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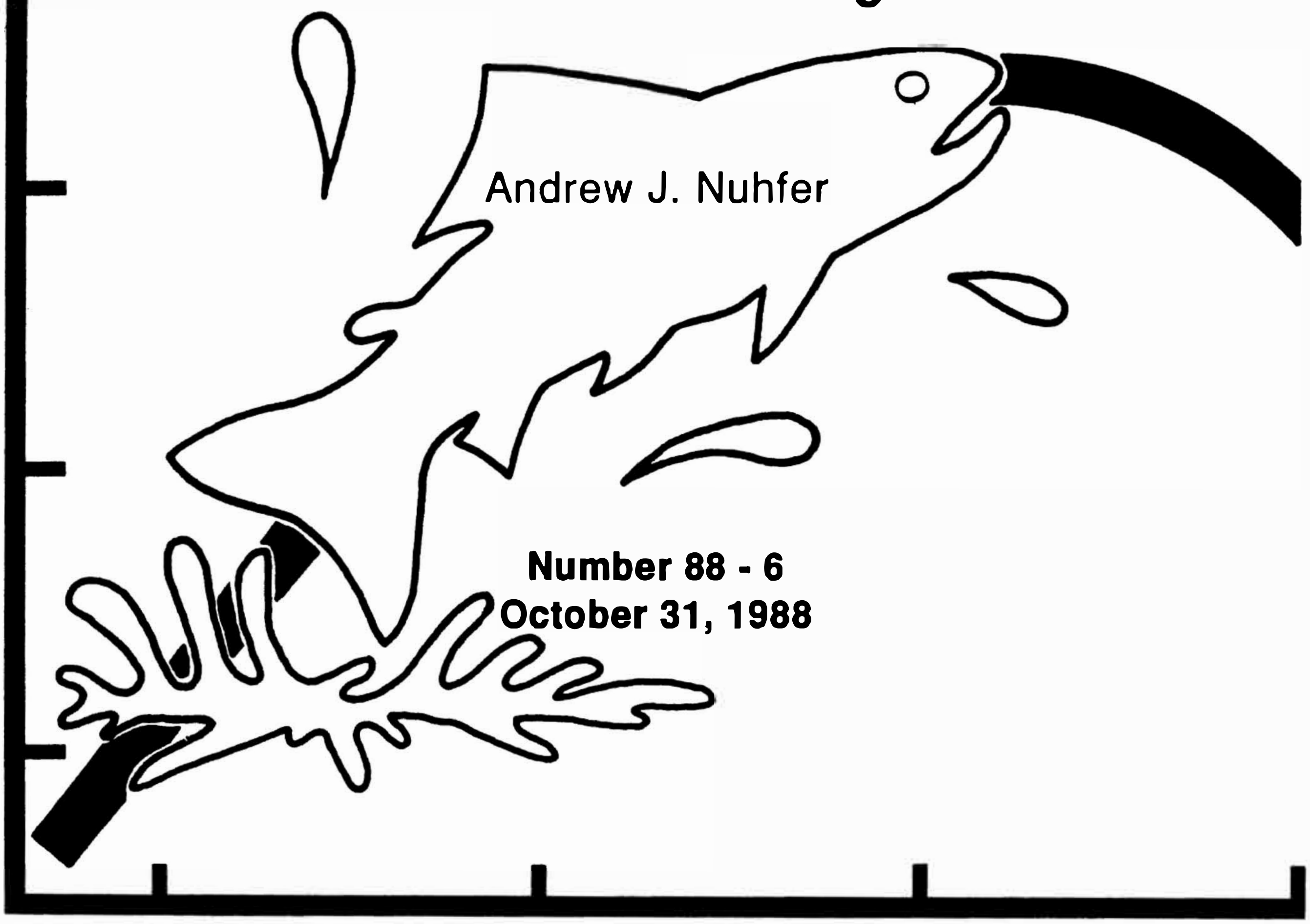

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MICHIGAN DEPARTMENT OF NATURAL RESOURCES
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A COMPARISON OF GROWTH OF BROWN TROUT FROM SELECTED WESTERN RIVERS WITH GROWTH OF BROWN TROUT FROM MICHIGAN RIVERS[1]

Andrew J. Nuhfer

[1]A contribution from Dingell-Johnson Project F-35-R, Michigan.

ABSTRACT

Growth of brown trout has declined in the Mainstream Au Sable River, Michigan, since the early 1970s. Many anglers of the Au Sable River have become interested in possible genetic improvement of the brown trout stock as a method for increasing the number of trophy-sized fish. Wild brown trout from streams in the western United States have been suggested as the source for "genetically fast-growing" brown trout. Data on age, growth, density, and other parameters were assembled and reviewed for an array of western "blue-ribbon" trout streams. A variety of western and Michigan stream segments were ranked based on the growth characteristics of their brown trout populations. Selection of wild riverine stocks for possible importation and testing in Michigan waters was based primarily on factors such as growth, potential disease threats, absence of recently stocked brown trout, and potential availability. A two-phased experimental design to compare the survival and growth potential of selected Montana strain brown trout and Mainstream Au Sable River brown trout in Michigan waters was developed and described. The feasibility of this proposed study will ultimately depend upon the cooperation of the State of Montana and the disease status of the wild brown trout stocks.

INTRODUCTION

The growth rates of brown trout in both the South and Main branches of the Au Sable River have declined from 1960s rates (Alexander et al. 1979; Merron 1982). The two major hypotheses advanced to explain the reduced growth rates are a decline in genetic growth potential (Favro et al. 1979; Favro et al. 1982) and a decline in river productivity which occurred after domestic sewage was diverted (Merron 1982). Alexander's study (1987) suggested that both environmental and genetic factors may have contributed to the growth decline.

Biologists and anglers have observed that some river populations of brown trout in the western United States exhibit fast growth. Some believe that the faster growth is due at least in part to genetics and it has been suggested that the growth rate of brown trout in the Au Sable and other Michigan rivers might be improved by introducing trout from these western rivers.

In this report I summarize available growth data from an array of rivers in the West which have fast-growing brown trout. I make quantitative comparisons of brown trout growth among both western and Michigan trout populations and explore the possibility that the differences found are genetic or environmental. I also outline an experimental design to test the growth potential of selected stocks of brown trout in Michigan waters.

BACKGROUND

Possible effect of selective harvest on genetic growth potential

Over the years anglers and fisheries managers alike have speculated that the selective harvest of larger fish could depress the growth potential of fish populations. According to this theory stocks exposed to selective mortality of large individuals lose genes which promote rapid growth since large fish tend to be the faster-growing individuals. In addition it has been hypothesized that faster-growing individuals are more aggressive feeders and hence more vulnerable to sportfishing mortality. Cooper (1952) found that faster-growing brook trout of a cohort in the Pigeon River, Michigan, were more heavily exploited. Wolfarth (1986) noted that the long-term genetic effect of negative selection depends on fishing intensity, phenotypic variation, and heritability of growth.

Favro et al. (1979) constructed a genetic model assigning growth rates to two unlinked loci with two alleles at each locus and used it to project hypothetical changes which could occur in Au Sable River brown trout populations due to selective angling removal of faster-growing individuals. They concluded that their genetic model was capable of reproducing the observed changes in the Au Sable River brown trout populations. Favro et al. (1982) next extended their modeling effort to include more active loci and again concluded that agreement between the calculated and observed population changes were consistent with their previous genetic hypothesis.

Alexander (1987) tested the growth potential of wild brown trout stocks from the Au Sable River and other populations with lower historical exploitation rates. He found that growth rates of the stocks were inversely related to the degree of exploitation. Although the results suggested angler exploitation may alter the genetic potential for growth of wild trout populations, he concluded the observed reduction in Au Sable River brown trout growth was mainly due to environmental factors related to reduced input of sewage effluents. The fact that the relative growth rank of these four wild stocks in their native streams was different than their growth rank when they grew together in the same research waters further illustrates that an interaction of environmental and genetic factors determined size at age (Alexander, personal communication, 1988, Michigan Department of Natural Resources, Lewiston). Genetic change induced by high exploitation of larger individuals is more likely to occur in species which are harvested before they have an opportunity to reproduce. Ricker (1981) cited genetic effects as the cause of declines in the size of coho and pink salmon in British Columbia which are subject to heavy commercial exploitation before they are sexually mature. Hanford et al. (1977) believed that a gill-net fishery for whitefish in Lesser Slave Lake, Alberta, which was highly selective of large, robust, fast-growing individuals, was capable of inducing an evolutionary response which would express itself as changes in patterns of growth and age in the stock. He concluded that the observed reductions in whitefish size and condition at age over time could have been caused primarily by selection. As a result of these and other studies many anglers of the Au Sable River became interested in possible genetic improvement of its brown trout stock. Many ascribe to the belief that genetic improvements and no-kill regulations could produce good populations of large brown trout such as those found in some blue-ribbon western trout streams.

It should be noted that in contrast to the theories of growth suppression due to genetic effects, heavily exploited fish populations frequently exhibit increased growth rates because of decreased fish densities. However, when exploitation ceases growth rates and other characteristics of these populations quickly revert to pre-exploitation levels (Miller 1957). Behnke (1987) observed that cutthroat trout in both Yellowstone Lake and Yellowstone River were exposed to perhaps the most intense level of exploitation of any major wild trout fishery in the country for many years, but there was no apparent hereditary change toward slower growth. He noted that there was no detectable difference in the average and maximum fish size in the present populations of cutthroat trout (now protected by special regulations) and those trout caught in "the old days" before high exploitation occurred.

Effects of environmental factors on growth

Because growth is strongly influenced by environmental factors such as food type and availability, water temperature, and fish density, differences or changes in growth rates in wild populations cannot readily be ascribed to genetic differences or changes. Dramatic examples of the growth plasticity of brown trout produced in Michigan hatcheries is evident from comparisons of their growth when they are stocked in different waters. Domestic brown trout stocked in Lake Huron near Alpena, Michigan, achieve an average size of 18.8 inches and 3.5 pounds during the summer at age 2 (Weber, personal communication, 1988, Michigan Department of Natural Resources, Alpena). Domestic brown trout stocked in sinkhole lakes in the Pigeon River State Forest were 12 inches long and weighed 0.6 pound in October at age 2 (Alexander 1987). Au Sable River brown trout which grew at the same rate as domestic brown trout in the Pigeon River lakes average 9.3 inches long in the Mainstream Au Sable River in October at age 2 (Alexander et al. 1979). In western blue-ribbon trout streams there is considerable variation in brown trout growth rates from stream to stream and between sections within the same river (Sosiak 1984; Oswald 1986a, 1986b; Vincent, personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Bozeman). Factors believed to account for the different apparent growth rates in these streams include fish density, inherent productivity, water temperature, and regulations.

One way to determine if some western strains of brown trout grow faster than Mainstream Au Sable River strain fish due to genetic factors is to stock equal numbers of both strains in the same Michigan waters. Comparisons of the growth and population structure of these stocks when they reside in different waters is only an indicator as both biotic and abiotic conditions affecting trout stocks in the respective states, or even within states, vary substantially.

Heritability

The fisheries literature contains abundant evidence that growth rate, survival, thermal tolerance, disease resistance, age at maturity, egg production, and other characteristics are heritable and alterable through selective breeding (Donaldson and Olson 1955; Donaldson and Olson 1957; Donaldson and Menasveta 1961; Aulstad et al. 1972; Ihssen 1973; Kincaid et al. 1977). Kinghorn (1983), who reviewed studies of quantitative genetics in fish breeding, believed that the scope for genetic improvement of fish compared favorably with that for domestic mammals and poultry. He noted that although the heritability of growth traits in fish species is generally lower than in other domestic animals, growth is more variable in fish species and selection intensities can be very high. Gjedrem (1983) reviewed 16 selection experiments and likewise concluded that the possibilities for genetic improvements in fish were good. It must be noted, however, that the projected improvements discussed by the above authors pertain to captive stocks whose breeding options can be controlled, whereas little control can be exercised over wild stocks.

METHODS

Data collection

Data on growth rates of brown trout in western streams were obtained by contacting university fisheries experts as well as state agency biologists in Montana, Colorado, Wyoming, Idaho, and Alberta, Canada. I indicated that we were specifically interested in wild, fast-growing, stream-dwelling brown trout populations. Thus the growth and sizes at age of brown trout from western streams discussed in this report represent those in the best streams rather than those in average western streams. Growth data from the Michigan rivers discussed in this report represent more of an average for trout streams located in the northern Lower Peninsula of Michigan. These were selected based on availability.

Since some investigators reported back-calculated lengths at annulus formation, while others reported average lengths at age for spring or fall brown trout collections, it was necessary to standardize the data before making comparisons between populations. Data sets showing average total lengths at age during spring or fall collections were standardized by first plotting the average length of brown trout at each age for each river section and month when the collections were made. Adjacent points were connected and linear projections of total fish length during the previous January were read from the graphs constructed for each population. It is recognized that seasonal trout growth is not linear, annuli frequently form in months other than January, and fishing mortality can result in "apparent" differences in growth where none exist. However, since all data sets were plotted in the same manner and since most collections were made during autumn months, the standardization procedure facilitated ranking of otherwise incomparable size-at-age data. Those brown trout data reported as back-calculated lengths at annulus formation were compared directly to the projected lengths in January (approximate time of annulus formation). Since trout grow little, if at all, during winter months the projected lengths at the beginning of each year should be essentially the same as the back-calculated lengths at annulus formation.

Ranking criteria

Brown trout growth data by age were tabulated and arranged in descending order based on the following criteria: (1) total length at age 2; (2) total length at age 3; (3) total length at age 4; (4) incremental total length increase from age 2 to age 3; and (5) incremental total length increase from age 3 to age 4. The stream sections from each of these five tables were ranked from 1 to 36 for each of the five criteria. The rank scores were summed to obtain a final value which incorporated all five criteria. Ranks for incremental total length increase were multiplied by 1.5 to allow calculation of a cumulative score which was 50% dependent upon length at age and 50% dependent on annual growth increments. This strategy was adopted to prevent undue weighting of total length at age which can be strongly influenced by environmental selection favoring larger fish at young ages. A final rank score for each river section was then obtained by dividing the sum of the rank scores for each growth measurement criterion by six.

After completing the above exercise, criteria such as trout density, sewage effluents, past and present stocking practices, disease problems, species composition in the rivers, and other factors were considered before arriving at final recommendations. Unfortunately, differences in river size, morphology, discharge, and temperature regimes; regulations; species complexes; and a host of other factors which can dramatically affect trout growth make it difficult to develop truly objective selection criteria. Moreover, for most rivers good measures of productivity are lacking. Thus, only obvious outlier values for such factors as density could be used to eliminate some rivers from consideration. Western rivers which have been stocked recently with hatchery brown trout were eliminated from consideration since it would not be possible to identify wild and domestic parents in these rivers. Finally, it was decided that if fertilized eggs can be obtained from more than one population it would be desirable to select populations that are separated by migration barriers.

RESULTS AND DISCUSSION

Total brown trout lengths at annulus formation for selected Michigan and western trout stream segments are presented in Table 1. The rivers are sorted such that the river segment listed first has the largest age-2 brown trout while the river listed last has the smallest. Similarly, rivers are listed in descending order in Tables 2 and 3 based on brown trout total lengths at age 3 and at age 4, respectively. In Table 4, the growth increments between ages 2 and 3 for the same river segments are listed in descending order and Table 5 is similarly arranged to show growth increments between ages 3 and 4.

A final list of the 36 stream segments with cumulative rank scores derived from Tables 1-5 is shown in Table 6. The top 10 stream segments listed in descending order are: Beaverhead River—Hildreth, Beaverhead River—Henneberry, Beaverhead River—Pipe Organ, Bow River, Bighorn River—below Yellowtail Afterbay Dam, South Fork Snake River, Madison River—Varney (1967), Au Sable River-South Branch (1960–61+73), Missouri River—Craig, and South Fork Madison River.

Some of the streams changed rank with time. Both the South Branch Au Sable River and the Varney section of the Madison River ranked lower based on their more recent growth characteristics. The Mainstream Au Sable River's growth during the early 1960s ranked 17, whereas, it ranked 30 for the 1974–76 time period (Table 6). Although the cumulative growth rank rating for the North and South Branches of the Au Sable River also declined over the same time period the change in rank for these river segments was only about half the magnitude of the Mainstream Au Sable River rank decline (Table 6).

Interpretation of the meaning of the differences in growth observed for the 36 stream sections examined is difficult due to the diverse character of the rivers involved. The three sections of the Beaverhead River in Montana (Hildreth, Henneberry, and Pipe Organ) were consistently ranked high regardless of the growth criterion applied. This large tailwater fishery located downstream from Clark Canyon Reservoir is nutrient rich and has near optimal thermal conditions for trout growth (Oswald 1986b). Spring population estimates for age-2 and older brown trout average nearly 1,500 fish per mile in the three sections. Age-4 and older brown trout comprise 15% of this total.

The next highest ranked river (Table 6) was the Bow River in Alberta, Canada which is another large nutrient-rich river that receives sewage effluent from the City of Calgary. Growth of brown trout in the Bow River is strongly influenced by the numerous reservoirs in the drainage (Kraft, personal communication, 1988, Alberta Forestry, Lands and Wildlife Department, Alberta, Canada). Rainbow trout are the most numerous salmonid species in the river. Fall density of age-2 and older brown trout is about 225 trout per mile (Sosiak 1984) with age-4 and older trout making up 17% of this total.

The Bighorn River downstream from the Yellowtail Afterbay Dam in Montana is another large productive stream with excellent thermal characteristics for trout production. Brown trout are the primary salmonid species in the sections downstream from the dam, with over 4,900 age-2 and older brown trout per mile estimated during the spring of 1985. Age-4 and older fish contributed 20% to this total (Fredenberg 1986).

The next highest ranked river was the South Fork of the Snake River in Idaho downstream from Palisades Reservoir. Age-2 and older cutthroat trout are 4.6 times as abundant as brown trout which number around 250 per mile in the fall (Moore and Schill 1984). Unfortunately, for purposes of this analysis the investigators found it difficult to accurately determine the age of fish of age-2 and older as many scales showed evidence of adsorption and re-growth with checks. The analysis was further complicated by immigration of fish from Palisades Reservoir during a spring 1982 drawdown. In addition, hatchery brown trout fry are stocked in both the South Fork Snake River and the tributary Rainey Creek.

The next best brown trout growth characteristics were found in the Varney section of the Madison River, Montana in 1967 (Table 6). However, growth characteristics of this population from 1981 rank 21 among the 36 stream segments listed in Table 6. Vincent (personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Bozeman) observed a significant negative correlation between brown trout growth and density in the Varney section of the Madison. Similarly, the brown trout growth characteristics in the South Branch Au Sable River, Michigan, prior to 1974 ranked 8 while for the 1974–77 period it ranked 14 out of 36 (Table 6). Merron (1982) believed that reduced food supplies following removal of sewage effluents in 1974 was the most plausible explanation for the abrupt reduction in brown trout growth.

The Craig section of the Missouri River which ranked 9 is a large river regulated by Holter Dam. Normal discharge is around 4,000 cfs with peak runoff flows near 20,000 cfs in some years. Temperature regimes are good for trout growth, insects are abundant, and this river section has about 6,000 "bite-sized" mountain whitefish per mile along with numerous sculpins. Rainbow trout are 10 times more abundant than brown trout, which number 300–400 per mile in this river section (Leathe, personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Billings).

Brown trout from the South Fork Madison River, which ranked 10, presently exhibit better growth than brown trout in the other sections of the Madison River drainage listed in Table 6. Vincent (personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Bozeman) believed that lower trout density in this stream segment might account for the faster growth. He stated further that scale characteristics suggest that a portion of the fish may be part-time residents of Hebgen Reservoir. The South Fork Madison River was colder and more sterile (less conductive) than the Snowball, Varney, and Norris sections of the Madison River, the East Gallatin River, the West Fork Madison River, and the Gallatin River (Vincent, personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Bozeman).

The Maiden Rock and Melrose sections of the Big Hole River in Montana ranked 11 and 13, respectively. The differences in population structure between these sections may be attributed to differences in regulations (Oswald 1986a). Age-2 and older brown trout number 1,000 and 850 per mile in the spring in the Melrose and Maiden Rock sections, respectively (Oswald 1986a). Although these two sections are adjacent to each other, on an annual basis brown trout comprise 70% of the estimated number and 75% of the biomass of trout in the Melrose section and only 43% of the estimated number but 62% of the biomass of trout in the Maiden Rock section.

RECOMMENDATIONS

The above discussion illustrates some of the diversity among the trout populations of a cross section of "blue-ribbon" western trout streams with the fastest-growing brown trout. It is clearly not possible to determine the relative effects of genetic growth potential and environmental factors on the size and growth rates of these brown trout populations by simply examining their performance in different streams. Therefore, I will briefly discuss my rationale for eliminating some streams from immediate consideration as sources of brown trout to test in Michigan waters.

The Bow River in Alberta, Canada should be removed from consideration because of the documented enhancement of growth by sewage effluents and reservoir effects. Moreover, it is difficult to import fish from another country due to complicated "disease-free" certification requirements.

The South Fork Snake River should be eliminated as its population is augmented with hatchery fish which could not be readily identified in collections. In addition size-at-age data were believed to be unreliable. Moreover, Michigan does not currently import fish from waters west of the continental divide due to the possibility that these stocks may be infected with infectious hematopoietic necrosis disease which is not known to occur in Michigan.

The Craig section of the Missouri River ranks high based on growth characteristics. However, the brown trout population is relatively small in this stream segment averaging about 300–400 fish per mile (Leathe, personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Billings). Ryman and Stahl (1980) recommended that a minimum random sample of 30 parents of each sex should be used when founding or transplanting a stock to minimize the probability that alleles which may be important in the new environment are not lost. Leathe (personal communication, 1988, Montana Department of Fish, Wildlife, and Parks, Billings) believes that brown trout abundance in this river section is probably limited by low recruitment and overharvest. Since it may be necessary to sacrifice and dissect the parents as part of the disease status certification process it would probably be considered undesirable to remove so many adults. Current requirements for importation of fish or eggs into Michigan which do not have a documented disease status history include the sacrifice and examination of internal tissues from 60 fish for 2 consecutive years. These fish may be of any age or sex. In addition ovarian fluid must be collected and examined from up to 150 ripe females for 2 years. Such collections could be difficult where populations are not abundant.

Because of the length of time required to properly test the growth potential of new strains it would be desirable to import western strains of brown trout from more than one western drainage as this will increase the chances of picking the "best one". Brown trout from the Beaverhead River would appear to be one good choice. The Big Hole River would probably be an equally good source of brown trout. The growth rank of Big Hole River brown trout in both the Maiden Rock and Melrose sections is quite high. The genetic characteristics of these fish may be similar to Beaverhead River brown trout since the Big Hole and Beaverhead rivers join to form the Jefferson River and breeding populations in the two rivers are not separated by physical barriers.

Brown trout from the Bighorn River below Yellowtail Afterbay Dam are another promising choice to test in Michigan waters. However, if two stocks of Montana strain trout are obtainable, I believe that no more than one should come from river segments immediately downstream from large reservoirs. It would be desirable to pick at least one stock from a stream less obviously affected by a reservoir. In this regard, I believe that brown trout from the South Fork Madison River could be the best choice. The Madison River drainage is highly regarded by many Michigan anglers. Since the sports anglers of Michigan provided much of the impetus for this study proposal, I believe it is appropriate to strongly consider their view of which fish should be tested.

The ultimate choice of brown trout strains will depend upon the cooperation of the State of Montana and logistical constraints such as disease status.

EXPERIMENTAL DESIGN

I propose a two-phase design to test the genetic growth potential of selected Montana strain brown trout in Michigan waters. Performance of the second phase of the study would be contingent upon the results of the first phase tests.

Phase One

Determine disease status.—The disease status of both Montana donor stocks and Mainstream Au Sable River fish must be determined before they can be brought into Michigan's hatchery system.

Obtain fish.—During fall 1990, obtain approximately 130,000 fertilized brown trout eggs from each of two different strains of wild Montana brown trout and from Mainstream Au Sable River strain brown trout. Assuming normal hatching success this would be a sufficient number to provide 100,000 fish of each strain.

Rear and stock.—Rear each strain in a separate raceway under the most identical conditions possible to spring or fall fingerling size depending upon the experimental stocking site. After giving each strain a distinctive fin clip, stock equal numbers of each strain of brown trout into four research lakes which are closed to fishing. A portion of the remaining fall fingerlings should be reared to yearling size for use in a test of growth potential in streams. The remaining fall fingerlings could be used for routine stocking of various state trout waters or they could be reared to yearling size depending upon management program needs.

A test of the performance of the different strains in a riverine environment similar to the Au Sable River would be highly desirable. A first priority stream for yearling fish should be the Manistee River which is presently stocked annually with domestic strain brown trout. Equal numbers of each strain should be stocked at each stocking site.

Evaluation.—At the end of three growing seasons (1993) survival and growth of brown trout stocked into lakes closed to fishing should be determined. Survival and growth in the Manistee River should be evaluated annually via a volunteer angler log system and by annual fall mark-and-recapture population estimates at a minimum of three stations.

Phase Two

If the results of the first phase of this study indicate that the Montana strains have characteristics which would be beneficial to Michigan stocks, the second phase of the study would involve testing of the performance of crosses of Montana and Michigan strains. This phase will give a measure of the expected growth and survival of first generation fish which would be produced if Montana strain fish were stocked into streams with resident brown trout populations. While there are many possible combinations of crosses, at a minimum it would be desirable to test the survival and growth performance of Montana x Mainstream Au Sable strain crosses. Each test of hybrid performance should include stocking of matched numbers of pure parental strain fish with the hybrid at each Michigan site which can be evaluated. Comparisons of the performance of hybrid strains to the parental strain performance in phase one of this study could lead to erroneous conclusions due to temporal variability of environmental conditions in test waters.

It would also be desirable to test the performance of hybrids of Montana strains and domestic strains of brown trout. The production logistics of such crosses would be simpler to carry out since collections from the wild would be required for only one parental line. Although progeny from crosses of domestic and wild trout strains frequently perform as well or better than progeny of all wild parents in natural waters (Moav et al. 1978; Fraser 1981; Gowing 1986; and Wolfarth 1986) the performance of a particular hybrid is difficult to predict.

Disease status certification, rearing, stocking, and evaluation would be necessary for the hybrids as in phase one of the study of wild strains.

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Table 1. Total length in inches at annulus formation for brown trout from selected Michigan and western United States rivers. Rivers are arranged in descending order based on brown trout length at age-2 annulus formation.

River	Section	Year(s)	Age 1	2	3	4	5	Reference
Beaverhead, MT	Hildreth	1970–84	—	12.10	15.80	19.50[1]	—	Oswald (1986b)
Missouri, MT	Craig	1984–87	8.00	11.70	15.20	17.90	—	Leathe, pers. com.
Beaverhead, MT	Henneberry	1984	—	11.60	15.40	19.20[1]	—	Oswald (1986b)
Beaverhead, MT	Pipe Organ	1984	—	10.70	14.70	18.00[1]	—	Oswald (1986b)
Bow, Alberta	1 & 2 combined	1981–83	5.70	10.60	15.20	18.20	20.40	Sosiak (1984)
Bighorn, MT	Below Afterbay	1983–86	5.40	10.20	14.80	17.70	19.80[2]	Fredenberg (1987)
Big Hole, MT	Melrose		6.40	9.90	13.30	15.90[1]	—	Oswald (1986a)
Big Hole, MT	Maiden Rock		6.70	9.80	13.20	16.40[1]	—	Oswald (1986a)
Au Sable, MI	North Branch		6.90	9.80	12.20	14.50	17.80	Gowing & Alexander (1980)
Au Sable, MI	Mainstream	1960–61	5.00	9.30	12.10	14.90[3]	—	Merron (1982)
Au Sable, MI	South Branch	1960–61 + 73	5.10	9.30	12.90	16.50[3]	—	Merron (1982)
Madison, MT	Varney	1967	—	9.30	14.10	17.10	19.30	Vincent, pers. com.
Pere Marquette, MI	Little S. Branch	1960–61	7.00	9.30	11.60	14.80	18.40	Gowing & Alexander (1980)
Madison, MT	Norris		—	9.20	11.30	14.50	15.70	Vincent, pers. com.
O'Dell Spring Creek, MT			5.70	9.20	12.50	15.00	16.60	Vincent, pers. com.
South Fork Snake, ID		1979–81	3.80	9.20	14.60	17.80	21.70	Moore & Schill (1984)
Madison, MT	Varney	1981	—	8.80	11.90	14.10	15.80	Vincent, pers. com.
Au Sable, MI	South Branch	1974–77	5.50	8.80	11.90	15.50	20.40	Gowing & Alexander (1980)
Au Sable, MI	North Branch	1960–61	4.50	8.70	12.00	15.20[3]	—	Merron (1982)

Table 1. Continued:

River	Section	Year(s)	Age 1	2	3	4	5	Reference
Pigeon, MI		1961–64	4.90	8.60	12.50	15.80	18.60	Gowing & Alexander (1980)
Madison, MT	Snowball		—	8.50	11.30	13.90	15.40	Vincent, pers. com.
Rifle, MI		1957–62	6.40	8.50	10.90	13.70	16.70	Gowing & Alexander (1980)
New Fork, WY	Airport-School	1982	3.30	8.10	12.40	15.20	16.80	Kurtz (1964)
Boardman, MI	Mainstream	1960–61	5.50	8.10	10.70	13.10	16.50	Gowing & Alexander (1980)
South Fork Madison, MT			—	8.00	12.00	16.50	18.70	Vincent, pers. com.
East Gallatin, MT	Bozeman		—	7.70	9.80	11.80	14.70	Vincent, pers. com.
Houghton Creek, MI		1954–61	5.30	7.60	9.70	11.90	14.80	Gowing & Alexander (1980)
Boardman, MI	North Branch	1973–76	4.60	7.30	9.80	12.40	15.50	Gowing & Alexander (1980)
Poplar Creek, MI		1972–74	4.10	7.30	10.00	12.40	14.40	Gowing & Alexander (1980)
Au Sable, MI	Mainstream	1974–76	5.20	7.20	9.90	12.00	14.80	Gowing & Alexander (1980)
Boardman, MI	South Branch	1973–76	4.90	7.20	9.30	11.00	13.80	Gowing & Alexander (1980)
Henrys Fork, ID		1984	4.30	7.10	10.10	12.70	14.70	Brostrom & Spateholts (1985)
Williamsburg Cr., MI		1975–76	4.40	7.00	9.40	11.60	13.90	Gowing & Alexander (1980)
Gamble Creek, MI		1961–65	4.60	6.70	8.70	10.90	13.00	Gowing & Alexander (1980)
West Fork Madison, WI			—	6.10	8.80	13.10	16.10	Vincent, pers. com.
Gallatin, MT			—	6.10	9.00	10.90	13.10	Vincent, pers. com.

[1]Brown trout of age-4 and older are included in mean-length calculations.
[2]Brown trout of age-5 and older are included in mean-length calculations.
[3]Projected age-4 length at annulus.

Table 2. Total length in inches at annulus formation for brown trout from selected Michigan and western United States rivers. Rivers are arranged in descending order based on brown trout length at age-3 annulus formation.

River	Section	Year(s)	Age 1	2	3	4	5	Reference
Beaverhead, MT	Hildreth	1970–84	—	12.10	15.80	19.50[1]	—	Oswald (1986b)
Beaverhead, MT	Henneberry	1984	—	11.60	15.40	19.20[1]	—	Oswald (1986b)
Bow, Alberta	1 & 2 combined	1981–83	5.70	10.60	15.20	18.20	20.40	Sosiak (1984)
Missouri, MT	Craig	1984–87	8.00	11.70	15.20	17.90	—	Leathe, pers. com.
Bighorn, MT	Below Afterbay	1983–86	5.40	10.20	14.80	17.70	19.80[2]	Fredenberg (1987)
Beaverhead, MT	Pipe Organ	1984	—	10.70	14.70	18.00[1]	—	Oswald (1986b)
South Fork Snake, ID		1979–81	3.80	9.20	14.60	17.80	21.70	Moore & Schill (1984)
Madison, MT	Varney	1967	—	9.30	14.10	17.10	19.30	Vincent, pers. com.
Big Hole, MT	Melrose		6.40	9.90	13.30	15.90[1]	—	Oswald (1986a)
Big Hole, MT	Maiden Rock		6.70	9.80	13.20	1640[1]	—	Oswald (1986a)
Au Sable, MI	South Branch	1960–61 + 73	5.10	9.30	12.90	16.50[3]	—	Merron (1982)
Pigeon, MI		1961–64	4.90	8.60	12.50	15.80	18.60	Gowing & Alexander (1980)
O'Dell Spring Creek, MT			5.70	9.20	12.50	15.00	16.60	Vincent, pers. com.
New Fork, WY	Airport-School	1982	3.30	8.10	12.40	15.20	16.80	Kurtz (1984)
Au Sable, MI	North Branch	1961–67	6.90	9.80	12.20	14.50	17.80	Gowing & Alexander (1980)
Au Sable, MI	Mainstream	1960–61	5.00	9.30	12.10	14.90[3]	—	Merron (1982)
South Fork Madison, MT			—	8.00	12.00	16.50	18.70	Vincent, pers. com.
Au Sable, MI	North Branch	1960–61	4.50	8.70	12.00	15.20[3]	—	Merron (1982)
Madison, MT	Varney	1981	—	8.80	11.90	14.10	15.80	Vincent, pers. com.

Table 2. Continued:

River	Section	Year(s)	Age 1	2	3	4	5	Reference
Au Sable, MI	South Branch	1974–77	5.50	8.80	11.90	15.50	20.40	Gowing & Alexander (1980)
Pere Marquette, MI	Little S. Branch	1960–61	7.00	9.30	11.80	14.80	18.40	Gowing & Alexander (1980)
Madison, MT	Snowball		—	8.50	11.30	13.90	15.40	Vincent, pers. com.
Madison, MT	Norris		—	9.20	11.30	14.50	15.70	Vincent, pers. com.
Rifle, MI		1957–62	6.40	8.50	10.90	13.70	16.70	Gowing & Alexander (1980)
Boardman, MI	Mainstream	1960–61	5.50	8.10	10.70	13.10	16.50	Gowing & Alexander (1980)
Henrys Fork, ID		1984	4.30	7.10	10.10	12.70	14.70	Brostrom & Spateholts (1985)
Poplar Creek, MI		1972–74	4.10	7.30	10.00	12.40	14.40	Gowing & Alexander (1980)
Au Sable, MI	Mainstream	1974–76	5.20	7.20	9.90	12.00	14.80	Gowing & Alexander (1980)
Boardman, MI	North Branch	1973–76	4.60	7.30	9.80	12.40	15.50	Gowing & Alexander (1980)
East Gallatin, MT	Bozeman		—	7.70	9.80	11.80	14.70	Vincent, pers. com.
Houghton Creek, MI		1954–61	5.30	7.60	9.70	11.90	14.80	Gowing & Alexander (1980)
Williamsburg Creek, MI		1975–76	4.40	7.00	9.40	11.60	13.90	Gowing & Alexander (1980)
Boardman, MI	South Branch	1973–76	4.70	7.20	9.30	11.00	13.80	Gowing & Alexander (1980)
Gallatin, MT			—	6.10	9.00	10.90	13.10	Vincent, pers. com.
West Fork Madison, MT			—	6.10	8.80	13.10	16.10	Vincent, pers. com.
Gamble Creek, MI		1961–65	4.60	6.70	8.70	10.90	13.00	Gowing & Alexander (1980)

[1]Brown trout of age-4 and older are included in mean-length calculations.
[2]Brown trout of age-5 and older are included in mean-length calculations.
[3]Projected age-4 length at annulus.

Table 3. Total length in inches at annulus formation for brown trout from selected Michigan and western United States rivers. Rivers are arranged in descending order based on brown trout length at age-4 annulus formation.

River	Section	Year(s)	Age 1	Age 2	Age 3	Age 4	Age 5	Reference
Beaverhead, MT	Hildreth	1970–84	—	12.10	15.80	19.50[1]	—	Oswald (1986b)
Beaverhead, MT	Henneberry	1984	—	11.60	15.40	19.20[1]	—	Oswald (1986b)
Bow, Alberta	1 & 2 combined	1981–83	5.70	10.60	15.20	18.20	20.40	Sosiak (1984)
Beaverhead, MT	Pipe Organ	1984	—	10.70	14.70	18.00[1]	—	Oswald (1986b)
Missouri, MT	Craig	1984–87	8.00	11.70	15.20	17.90	—	Leathe, pers. com.
South Fork Snake, ID		1979–81	3.80	9.20	14.60	17.80	21.70	Moore & Schill (1984)
Bighorn, MT	Below Afterbay	1983–86	5.40	10.20	14.80	17.70	19.80[2]	Fredenberg (1987)
Madison, MT	Varney	1967	—	9.30	14.10	17.10	19.30	Vincent, pers. com.
Au Sable, MI	South Branch	1960–61 + 73	5.10	9.30	12.90	16.50[3]	—	Merron (1982)
South Fork Madison, MT			—	8.00	12.00	16.50	18.70	Vincent, pers. com.
Big Hole, MT	Maiden Rock		6.70	9.80	13.20	16.40[1]	—	Oswald (1986a)
Big Hole, MT	Melrose		6.40	9.90	13.30	15.90[1]	—	Oswald (1986a)
Pigeon, MI		1961–64	4.90	8.60	12.50	15.80	18.60	Gowing & Alexander (1980)
Au Sable, MI	South Branch	1974–77	5.50	8.80	11.90	15.50	20.40	Gowing & Alexander (1980)
Au Sable, MI	North Branch	1960–61	4.50	8.70	12.00	15.20[3]	—	Merron (1982)
New Fork, WY	Airport-School	1982	3.30	8.10	12.40	15.20	16.80	Kurtz (1984)
O'Dell Spring Creek, MT			5.70	9.20	12.50	15.00	16.60	Vincent, pers. com.
Au Sable, MI	Mainstream	1960–61	5.00	9.30	12.10	14.90[3]	—	Merron (1982)
Pere Marquette, MI	Little S. Branch	1960–61	7.00	9.30	11.80	14.80	18.40	Gowing & Alexander (1980)

Table 3. Continued:

River	Section	Year(s)	Age 1	2	3	4	5	Reference
Madison, MT	Norris		—	9.20	11.30	14.50	15.70	Vincent, pers. com.
Au Sable, MI	North Branch	1961–67	6.90	9.80	12.20	14.50	17.80	Gowing & Alexander (1980)
Madison, MT	Varney	1981	—	8.80	11.90	14.10	15.80	Vincent, pers. com.
Madison, MT	Snowball		—	8.50	11.30	13.90	15.40	Vincent, pers. com.
Rifle, MI		1957–62	6.40	8.50	10.90	13.70	16.70	Gowing & Alexander (1980)
West Fork Madison, MT			—	6.10	8.80	13.10	16.10	Vincent, pers. com.
Boardman, MI	Mainstream	1960–61	5.50	8.10	10.70	13.10	16.50	Gowing & Alexander (1980)
Henrys Fork, ID		1984	4.30	7.10	10.10	12.70	14.70	Brostrom & Spateholts (1985)
Boardman, MI	North Branch	1973–76	4.60	7.30	9.80	12.40	15.50	Gowing & Alexander (1980)
Poplar Creek, MI		1972–74	4.10	7.30	10.00	12.40	14.40	Gowing & Alexander (1980)
Au Sable, MI	Mainstream	1974–76	5.20	7.20	9.90	12.00	14.80	Gowing & Alexander (1980)
Houghton Creek, MI		1954–61	5.30	7.60	9.70	11.90	14.80	Gowing & Alexander (1980)
East Gallatin, MT	Bozeman		—	7.70	9.80	11.80	14.70	Vincent, pers. com.
Williamsburg Creek, MI		1975–76	4.40	7.00	9.40	11.60	13.90	Gowing & Alexander (1980)
Boardman, MI	South Branch	1973–76	4.90	7.20	9.30	11.00	13.80	Gowing & Alexander (1980)
Gamble Creek, MI		1961–65	4.60	6.70	8.70	10.90	13.00	Gowing & Alexander (1980)
Gallatin, MT			—	6.10	9.00	10.90	13.10	Vincent, pers. com.

[1]Brown trout of age-4 and older are included in mean-length calculations.
[2]Brown trout of age-5 and older are included in mean-length calculations.
[3]Projected age-4 length at annulus.

Table 4. Incremental growth in inches between age 2 and age 3 for brown trout from selected Michigan and western United States rivers.

River	Section	Year(s)	Increment	Reference
South Fork Snake, ID		1979–81	5.40	Moore & Schill (1984)
Madison, MT	Varney	1967	4.80	Vincent, pers. com.
Bighorn, MT	Below Afterbay	1983–86	4.60	Fredenberg (1987)
Bow, Alberta	1 & 2 combined	1981–83	4.60	Sosiak (1984)
New Fork, WY	Airport-School	1982	4.30	Kurtz (1984)
South Fork Madison, MT			4.00	Vincent, pers. com.
Beaverhead, MT	Pipe Organ	1984	4.00	Oswald (1986b)
Pigeon, MI		1961–64	3.90	Gowing & Alexander (1980)
Beaverhead, MT	Henneberry	1984	3.80	Oswald (1986b)
Beaverhead, MT	Hildreth	1970–84	3.70	Oswald (1986b)
Au Sable, MI	South Branch	1960–61 + 73	3.60	Merron (1982)
Missouri, MT	Craig	1984–87	3.50	Leathe, pers. com.
Big Hole, MT	Maiden Rock		3.40	Oswald (1986a)
Big Hole, MT	Melrose		3.40	Oswald (1986a)
Au Sable, MI	North Branch	1960–61	3.30	Merron (1982)
O'Dell Spring Creek, MT			3.30	Vincent, pers. com.
Madison, MT	Varney	1981	3.10	Vincent, pers. com.
Au Sable, MI	South Branch	1974–77	3.10	Gowing & Alexander (1980)
Henrys Fork, ID		1984	3.00	Brostrom & Spateholts (1985)
Gallatin, MT			2.90	Vincent, pers. com.
Madison, MT	Snowball		2.80	Vincent, pers. com.

Table 4. Continued:

River	Section	Year(s)	Increment	Reference
Au Sable, MI	Mainstream	1960–61	2.80	Merron (1982)
West Fork Madison, MT			2.70	Vincent, pers. com.
Au Sable, MI	Mainstream	1974–76	2.70	Gowing & Alexander (1980)
Poplar Creek, MI		1972–74	2.70	Gowing & Alexander (1980)
Boardman, MI	Mainstream	1960–61	2.60	Gowing & Alexander (1980)
Boardman, MI	North Branch	1973–76	2.50	Gowing & Alexander (1980)
Pere Marquette, MI	Little S. Branch	1960–61	2.50	Gowing & Alexander (1980)
Williamsburg Creek, MI		1975–76	2.40	Gowing & Alexander (1980)
Rifle, MI		1957–62	2.40	Gowing & Alexander (1980)
Au Sable, MI	North Branch	1961–67	2.40	Gowing & Alexander (1980)
Boardman, MI	South Branch	1973–76	2.10	Gowing & Alexander (1980)
Houghton Creek, MI		1954–61	2.10	Gowing & Alexander (1980)
East Gallatin, MT	Bozeman		2.10	Vincent, pers. com.
Madison, MT	Norris		2.10	Vincent, pers. com.
Gamble Creek, MI		1961–65	2.00	Gowing & Alexander (1980)

Table 5. Incremental growth in inches between age 3 and age 4 for brown trout from selected Michigan and western United States rivers.

River	Section	Year(s)	Increment	Reference
South Fork Madison, MT			4.50	Vincent, pers. com.
West Fork Madison, MT			4.30	Vincent, pers. com.
Beaverhead, MT	Henneberry	1984	3.80	Oswald (1986b)
Beaverhead, MT	Hildreth	1970–84	3.70	Oswald (1986b)
Au Sable, MI	South Branch	1974–77	3.60	Gowing & Alexander (1980)
Au Sable, MI	South Branch	1960–61 + 73	3.60	Merron (1982)
Pigeon, MI		1961–64	3.30	Gowing & Alexander (1980)
Beaverhead, MT	Pipe Organ	1984	3.30	Oswald (1986b)
Au Sable, MI	North Branch	1960–61	3.20	Merron (1982)
Madison, MT	Norris		3.20	Vincent, pers. com.
South Fork Snake, ID		1979–81	3.20	Moore & Schill (1984)
Big Hole, MT	Maiden Rock		3.20	Oswald (1986a)
Bow, Alberta	1& 2 combined	1981–83	3.00	Sosiak (1984)
Madison, MT	Varney	1967	3.00	Vincent, pers. com.
Pere Marquette, MI	Little S. Branch	1960–61	3.00	Gowing & Alexander (1980)
Bighorn, MT	Below Afterbay	1983–86	2.90	Fredenberg (1987)
Au Sable, MI	Mainstream	1960–61	2.80	Merron (1982)
New Fork, WY	Airport-School	1982	2.80	Kurtz (1984)
Rifle, MI		1957–62	2.80	Gowing & Alexander (1980)
Missouri, MT	Craig	1984–87	2.70	Leathe, pers. com.
Henrys Fork, ID		1984	2.60	Brostrom & Spateholts (1985)

Table 5. Continued:

River	Section	Year(s)	Increment	Reference
Boardman, MI	North Branch	1973–76	2.60	Gowing & Alexander (1980)
Madison, MT	Snowball		2.60	Vincent, pers. com.
Big Hole, MT	Melrose		2.60	Oswald (1986a)
O'Dell Spring Creek, MT			2.50	Vincent, pers. com.
Poplar Creek, MI		1972–74	2.40	Gowing & Alexander (1980)
Boardman, MI	Mainstream	1960–61	2.40	Gowing & Alexander (1980)
Au Sable, MI	North Branch	1961–67	2.30	Gowing & Alexander (1980)
Gamble Creek, MI		1961–65	2.20	Gowing & Alexander (1980)
Williamsburg Creek, MI		1975–76	2.20	Gowing & Alexander (1980)
Houghton Creek, MI		1954–61	2.20	Gowing & Alexander (1980)
Madison, MT	Varney	1981	2.20	Vincent, pers. com.
Au Sable, MI	Mainstream	1974–76	2.10	Gowing & Alexander (1980)
East Gallatin, MT	Bozeman		2.00	Vincent, pers. com.
Gallatin, MT			1.90	Vincent, pers. com.
Boardman, MI	South Branch	1973–76	1.70	Gowing & Alexander (1980)

Table 6. Cumulative rank scores for brown trout growth in selected Michigan and western United States streams.

River	Section	Year(s)	Rank score	Reference
Beaverhead, MT	Hildreth	1970–84	4.00	Oswald (1986b)
Beaverhead, MT	Henneberry	1984	4.20	Oswald (1986b)
Beaverhead, MT	Pipe Organ	1984	6.10	Oswald (1986b)
Bow, Alberta	1 & 2 combined	1981–83	6.10	Sosiak (1984)
Bighorn, MT	Below Afterbay	1983–86	7.80	Fredenberg (1987)
South Fork Snake, ID		1979–81	7.80	Moore & Schill (1984)
Madison, MT	Varney	1967	8.70	Vincent, pers. com.
Au Sable, MI	South Branch	1960–61 + 73	9.40	Merron (1982)
Missouri, MT	Craig	1984–87	9.80	Leathe, pers. com.
South Fork Madison, MT			10.40	Vincent, pers. com.
Big Hole, MT	Maiden Rock		11.10	Oswald (1986a)
Pigeon, MI		1961–64	11.30	Gowing & Alexander (1980)
Big Hole, MT	Melrose		14.20	Oswald (1986a)
Au Sable, MI	South Branch	1974–77	14.40	Gowing & Alexander (1980)
New Fork, WY	Airport-School	1982	14.60	Kurtz (1984)
Au Sable, MI	North Branch	1960–61	14.70	Merron (1982)
Au Sable, MI	Mainstream	1960–61	17.10	Merron (1982)
O'Dell Spring Creek, MT			17.80	Vincent, pers. com.
Pere Marquette, MI	Little S. Branch	1960–61	19.60	Gowing & Alexander (1980)
Madison, MT	Norris		20.80	Vincent, pers. com.

Table 6. Continued:

River	Section	Year(s)	Rank score	Reference
Madison, MT	Varney	1981	21.90	Vincent, pers. com.
Madison, MT	Snowball		22.00	Vincent, pers. com.
West Fork Madison, MT			22.10	Vincent, pers. com.
Au Sable, MI	North Branch	1961–67	22.30	Gowing & Alexander (1980)
Rifle, MI		1957–62	23.90	Gowing & Alexander (1980)
Henrys Fork, ID		1984	24.20	Brostrom & Spateholts (1985)
Boardman, MI	Mainstream	1960–61	25.80	Gowing & Alexander (1980)
Boardman, MI	North Branch	1973–76	26.40	Gowing & Alexander (1980)
Poplar Creek, MI		1972–74	26.90	Gowing & Alexander (1980)
Au Sable, MI	Mainstream	1974–76	28.90	Gowing & Alexander (1980)
Houghton Creek, MI		1954–61	30.80	Gowing & Alexander (1980)
Williamsburg Creek, MI		1975–76	31.10	Gowing & Alexander (1980)
Gallatin, MT			31.40	Vincent, pers. com.
East Gallatin, MT	Bozeman		31.70	Vincent, pers. com.
Boardman, MI	South Branch	1973–76	33.30	Gowing & Alexander (1980)
Gamble Creek, MI		1961–65	33.80	Gowing & Alexander (1980)

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