of magnitude lower than those in the Little Manistee River, Pine Creek, and Bear Creek (Table 3). These systems have colder July mean temperatures, significantly higher daily temperature fluctuations, and less accumulated degree-days than the Manistee River site below Tippy Dam (Table 8). In Fall 1997, Manistee River steelhead density was on the same order of magnitude as YOY density in the Betsie River, a thermally stressed system (summer mean = 19.7°C) (Table 9). Fall 1997 estimates of YOY steelhead density in the Little Manistee River and Pine and Bear creeks were on the same order of magnitude as other Great Lakes tributaries (Table 9). Only the Manistee and Betsie rivers had relatively low fall YOY steelhead densities (Table 9).

Production

Production of steelhead parr in the Manistee River was limited to the early life stages. Most YOY steelhead simply did not persist long enough beyond July to add to the production estimate; only 1.7% of YOY steelhead survived their first month below Tippy Dam (Table 6). Therefore, the majority of YOY production came from newly-hatched fish and not subsequent fish growth. In the Little Manistee River, YOY and age-1 fish survived longer, grew, and contributed to the production estimate. Much of the production estimate in the Little Manistee came from growth of age-1 fish. Age-1 fish did not contribute to the production estimate in the Manistee River.

Production estimates for the Manistee and Little Manistee rivers compared favorably to steelhead production estimates in the Salmon River, a coldwater system in New York known for its yearly steelhead and salmon spawning runs (Wisniewski 1990). Production of juvenile steelhead in the Salmon system from June to November 1986 ranged from 0.6 to 1.72 g/m^2 (Wisniewski 1990). Based on production estimates, the Manistee, Little Manistee, and Salmon rivers appear to be almost equally productive. However, like the Little Manistee River, age-1 steelhead persist in the Salmon River and contribute to the production estimate.

Our YOY steelhead survival and production estimates for the Manistee River were not likely biased by emigration out of the study area. Emigration from the study area was unlikely for four reasons. First, the mark-recapture data suggest that steelhead parr moved less than 600 m from the point of marking, and areas in the mainstem Manistee River below the study area have potentially stressful thermal parameters similar to those below Tippy Dam (Table 8). Secondly, we did not find any marked steelhead parr in the tributaries, and it is unlikely that mainstem fish would settle there due to the high densities of resident steelhead parr in the tributaries (Table 2). Thirdly, migration or smolting at such a small size (July total length = 3.8 ± 1.4 cm) would likely lead to high levels of mortality along the migration route or in Lake Michigan. Seelbach et al. (1994) showed that smolt survival was strongly and positively correlated with size. Fourthly, only 30-50% of the adult steelhead catch in the Manistee River is comprised of wild fish, so it is unlikely that many naturally-produced steelhead parr from the Manistee River survive.

A future examination of otoliths of steelhead parr captured in Pine and Bear creeks may show the natal origin of these fish and further support or refute the above assumptions. An otolith or scale analysis of oxygen isotope signatures of mainstem-caught adult fish may determine the natal origin of these fish as well (Patterson 1998). It is possible that some of the adult fish caught in the mainstem Manistee River are strays from other systems or from Pine and Bear creeks. If this were the case, it would further support our argument of low parr survival of Manistee River steelhead.

Factors Affecting YOY Steelhead Survival and Production

River Temperature–Increased temperature and the resulting increases in metabolism likely caused decreases in fish growth or survival below Tippy Dam. Most fishes are ectothermic poikilotherms, and their metabolic rates are positively correlated with water temperature (Diana 1995). Standard metabolic rate is just one part of a fish's total energy budget that includes locomotion, excretion, reproduction, and growth costs among others (Webb 1978). If one term of this energy budget increases (i.e. metabolism), fish either have to decrease other terms (i.e. growth) or eat more to offset the increased energy demand. Swimming to attain food can be energetically costly (Diana 1995), and may lead to increased exposure to predators and decreased survival. Decreases in either growth or survival will lead to decreases in production.

Water temperature is an important factor determining the distribution of fish species, and most fish species inhabit preferred temperature ranges. Coutant (1977) showed that juvenile steelhead prefer temperatures ranging from 11 to

21°C, and Hokanson et al. (1977) showed that steelhead achieve maximum specific growth rates between 15.0 and 17.2°C. Hokanson et al. (1977) also showed that growth rates can be increased for juvenile steelhead when mean temperatures vary ± 3.8°C around the mean. This positive effect of temperature variation only occurred at mean temperatures below 17.2°C. Above 17.2°C, temperature variation caused decreased specific growth. This occurred because fish spent half of their time above the maximum temperature for growth with a temperature regime of 17.2 ± 3.8°C. Similar temperature variation likely explains why steelhead can persist and grow well in streams like Pine Creek and Bear Creek, whose mean July temperatures were above the range of maximum steelhead growth (Table 8). Bear Creek also had a relatively high daily temperature fluctuation (5.4 ± 3.0°C, Pine Creek data were unavailable due to recorder malfunction) in July 1997 (Table 8). This fluctuation was the result of diurnal cooling and allowed juvenile steelhead to occupy their preferred temperature regime for at least part of each day. Juvenile steelhead were not able to occupy their preferred temperature range below Tippy Dam, since mean July temperature below the dam was well above the preferred range (Figure 13), and the low daily fluctuation (0.8 ± 0.6°C) did not allow river temperatures to overlap the preferred range (Table 8).

Local distributions of steelhead parr in the Manistee River also indicated thermal stress was important. Fishes display the ability to regulate their body temperatures by actively moving between areas of different temperatures. In lab studies, McCauley and Huggins (1976) showed that juvenile steelhead will move between areas of warm and cold water to regulate their internal body temperature at 16.3°C. This type of behavioral thermoregulation is only possible if a variety of thermal habitats exist. Thermal habitat can vary diurnally, seasonally, and spatially due to water contributions from other sources like tributaries or local groundwater seeps. Seasonal variation in temperature is not the issue of concern below Tippy Dam. YOY steelhead abundance dropped over a very short period of time (2-3 weeks in July), so little seasonal variation occurred. Diurnal variation in temperature is virtually eliminated by the top draw of the dam and stratification of the reservoir, and daily temperature fluctuation below the dam averaged only 0.8 ± 0.6°C in July 1997 (Table 8). Groundwater may provide localized cold water refugia for steelhead below Tippy Dam. Groundwater seeps are common in the first 1.5 km of river below Tippy Dam, and the average temperature of these seeps was 15.0°C in July 1997 (A. P. Woldt, The University of Michigan, unpublished data). In July and August, large concentrations of juvenile steelhead were found in groundwater plumes below Tippy, while few fish were found in areas adjacent to the plumes (A. P. Woldt, The University of Michigan, unpublished data).

Steelhead parr dynamics in the Manistee River are similar to parr dynamics in the Betsie River, where parr survival also is limited by high summer temperatures (Newcomb 1998). To illustrate the effect of temperature on steelhead survival and subsequent production, we used Newcomb's (1998) regression relationship between maximum summer temperature (x-axis) and YOY steelhead density (y-axis) in the Betsie River. Assuming the maximum summer temperature in the Manistee River could be lowered by 4°C from 21.7°C, the density of surviving parr could be increased by 10-fold. This increase in survival would lead to an increase in production in the Manistee River, since low survival, not growth, contributes to low production below Tippy Dam.

Finally, evidence for temperature limitation on steelhead production in the Manistee River is provided by the contrast with current chinook salmon production below Tippy Dam. Adult chinook run up the Manistee River in fall to spawn, fry hatch in March, April, and May, and YOY leave the system as 1-3 month old smolts in late May and early June. In 1997, the peak of the chinook smolt run on the Manistee River was May 31 (Rutherford et al. 1998). While in the nursery area, juvenile salmon appear to survive much better than juvenile steelhead, especially after 1990 when hydropower dam operations were changed from peaking to run-of-river. Estimated number of 1-3 month old chinook fry produced below Tippy Dam increased from 100,000 fry (2,105/ha) in 1979 to 389,000 fry (8,190/ha) in 1993 (Carl 1980; E. S. Rutherford, The University of Michigan, unpublished data). This is much higher than the

51,000 YOY (1,100/ha) steelhead that remained approximately 1 month after emergence or the 16,000 YOY (338/ha) steelhead that remained approximately 2 months after emergence in July 1997 (Tables 2 and 3). The greatest difference in habitat in the Manistee River between May and July was mean water temperature. The mean water temperature below Tippy Dam in May 1997 was 10.4°C, while the mean July temperature was 20.3°C. Approximately 70% of the adult chinook returning to spawn below Tippy Dam in 1995 were of wild origin as well (Michigan Department of Natural Resources, Fisheries Division, unpublished data), indicating chinook salmon parr appear to survive better than steelhead parr in the Manistee River system.

Microhabitat Parameters–Many studies (Bjornn 1971; Bowlby and Roff 1986; Leider et al. 1986; Loch et al. 1988; Close and Anderson 1997; Newcomb 1998) have indicated that habitat quantity and quality can limit the abundance, survival, and production of steelhead. The habitat parameters examined (temperature, conductivity, pH, depth, flow, bottom composition, vegetative cover, woody debris, and shade) helped explain some of the variation in steelhead abundance on the Manistee and Little Manistee rivers.

In August 1997, temperature explained 22% of the variation in YOY steelhead abundance in the Manistee River (Table 7). Temperature did not affect YOY abundance in the expected direction, however. We used temperature as an indicator of groundwater. In July, Michigan groundwater is colder than ambient river water and may offer refuge to coldwater fish like steelhead. Thus, we expected temperature to have a negative relationship with YOY steelhead abundance.

The positive effect of temperature was likely due to the fact that we measured an instantaneous temperature at each site. It was not possible to measure continuous temperature at all study sites. River temperature varies, sometimes greatly (Table 8) over the course of a day. Cool and coldwater fish can persist in systems that get too warm by being inactive during the warmest parts of the day or by finding nearby thermal refugia (Diana 1995). We could have biased our habitat results by measuring the temperature of a site during the hottest part of the day and finding many fish there because they were being inactive or because there was a nearby thermal refuge (i.e. groundwater plume).

As juvenile steelhead got older on the Manistee River (September and March), % boulder in substrate became a significant predictor of YOY steelhead abundance as well. Percentage boulder explained 30% of the variation in YOY steelhead abundance in September, and % boulder (54%) and temperature (6%) explained 60% of the variation in YOY steelhead abundance in March (Table 7). Percentage boulder affected YOY steelhead abundance in an intuitive direction. Percentage boulder was positively correlated with YOY abundance, because YOY use boulder for cover (Bjornn 1971).

In the Little Manistee River, % gravel in substrate explained 37% of the variation in YOY steelhead abundance in July 1997 (Table 7). This model and the direction of the parameter coefficient have biological significance. Adult steelhead spawn in gravel, and young are often found adjacent to spawning beds.

In the October 1997 habitat model for the Little Manistee River, pH (27%) and depth (15%) explained 42% of the variation in YOY steelhead abundance (Table 7). pH did not affect YOY steelhead abundance in the expected direction, however. We assumed pH was an indicator of groundwater. We expected groundwater to have a higher pH than stream water due to its contact with, and leaching of, ions from underlying bedrock. We did not measure the pH of groundwater in the Little Manistee River system, however, so we do not know if this expectation is valid. If groundwater passed quickly through the ground, it may not have had the opportunity to take on the chemical properties of the bedrock. The negative effect of depth was expected. YOY steelhead aggregate in shallow water near stream margins. We did not find a single YOY steelhead >3 m from shore in our sampling runs.

In the March 1998 habitat model for the Little Manistee River, % vegetation (37%) and pH (19%) explained 56% of the variation in YOY steelhead abundance (Table 7). The significant positive effect of vegetation has biological significance. At several of the sites sampled in the Little Manistee River, YOY steelhead used weed beds for cover, especially at sites where instream cover was scarce. The negative effect of pH has already been explained.

Two important conclusions can be gleaned from the above habitat analysis. The first is that habitat factors other than the ones measured probably affect YOY steelhead abundance on these streams and should be investigated. The best-fit model predicting YOY steelhead abundance for the Manistee River explained 60% of the variation in YOY steelhead abundance, but most models explained only 22-56% of the variation. Factors such as temperature variation, biomass of benthic invertebrates, or biomass of drift organisms among others may account for the remainder of the variation. In fact, Poff and Ward (1989) contend that discharge is the most important characteristic affecting stream organisms. If true, this is very important in a flow-regulated system like the Manistee River. An emergency release of water at the wrong time could greatly influence the aquatic organisms below a dam. This was seen for steelhead in July of 1996. A FERC mandated, discharge-stage study flushed thousands of juvenile steelhead out of the nursery area below Tippy Dam (A. P. Woldt, The University of Michigan, unpublished data). These fish were not seen again, and it is likely that they died.

Secondly, % boulder in substrate was a significant factor affecting YOY steelhead abundance in 2 of 3 Manistee River models (Table 7). Boulder habitat was scarce below the dam. Only 4% of the nearshore area in the first 1.5 km below Tippy Dam contained boulder habitat, but YOY steelhead selected it for cover. This area produced 60% of the 1997 YOY steelhead in the Manistee River.

Management Implications

Three important management implications can be drawn from this study. These implications can be addressed through the management practices discussed below. It is likely that a combination of these management practices would yield the optimum improvement in the steelhead resource.

First, due to the stratification of Tippy Dam's reservoir and the top draw of the dam, waters below Tippy Dam may be warmer than they would be without the dam's presence. Much of the water on the bottom of the reservoir just behind Tippy Dam appears to be groundwater, because it has properties (July temperature = 9-10°C, and oxygen concentration = 0.2-2 ppm) consistent with those of groundwater (Michigan Department of Natural Resources, Fisheries Division, unpublished data). If this water were not impounded it would flow into the region below Tippy Dam, perhaps lowering the mean water temperature and increasing the amount of thermal habitat available to juvenile steelhead below Tippy Dam. Increasing the amount of thermal habitat may increase the amount of juvenile steelhead production below Tippy Dam. Christie and Reiger (1988) have shown that commercial yield of lake trout was positively correlated to quantity of available thermal habitat in Canadian lakes.

Some mechanism to pass hypolimnetic water (i.e. draft tubes) over Tippy Dam could be installed. A continuous hypolimnetic draw would provide a constant flow of cold water over the dam. Under this regime, the daily fluctuation in river temperature would remain small, but the mean temperature would decrease. A second plausible regime would be to pass cold, hypolimnetic water over the dam only at night to simulate diurnal cooling. This would give young steelhead some thermal refuge, and it would limit the amount of energy needed to pump water up from the bottom of the reservoir and over Tippy Dam. Both bottom draw regimes would only need to be performed in the summer months (June-August) when temperatures are hottest below Tippy Dam.

A hydrologic modeling analysis of the Manistee River would be needed to assess the feasibility of putting a bottom draw on Tippy Dam. It would be necessary to estimate the size and amount of cold groundwater that exists behind Tippy Dam, because it is possible that there is not enough groundwater impounded behind Tippy Dam to effectively lower the water temperature in the downstream area. It is also possible that the low amount of dissolved oxygen in this cold water could limit the survival of trout beneath the dam. Passing a mixture of hypolimnetic and epilimnetic water over the dam could likely solve this problem, but the relative amounts of each would need to be estimated.

Secondly, increasing the amount of boulder habitat, especially in the first 1.5 km below Tippy Dam, may increase YOY steelhead survival. Percentage boulder did not significantly influence YOY steelhead in the summer (August), but boulder habitat appeared to provide cover in September and March for those YOY that survived the summer die-off. Adding habitat to the Manistee River will not increase the low YOY survival (%S=1.7%) due to high temperature in July, but it may aid the survivors. Lack of habitat has been shown to limit the abundance and survival of juvenile steelhead in reservoirs and streams (Tabor and Wurtsbaugh 1991; Fausch and Northcote 1992).

Thirdly, discharges greater than those dictated by the run-of-river flow regime should be avoided whenever possible, especially during hatch-out periods of larval salmonids. Peaking discharges in times of electrical emergency (i.e. high electrical demand) are allowed under the 1994 licensing agreement between FERC and CPCo. These discharges are a necessary part of power generation, but could potentially be limited by drawing needed power from other facilities like the Ludington Pump Storage Facility. The negative effects (mortality and displacement) of peaking flows on larval fish have been well documented (Cushman 1985; Bain et al. 1988; Scheidegger and Bain 1995). Even a single peaking event, like the flow test of July 1996 that drove the majority of YOY steelhead from the primary rearing area below Tippy Dam, can limit salmonid abundance. The change from a peaking to a run-of-river flow regime has allowed chinook salmon fry to hatch and thrive, and it has allowed steelhead to hatch and survive, albeit briefly. Prior to 1989, YOY salmonids were not as abundant in the river, as they are now, below Tippy Dam (T.J. Rozich, Michigan Department of Natural Resources, personal communication). Adults spawned below Tippy Dam, but it is believed eggs and fry were washed away by peak flows. In order to best manage the fishery resource below Tippy Dam and avoid larval fish loss, efforts must be made to limit peak discharges.

Summary and Conclusions

A population bottleneck for steelhead parr exists below Tippy Dam on the Manistee River. Steelhead parr experience drastic declines in abundance due to low survival in summer. As a result, production of steelhead parr on the Manistee River is low, and the majority (50-70%) of adult steelhead catch in the Manistee River is comprised of hatchery fish.

High daily temperatures coupled with small daily temperature fluctuations seem to be the primary factors causing low YOY steelhead survival in the Manistee River. It may be possible to improve steelhead parr survival in the Manistee River by installing a hypolimnetic draw on Tippy dam to lower the mean temperature or increase the daily temperature fluctuation below the dam.

Acknowledgments

Funding for this project was provided from mitigation funds paid by Consumers Power Corporation (CPCo) as part of the 1994 re-licensing of the Tippy Dam Project.

We thank MDNR and Jim Gapczynski for technical assistance and equipment.

We thank the following individuals for assistance on field surveys: David Swank, Kevin Mooney, Jason “g” Lewis, Matt Tomlinson, Neal Godby, Tom Rozich, and Michigan DNR District 6 Fisheries personnel. We thank Michigan State University for providing summer housing at its Ludington Research Station, and the Chittenden Educational Center for providing housing during spring.

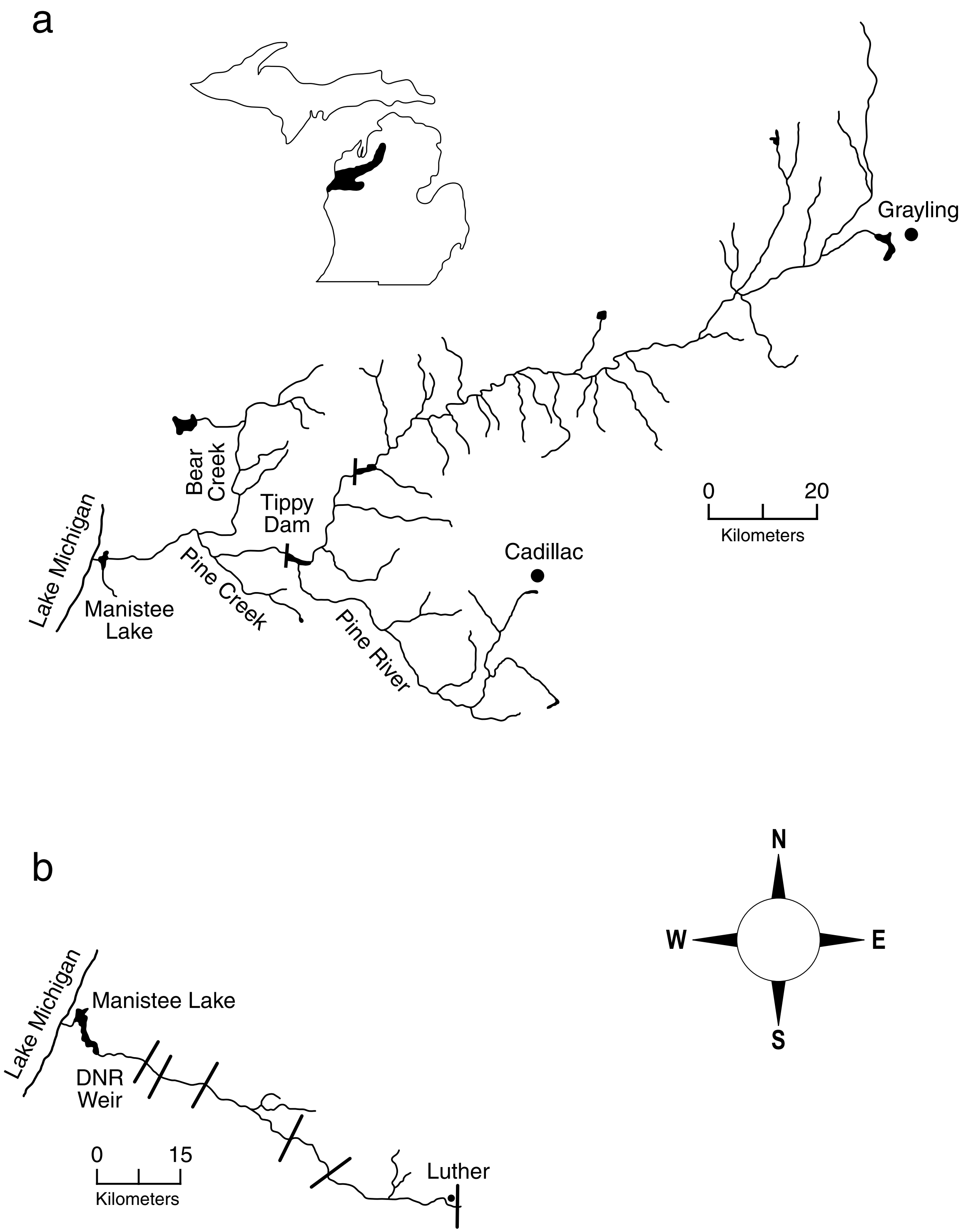

Figure 1.–Map of (a) Manistee River system, and (b) Little Manistee River system showing locations of the study strata. The downstream end of the study area was the DNR weir, and the upstream end of the study area was Luther Dam.

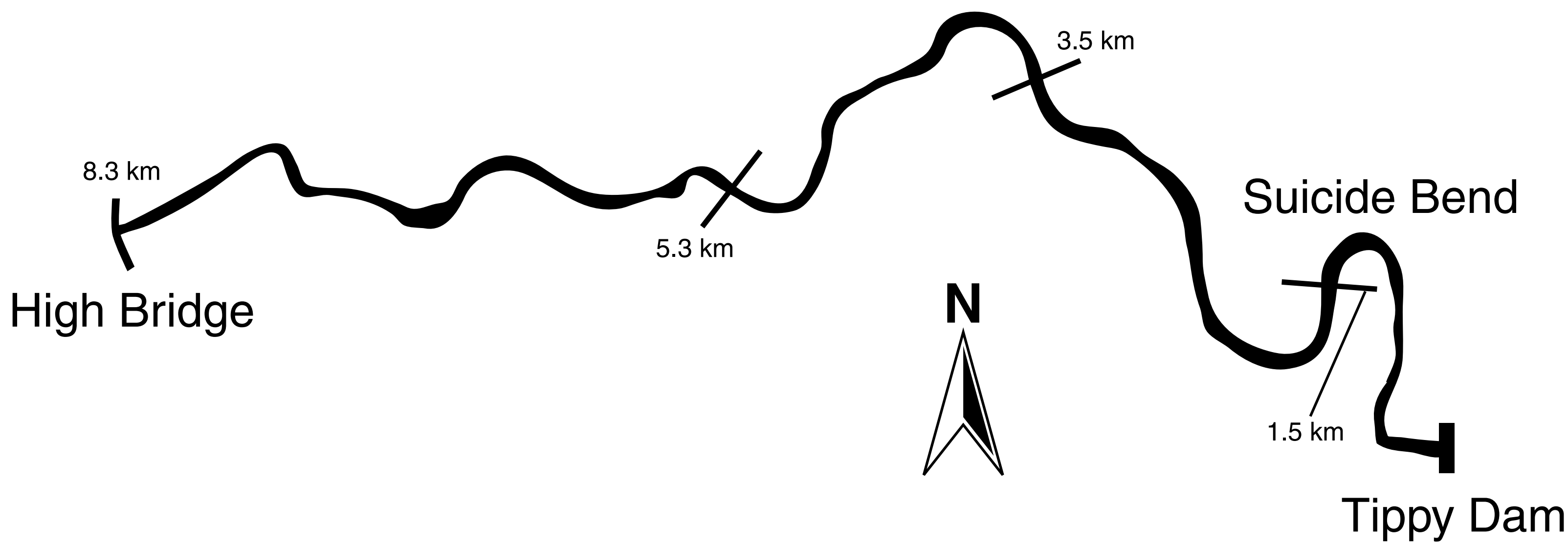

Figure 2.–Map of the Manistee River study site showing locations and lengths of the 4 study strata. The upstream limit of the study site was Tippy Dam and the downstream limit was High Bridge Road. Distances in the figure are cumulative distances measured from the base of Tippy Dam.

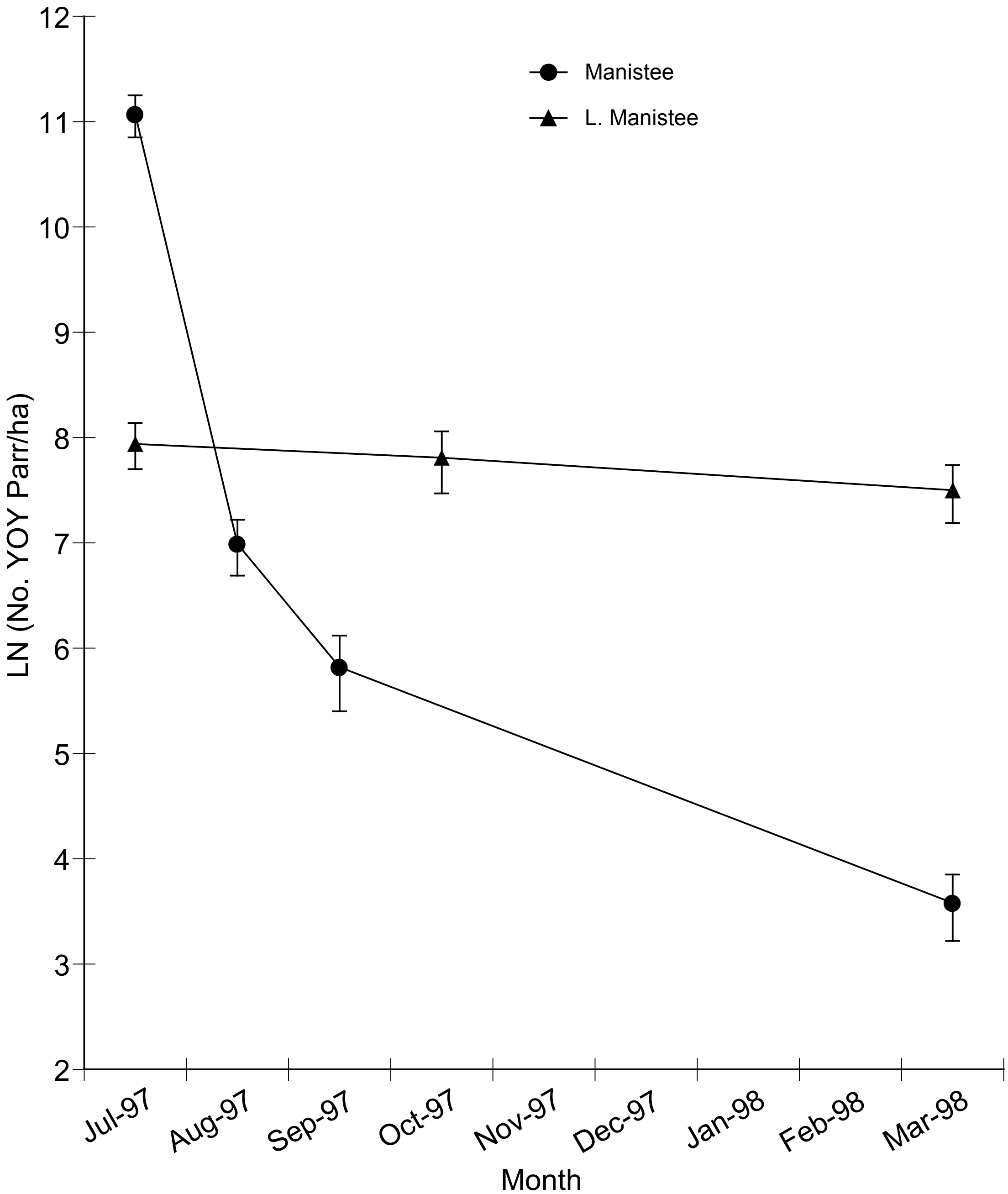

Figure 3.–Decline in young-of-the-year (YOY) steelhead $\log_e$-density over time in the Manistee and Little Manistee rivers. Error bars represent 95% confidence intervals around estimates.

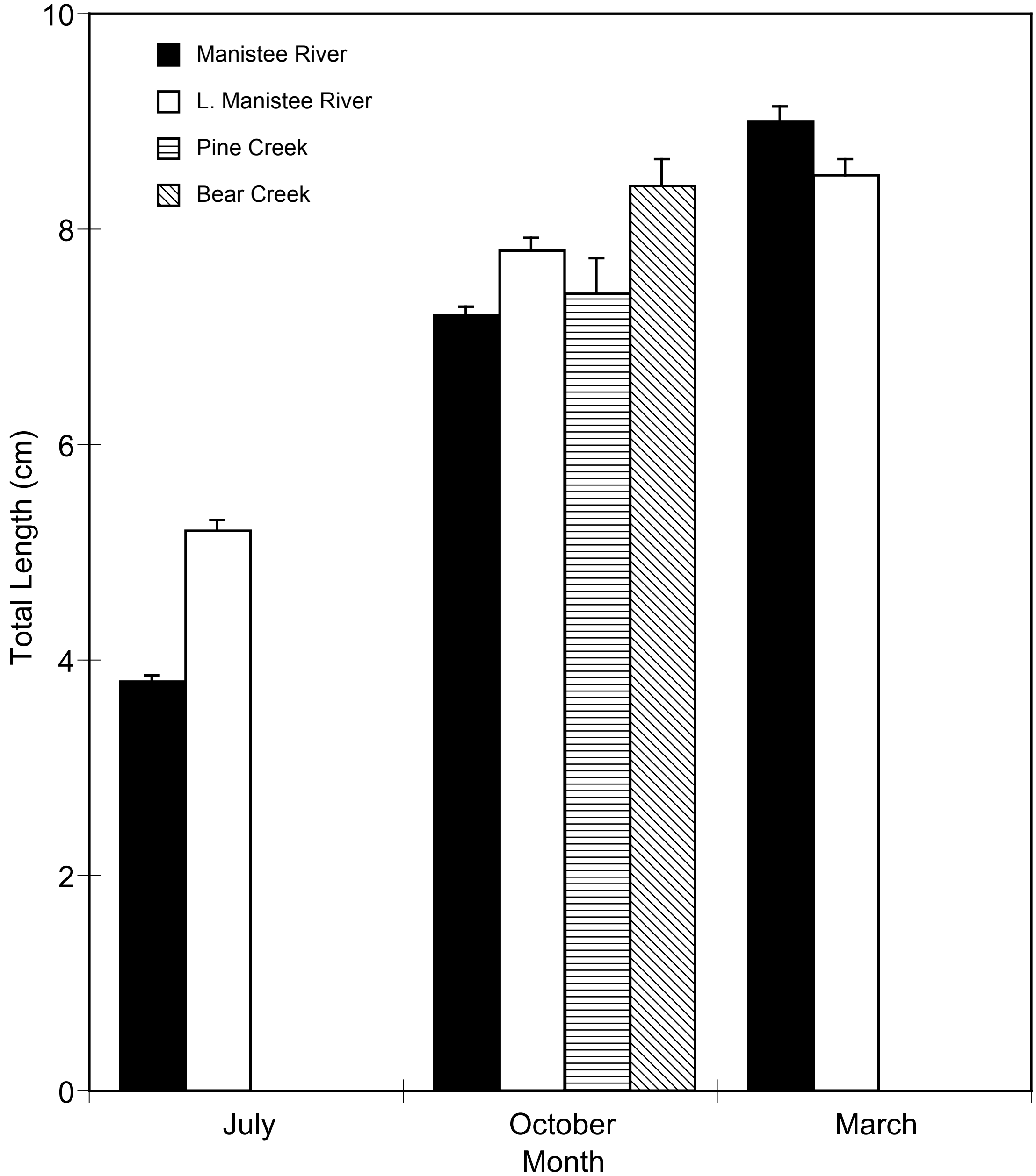

Figure 4.–Mean total length of young-of-the-year (YOY) steelhead from the Manistee River, Little Manistee River, Pine Creek, and Bear Creek in July and October 1997, and March 1998. Error bars represent 95% confidence intervals.

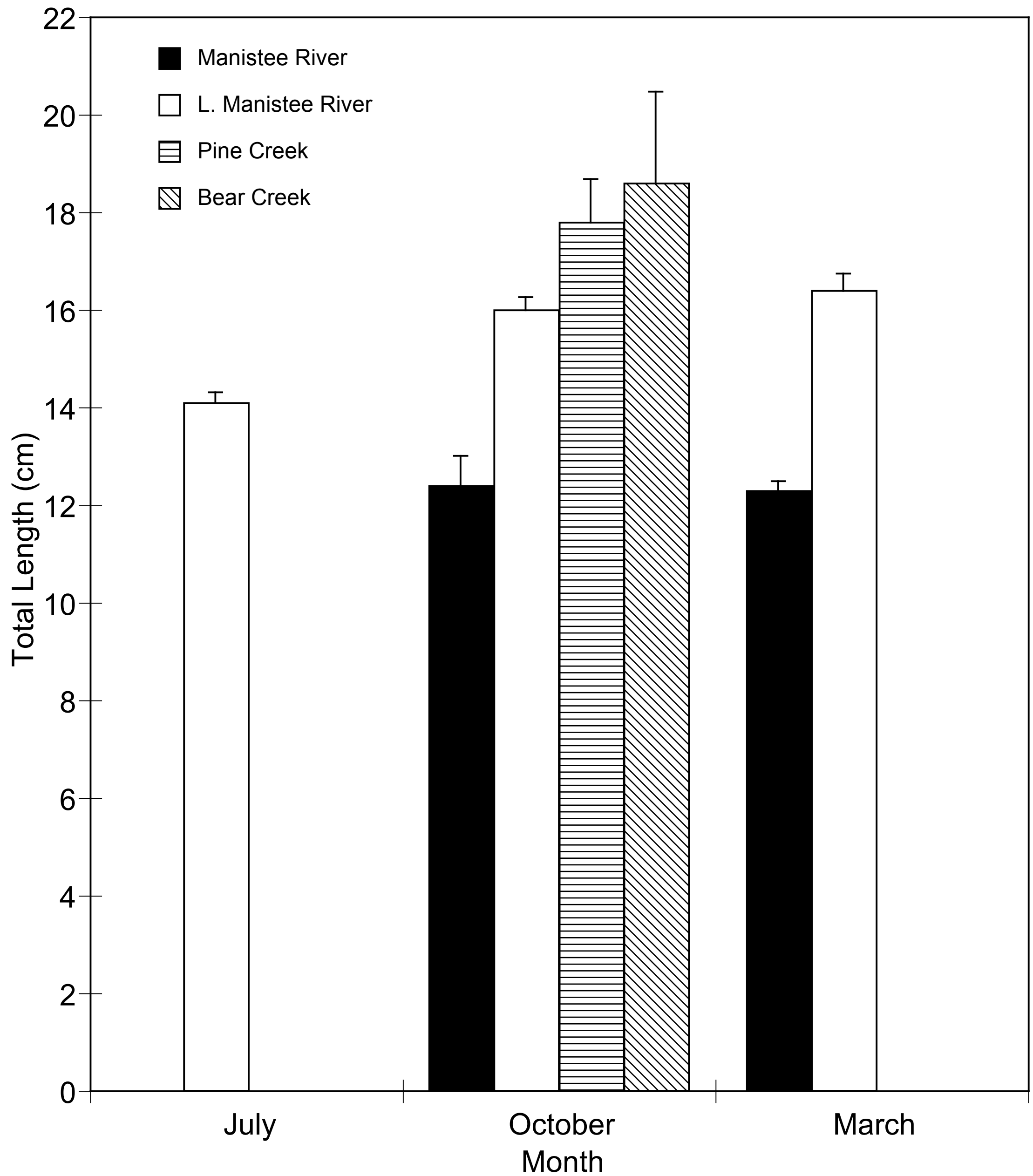

Figure 5.–Mean total length of age-1 steelhead from the Manistee River, Little Manistee River, Pine Creek, and Bear Creek in July and October 1997, and March 1998. Error bars represent 95% confidence intervals.

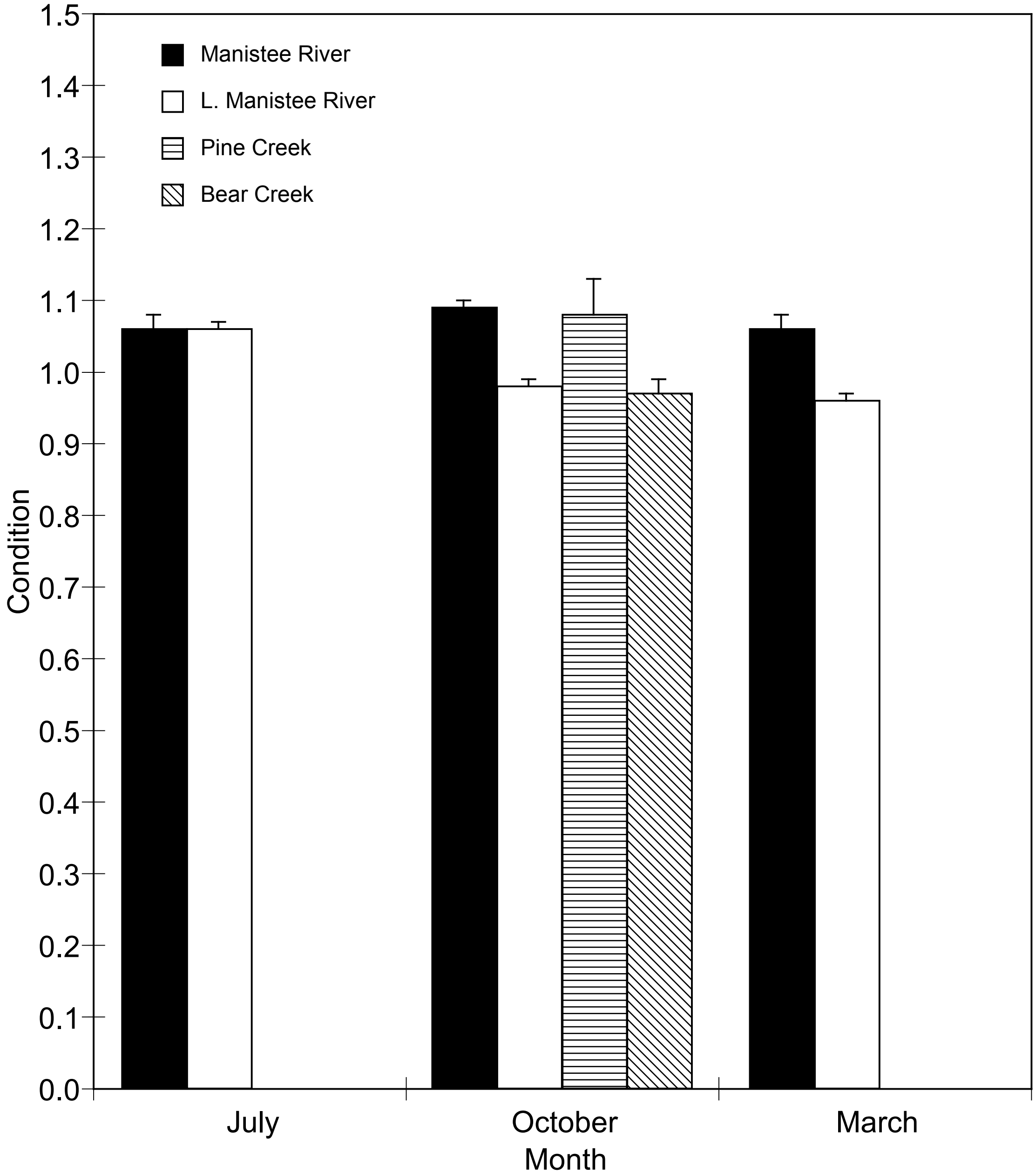

Figure 6.–Mean condition of young-of-the-year (YOY) steelhead from the Manistee River, Little Manistee River, Pine Creek, and Bear Creek in July and October 1997, and March 1998. Error bars represent 95% confidence intervals.

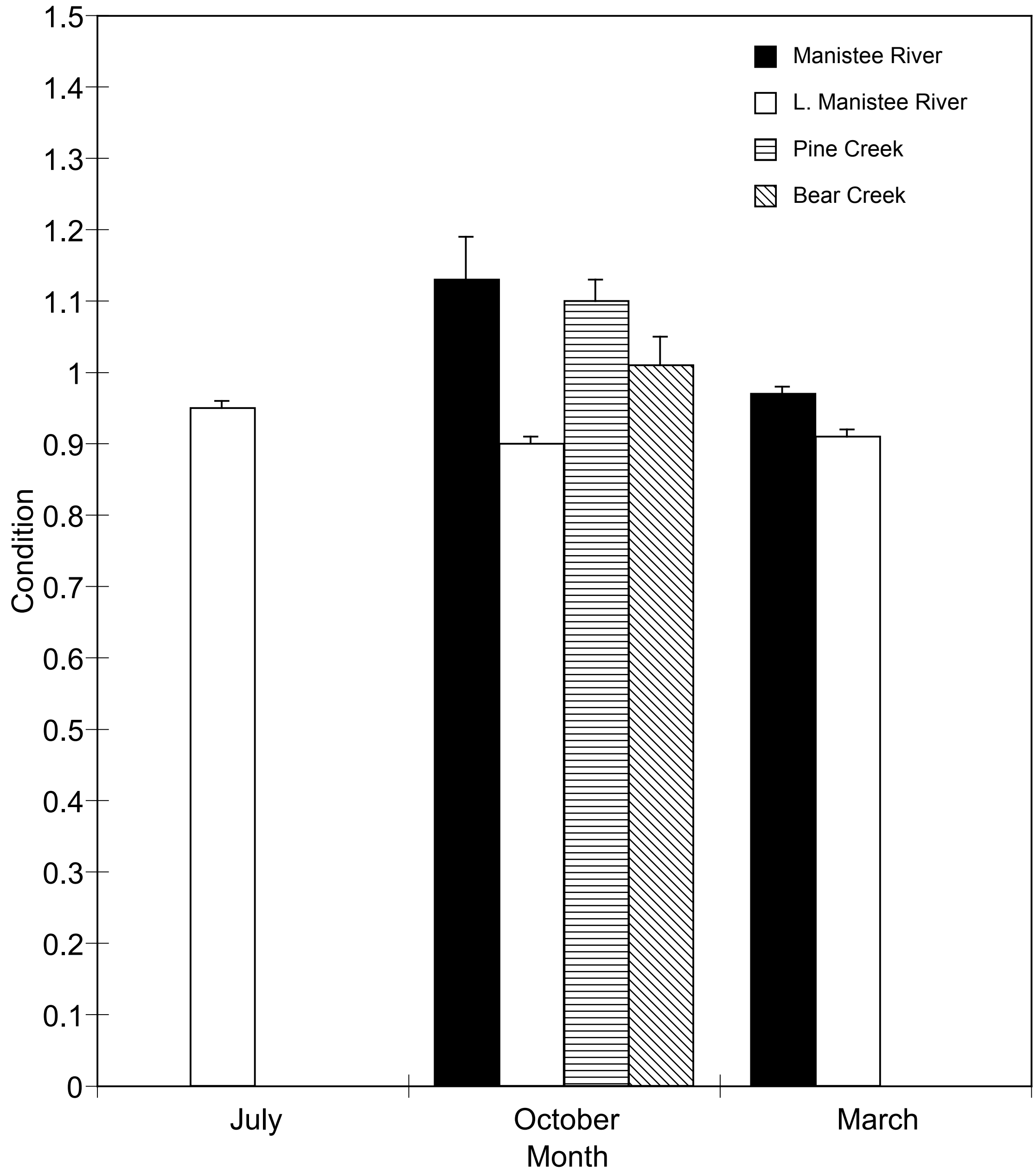

Figure 7.–Mean condition of age-1 steelhead from the Manistee River, Little Manistee River, Pine Creek, and Bear Creek in July and October 1997, and March 1998. Error bars represent 95% confidence intervals.

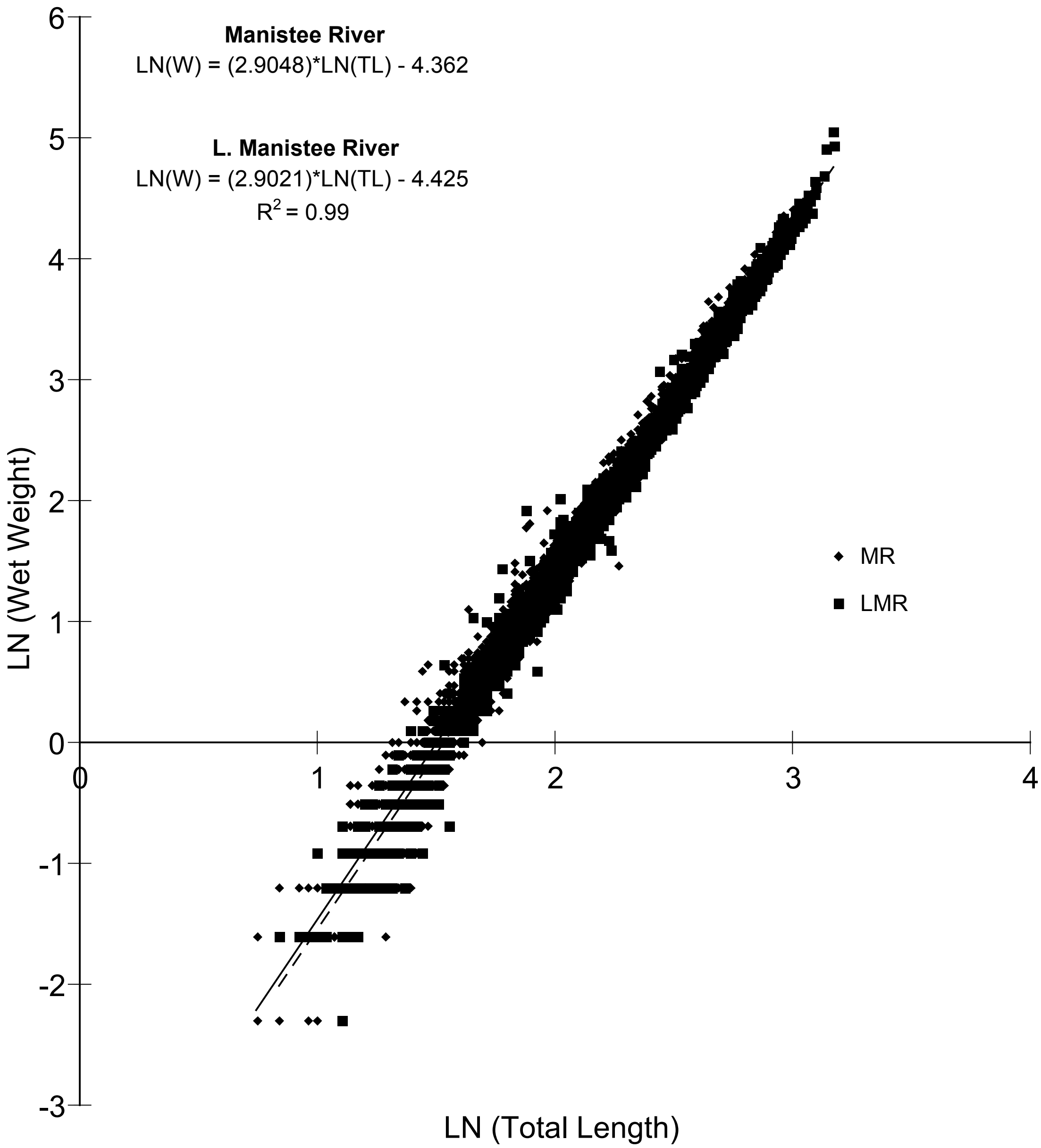

Figure 8.–Length-weight regression for steelhead parr in the Manistee (N = 4,342) and Little Manistee (N = 3,322) rivers, 1997-1998.

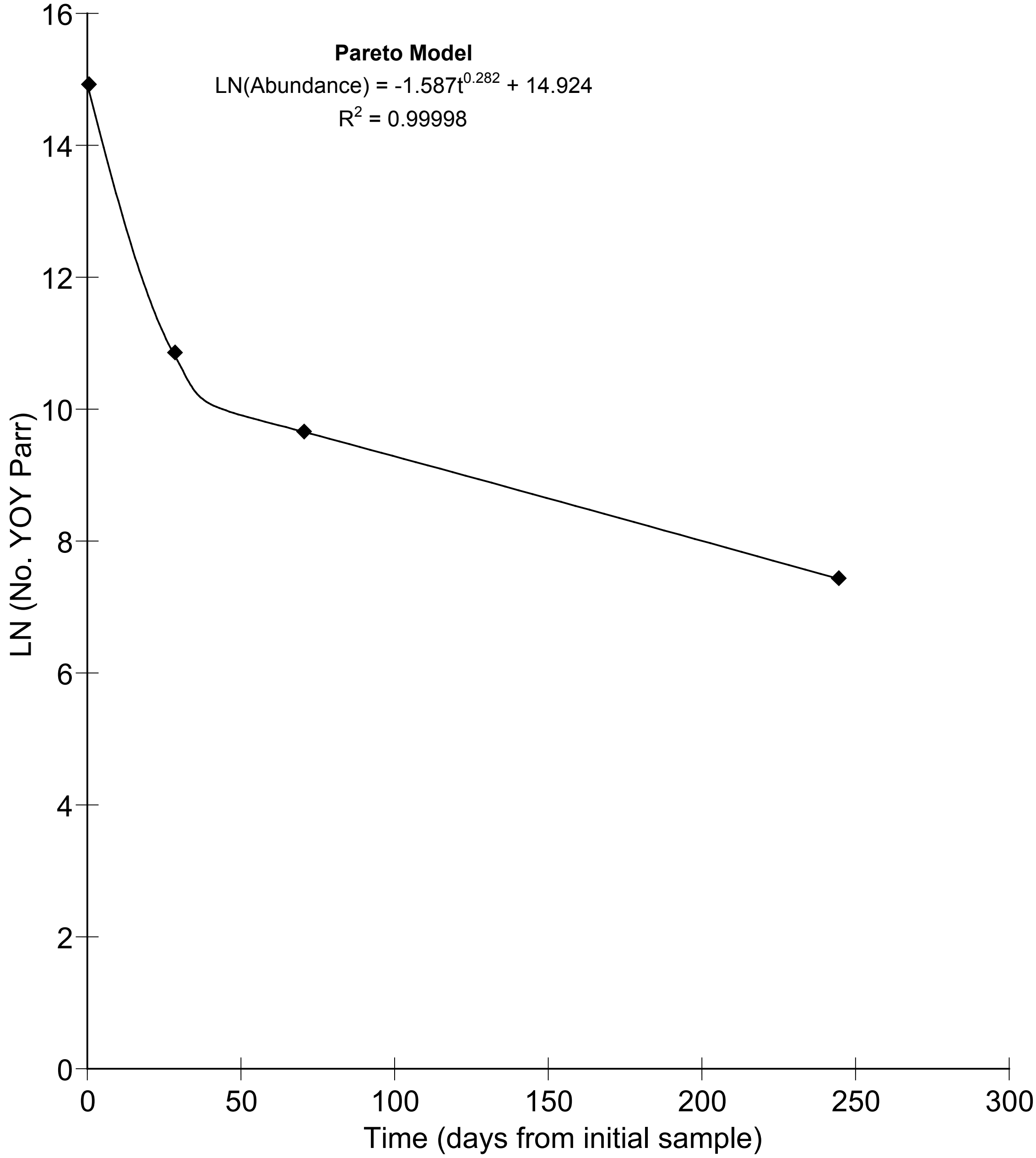

Figure 9.–Plot of young-of-the-year (YOY) steelhead $\log_e$-abundance over time in the Manistee River. Data points are fit with a Pareto Model that predicts LN abundance over time.

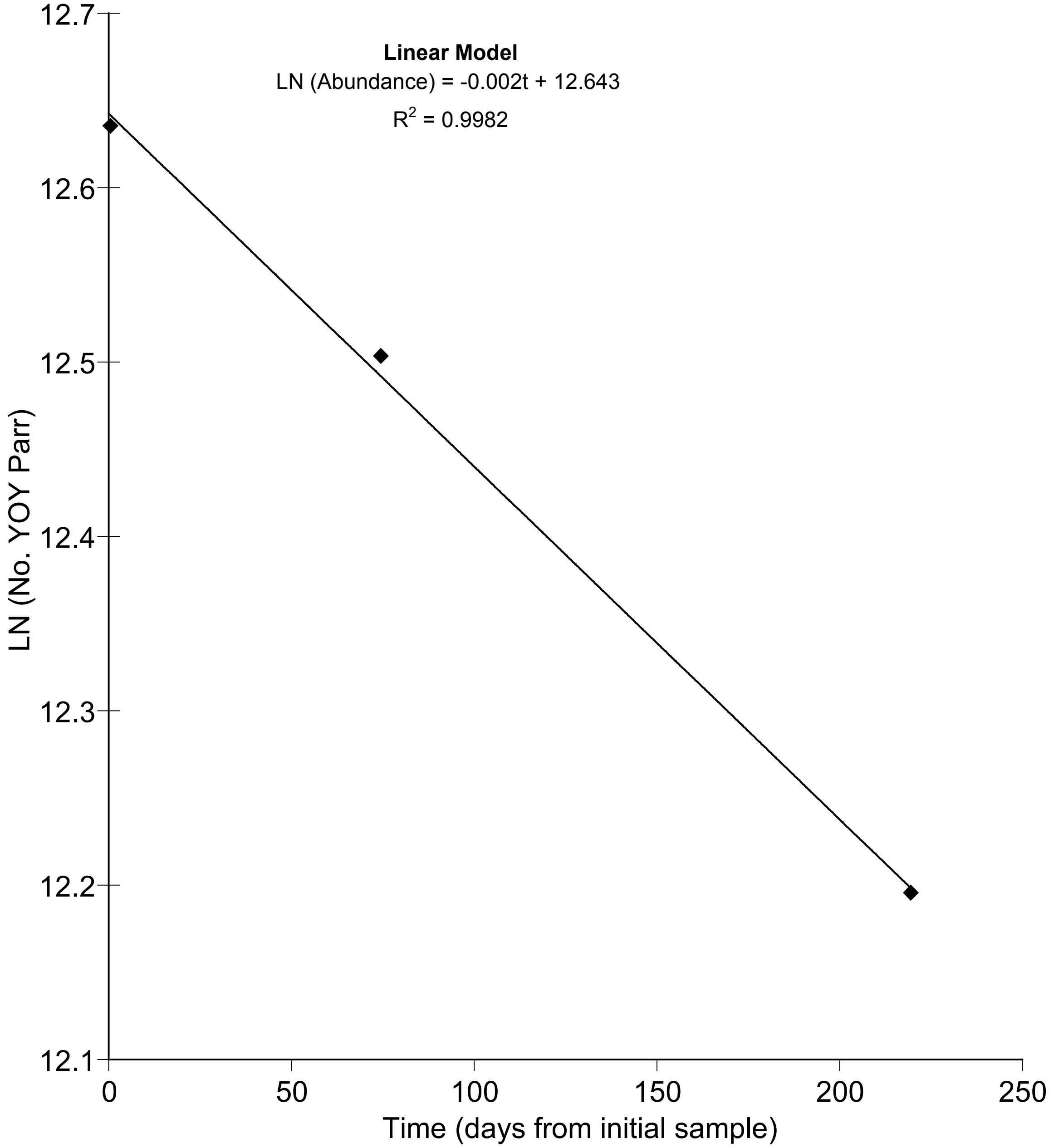

Figure 10.–Plot of young-of-the-year (YOY) steelhead $\log_e$-abundance over time in the Little Manistee River. Data points are fit with a linear least squares model that predicts LN abundance over time.

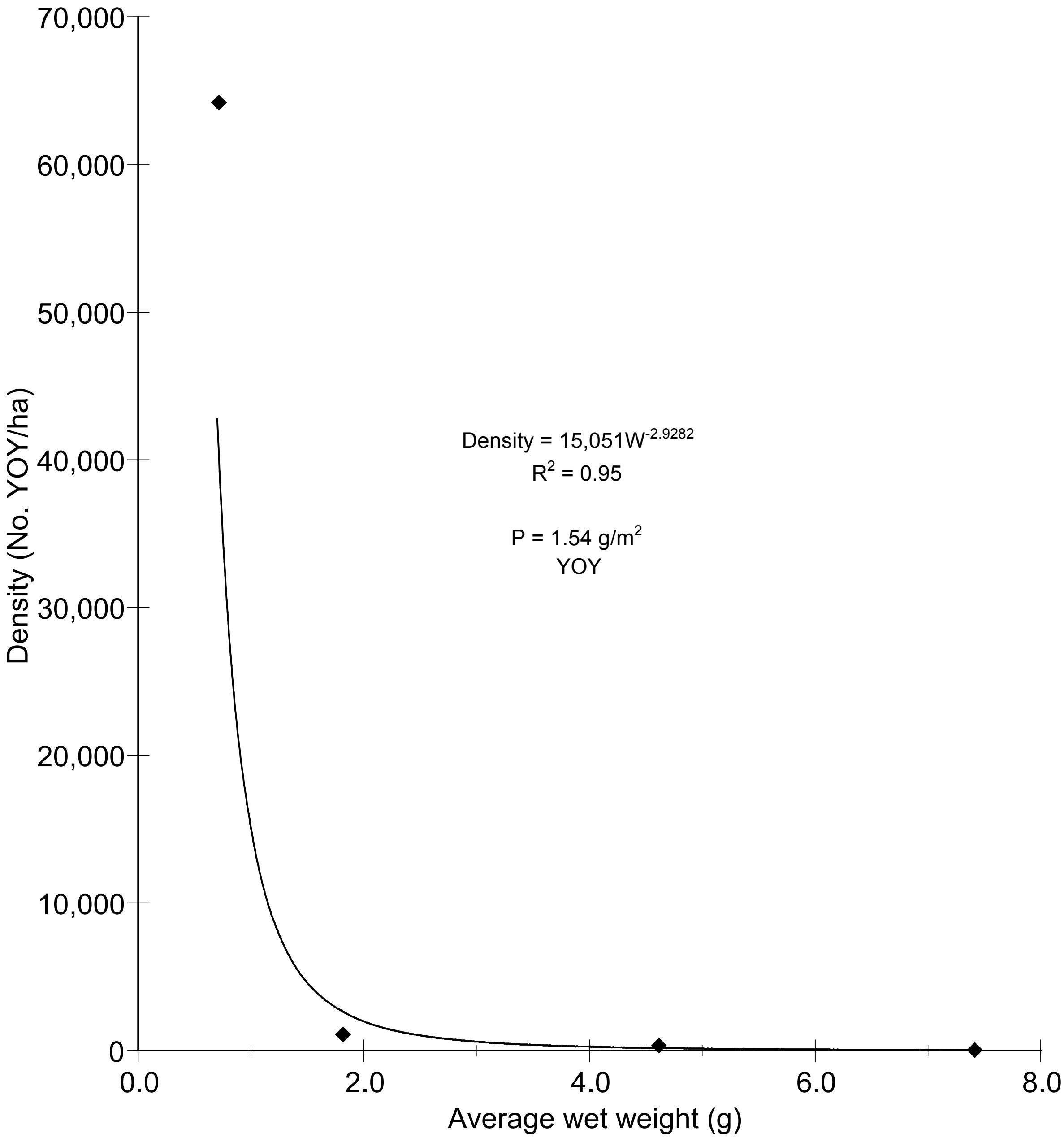

Figure 11.–Allen production curve for young-of-the-year (YOY) steelhead from the Manistee River, July 1997-March 1998. Area under the curve represents total YOY steelhead production (g/ha). Production values have been converted to g/m^2.

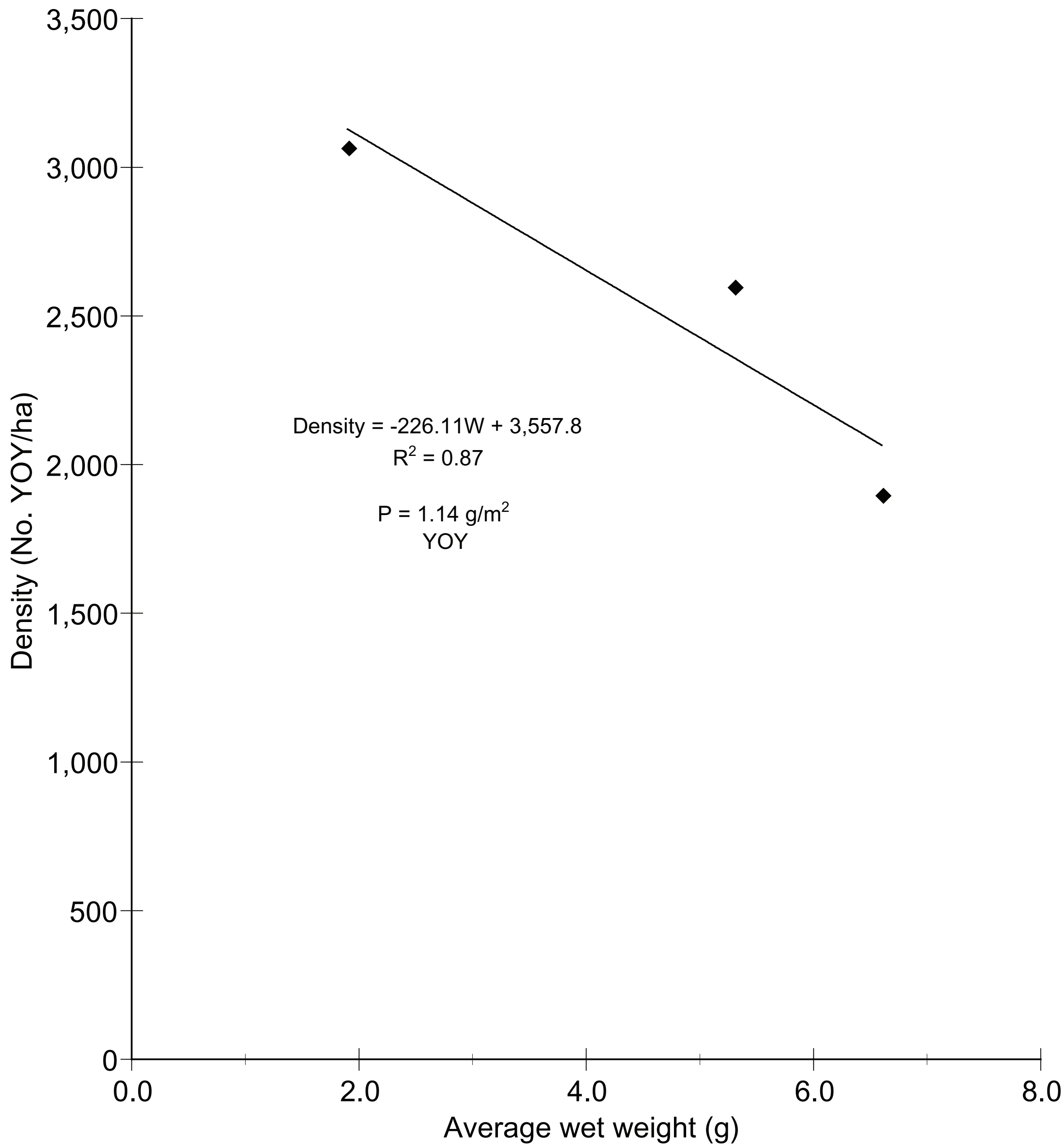

Figure 12.–Allen production curve for young-of-the-year (YOY) steelhead from the Little Manistee River, July 1997-March 1998. Area under the curve represents total YOY steelhead production (g/ha). Production values have been converted to g/m^2.

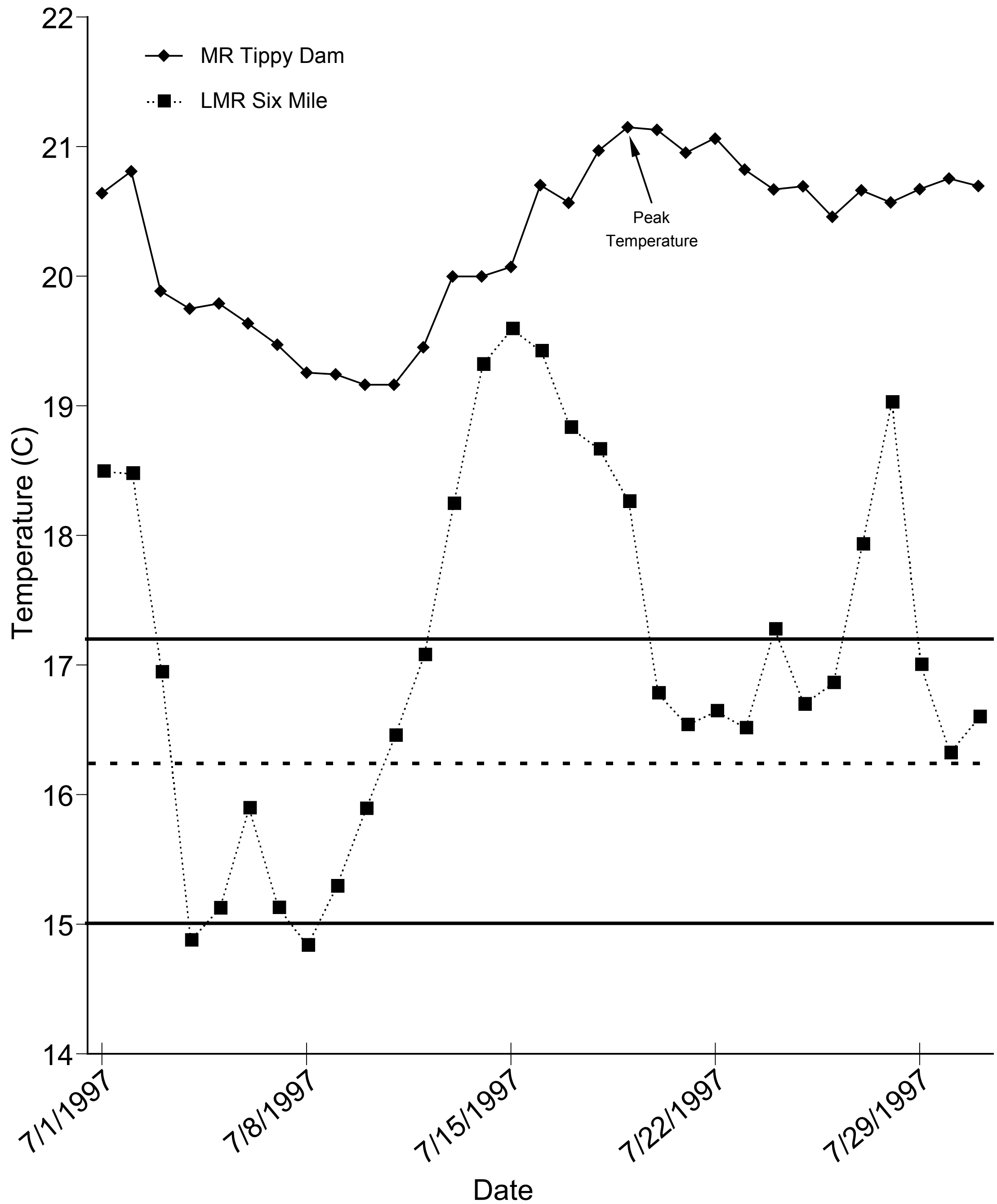

Figure 13.–Plot of daily mean temperature (°C) for July 1997 in the Manistee (MR, measured below Tippy Dam) and the Little Manistee rivers (LMR, measured at Six Mile Bridge). The area between the solid horizontal lines represents the optimal temperature range for steelhead growth (Hokanson et al. 1977). The dashed horizontal line represents the preferred body temperature of juvenile steelhead (McCauley and Huggins 1976). Mean river temperature peaked below Tippy on July 19th.

Table 1.–Summary of fish species collected in the Manistee River, Little Manistee River, Bear Creek, and Pine Creek in 1997-98 sampling (C = Common = species collected at >50% of sample sites, R = Rare = species collected at <10% of sample sites).

Species	Manistee River	Little Manistee River	Bear Creek	Pine Creek
Steelhead *Oncorhynchus mykiss*	C	C	C	C
Chinook salmon *Oncorhynchus tshawytscha*	C	C	C	C
Coho salmon *Oncorhynchus kisutch*	R	C	C	C
Brown trout *Salmo trutta*	R	C	C	C
Brook trout *Salvelinus fontinalis*	R		C	C
Sea lamprey *Petromyzon marinus*	C			
Lamprey spp. *Ichthyomyzon spp*.	C	C		R
Alewife *Alosa pseudoharengus*	R			
Common carp *Cyprinus carpio*	R			
Common shiner *Luxilus cornutus*	C			
River chub *Nocomis micropogon*			R	R
Golden shiner *Notemigonus crysoleucas*	C			
Spottail shiner *Notropis hudsonius*	C			
Emerald shiner *Notropis atherinoides*	C			
Bluntnose minnow *Pimephales promelas*	R			
Blacknose dace *Rhinichthys atratulus*		C	C	C
Longnose dace *Rhinichthys cataractae*	R		C	
Creek chub *Semotilus atromaculatus*	R	R	C	R
White sucker *Catastomous commersoni*	C	R	R	R
Shorthead redhorse *Moxostoma macrolepidotum*	C			
Redhorse spp. *Moxostoma spp.*	C			
Black bullhead *Ameiurus melas*				R
Yellow bullhead *Ameiurus natalis*		R		R
Northern pike *Esox lucius*	R			
Central mudminnow *Umbra limi*	R	R	R	R
Trout-perch *Percopsis omiscomaycus*	C			
Burbot *Lota lota*	C		R	R
Killifish *Fundulus spp*.	R			
Threespine stickleback *Gasterosteus aculeatus*	R	R	R	
Mottled sculpin *Cottus bairdi*	C	C	C	C
Rock bass *Ambloplites rupestris*	C			
Green sunfish *Lepomis cyanellus*	R		R	R
Pumpkinseed sunfish *Lepomis gibbosus*	R			R
Bluegill *Lepomis macrochirus*	R			
Smallmouth bass *Micropterus dolomieu*	C			
Largemouth bass *Micropterus salmoides*	R	R		
Black crappie *Pomoxis nigromaculatus*	R	R		
Johnny darter *Etheostoma nigrum*	C	R	R	
Blackside darter *Percina maculata*	C			R
Logperch *Percina caprodes*	C			
Yellow perch *Perca flavescens*	C	R		
Walleye *Stizostedion vitreum*	R			
Total Species	40	17	17	19

Table 2.–Estimated number of steelhead parr in the Manistee River and Little Manistee River study areas, 1997-1998. Confidence intervals (±95%) are included. Estimates are based on pass-depletion techniques.

Study area	Date	# YOY	# Age 1	# Age 2	# Age 3
Manistee	7/15/97	3,029,604 ± 589,803[1]	–	–	–
Manistee	8/12/97	108,795 ± 50,374[1]	–	–	–
Manistee	8/12/97	51,490 ± 13,389	–	–	–
Manistee	9/23/97	15,930 ± 5,545	59 ± 36	–	–
Manistee	3/16/98	–	1,692 ± 519	1,369 ± 492	2 ± 3
L. Manistee	7/26/97	307,259 ± 66,248	61,778 ± 16,272	586 ± 546	–
L. Manistee	10/8/97	269,290 ± 76,707	61,572 ± 29,576	99 ± 197	–
L. Manistee	3/2/98	–	197,935 ± 52,848	30,865 ± 13,297	187 ± 374

[1] Estimates are mark-recapture estimates.

Table 3.–Estimated densities of steelhead parr in the Manistee River and Little Manistee River study areas, 1997-1998, and average relative densities of steelhead parr in Pine and Bear creeks, 1997. Confidence intervals (±95%) are included. River estimates are based on pass-depletion techniques. All creek estimates are based on single pass, DC electrofishing.

Study area	Date	# YOY/ha	# Age 1/ha	# Age 2/ha	# Age 3/ha
Manistee	7/15/97	64,187 ± 12,496[1]	–	–	–
Manistee	8/12/97	2,305 ± 1,067[1]	–	–	–
Manistee	8/12/97	1,091 ± 284	–	–	–
Manistee	9/23/97	338 ± 117	1 ± 1	–	–
Manistee	3/16/98	–	36 ± 11	29 ± 10	1 ± 1
L. Manistee	7/26/97	2,819 ± 608	567 ± 149	5 ± 5	–
L. Manistee	10/8/97	2,471 ± 704	565 ± 271	1 ± 2	–
L. Manistee	3/2/98	–	1,816 ± 485	283 ± 122	2 ± 3
Pine Creek	8/26/97	1,667 ± 5,318	578 ± 1,776	11 ± 38	–
Pine Creek	10/25/97	1,344 ± 4,313	444 ± 1,482	–	–
Bear Creek	9/6/97	2,867 ± 3,587	167 ± 577	183 ± 635	–
Bear Creek	10/24/97	1,411 ± 1,405	133 ± 352	–	–

[1]Estimates are based on mark-recapture techniques.

Table 4.–Summary of absolute growth rates, relative growth rates, and instantaneous daily growth rates for young-of-the-year (YOY) steelhead in the Manistee River and for YOY and age-1 steelhead in the Little Manistee River, 1997-1998. Not enough age-1 and age-2 fish were captured in the Manistee River to generate growth estimates for these age classes, and not enough age-2 fish were captured in the Little Manistee River to generate growth estimates for this age class.

Study area	Cohort	Date	Absolute growth rate (g/d)	Relative growth rate ($g \cdot g^{-1} \cdot d^{-1}$)	Instantaneous daily growth rate
Manistee	YOY	7/15/97	–	–	–
Manistee	YOY	8/12/97	0.039	0.056	0.032
Manistee	YOY	9/23/97	0.067	0.037	0.024
Manistee	YOY	3/16/98	0.016	0.003	0.003
L. Manistee	YOY	7/26/97	–	–	–
L. Manistee	YOY	10/8/97	0.046	0.024	0.014
L. Manistee	YOY	3/2/98	0.009	0.002	0.002
L. Manistee	Age 1	7/26/97	–	–	–
L. Manistee	Age 1	10/8/97	0.153	0.005	0.005
L. Manistee	Age 1	3/2/98	0.017	0.0004	0.0004

Table 5.–Summary of average lengths, weights, conditions, and sample sizes for steelhead parr in Pine Creek and Bear Creek, 1997. Confidence intervals (±95%) are included.

Creek	Cohort	Date	Average L (cm)	Average W (g)	Average condition	N
Pine	YOY	8/26/97	5.2 ± 0.46	2.2 ± 0.60	1.22 ± 0.05	58
Pine	YOY	10/25/97	7.4 ± 0.33	5.0 ± 0.72	1.08 ± 0.05	92
Pine	Age 1	8/26/97	14.5 ± 0.62	30.3 ± 4.15	0.93 ± 0.02	52
Pine	Age 1	10/25/97	17.8 ± 0.89	66.3 ± 9.95	1.10 ± 0.03	40
Pine	Age 2	8/26/97	19.6	68.5	0.91	1
Pine	Age 2	10/25/97	–	–	–	0
Bear	YOY	9/6/97	6.7 ± 0.22	3.6 ± 0.35	1.08 ± 0.02	134
Bear	YOY	10/24/97	8.4 ± 0.25	6.3 ± 0.58	0.97 ± 0.02	126
Bear	Age 1	9/6/97	16.1 ± 0.44	40.4 ± 5.44	0.96 ± 0.09	10
Bear	Age 1	10/24/97	18.6 ± 1.88	71.1 ± 19.23	1.01 ± 0.04	12
Bear	Age 2	9/6/97	20.0 ± 0.42	71.7 ± 6.75	0.90 ± 0.04	11
Bear	Age 2	10/24/97	–	–	–	0

Table 6.–Summary of percent survival, instantaneous daily loss rates (Z), and percent of population lost per day for young-of-the-year (YOY) steelhead from the Manistee River and for YOY and age-1 steelhead from the Little Manistee River, 1997-1998. Not enough age-1 and age-2 fish were captured in the Manistee River to generate survival statistics for these age classes, and not enough age-2 fish were captured in the Little Manistee River to generate survival statistics for this age class.

Study area	Cohort	Date	% S	Z	% Population lost/day
Manistee	YOY	7/15/97	–	–	–
Manistee	YOY	8/12/97	1.7	0.146	13.543
Manistee	YOY	9/23/97	30.9	0.028	2.755
Manistee	YOY	3/16/98	10.6	0.013	1.280
L. Manistee	YOY	7/26/97	–	–	–
L. Manistee	YOY	10/8/97	87.6	0.002	0.178
L. Manistee	YOY	3/2/98	73.5	0.002	0.212
L. Manistee	YOY	7/26/97	–	–	–
L. Manistee	Age 1	10/8/97	99.7	0.00005	0.005
L. Manistee	Age 1	3/2/98	50.1	0.005	0.475

Table 7.–Summary of multiple linear regression (MLR) habitat models for the Manistee and Little Manistee rivers. Each model predicts young-of-the-year (YOY) steelhead abundance from habitat variables at the specified dates in 1997 and 1998. Note that predictive habitat variables vary between rivers and over time in an individual river. Asterisks denote $P < 0.05$*, $P < 0.01$**, or $P < 0.001$***.

	Independent variable			Model	
Date	Name	Coefficients	Adjusted R^2	P value	Adjusted R^2
		Manistee River			
August-97	Constant	-4,869.6*	–	P<0.01	0.22
	Temperature	275.6**	0.22		
September-97	Constant	137.7***	–	P<0.001	0.30
	% Boulder	14.8***	0.30		
March-98	Constant	-145.0*	–	P<0.001	0.60
	% Boulder	2.1***	0.54		
	Temperature	8.1*	0.06		
		Little Manistee River			
July-97	Constant	99.8*	–	P<0.05	0.37
	% Gravel	4.5*	0.37		
October-97	Constant	1,903.8*	–	P<0.05	0.42
	pH	-193.8*	0.27		
	Depth	-112.6*	0.15		
March-98	Constant	1,128.6*	–	P<0.01	0.56
	% Vegetation	5.0**	0.37		
	pH	-131.9*	0.19		

Table 8.–Summary of July 1997 mean daily temperatures, mean daily fluctuations, maximum temperatures, and accumulated degree days at sites in the Manistee River, Little Manistee River, and Bear Creek. Confidence intervals (±95%) are included for fluctuations. Pine Creek data are omitted due to recorder malfunction in July 1997. Manistee River sites are listed from the top of the watershed to the bottom. The Cameron Bridge and West Sharon Road sites are upstream of Tippy Dam. All other Manistee River sites are below Tippy Dam. Fluctuation = (daily maximum temperature – daily minimum temperature).

Site	Mean daily temperature (°C)	Mean daily fluctuation (°C)	Maximum temperature (°C)	Accumulated degree days
Manistee R. at Cameron Bridge	13.3	4.5 ± 2.6	18.7	413
Manistee R. at W. Sharon Road	17.9	3.6 ± 2.1	23.5	554
Manistee R. below Tippy Dam	20.3	0.8 ± 0.6	21.7	629
Manistee R. at High Bridge	21.0	2.3 ± 1.2	23.7	650
Manistee R. at River Road	21.2	3.0 ± 1.7	24.1	658
Manistee R. near river mouth	20.0	1.8 ± 1.3	22.9	620
L. Manistee R. at 6-Mile Bridge	17.0	3.5 ± 1.7	21.6	527
Bear Creek at Leffew Road	17.6	5.4 ± 3.0	24.3	544

Table 9.–Estimated fall densities of young-of-the-year (YOY) steelhead in other Great Lakes tributaries.

Water body	Density (# YOY/ha)	Author (year)
Betsie River, MI	835	Newcomb (1998)
Little Manistee River, MI	2,300	Seelbach (1986)
Pine Creek, MI	4,500	Carl (1983)
Black River, MI	6,900	Stauffer (1977)
Platte River, MI	1,500	Taube (1975)
Manistee River, MI	338 ± 117	This study
Little Manistee River, MI	2,471 ± 704	This study
Pine Creek	1,344 ± 4,313	This study
Bear Creek	1,411 ± 1,405	This study

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Appendix Table 1.–Summary of average lengths, weights, conditions, and sample sizes for steelhead parr from the Manistee River and Little Manistee River, 1997-1998. Confidence intervals (±95%) are included.

Study area	Cohort	Date	Average L (cm)	Average W (g)	Average condition	N
Manistee	YOY	7/15/97	3.8 ± 0.06	0.7 ± 0.04	1.06 ± 0.02	541
Manistee	YOY	8/12/97	5.1 ± 0.05	1.7 ± 0.07	1.14 ± 0.01	1706
Manistee	YOY	9/23/97	7.2 ± 0.08	4.6 ± 0.17	1.09 ± 0.01	1334
Manistee	YOY	3/16/98	9.0 ± 0.14	7.4 ± 0.36	1.06 ± 0.02	334
Manistee	Age 1	7/15/97	–	–	–	0
Manistee	Age 1	8/12/97	–	–	–	0
Manistee	Age 1	9/23/97	12.4 ± 0.62	22.4 ± 4.22	1.13 ± 0.06	17
Manistee	Age 1	3/16/98	12.3 ± 0.20	19.8 ± 1.17	0.97 ± 0.01	414
Manistee	Age 2	7/15/97	–	–	–	0
Manistee	Age 2	8/12/97	–	–	–	0
Manistee	Age 2	9/23/97	–	–	–	0
Manistee	Age 2	3/16/98	16.4	42.4	0.96	1
L. Manistee	YOY	7/26/97	5.2 ± 0.10	1.9 ± 0.13	1.06 ± 0.01	915
L. Manistee	YOY	10/8/97	7.8 ± 0.12	5.3 ± 0.24	0.98 ± 0.01	1036
L. Manistee	YOY	3/2/98	8.5 ± 0.15	6.6 ± 0.33	0.96 ± 0.01	596
L. Manistee	Age 1	7/26/97	14.1 ± 0.22	28.0 ± 1.35	0.95 ± 0.01	343
L. Manistee	Age 1	10/8/97	16.0 ± 0.27	39.3 ± 2.39	0.90 ± 0.01	293
L. Manistee	Age 1	3/2/98	16.4 ± 0.35	41.8 ± 2.67	0.91 ± 0.01	179
L. Manistee	Age 2	7/26/97	19.7 ± 0.96	71.9 ± 9.24	0.94 ± 0.04	4
L. Manistee	Age 2	10/8/97	17.9	46.4	0.81	1
L. Manistee	Age 2	3/2/98	20.6	79.9	0.91	1