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Dynamics in Lake Superior of Hatchery and Wild Steelhead Emigrating From the Huron River, Michigan

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Abstract.–We studied recruitment, survival and growth in Lake Superior of hatchery and wild steelhead *Oncorhynchus mykiss* emigrating from the Huron River, Michigan. We monitored the emigration of marked Little Manistee (Lake Michigan) stock hatchery smolts and wild emigrants with smolt traps near the river mouth in 1987-1988. Each spring 1988-1992 we monitored returns with a trap net in the lower river, and the riverine sport fishery with a census. Hatchery smolts survived transportation and stocking well, and migrated quickly from the river. Adult returns of stocked fish were low and contributed only about 3% to total adult runs. Survival in Lake Superior was 0.05% or less. Larger smolts (>210 mm) had relatively high survival, based on a comparison of smolt total lengths with those back-calculated from adult scales. Returns of marked fish from distant locations indicated a possible lack of homing to the Huron River. The yield of wild emigrant steelhead was low and variable between years. Age-1 parr and smolts made up a substantial portion (21-66%) of the emigrant population. Returning adult populations were likewise low in number. Survival in Lake Superior of wild emigrants was fairly high (at least 11%). We found no effects of size on survival of wild emigrants. In contrast, based on emigration dates back-calculated from adult scales, survival increased dramatically for fish that emigrated after about the third week in May. Age-1 emigrants, which migrated in June, had much higher survival rates than age-2 smolts, which migrated in May. Survival to repeat-spawn was high (about 75%) and 54% of all returning adults were repeat spawners, many of which had spawned several times. Poor returns of hatchery smolts may have been due to either early emigration when conditions for survival in the lake were poor (related to the abundance of predators or food) or poor imprinting. Survival of stocked fish may be enhanced by use of a local wild stock, more adapted to the rigorous Lake Superior environment, for supplementation of wild populations in this region.

Management of steelhead *Oncorhynchus mykiss* fisheries in Michigan tributaries of Lake Superior has historically focused on supplementing naturalized, wild stocks with hatchery-raised fish (Hansen and Stauffer 1971; Wagner and Stauffer 1978; Anonymous 1991a; Peck 1992). Currently, the Michigan Department of Natural Resources (MDNR) stocks about 75,000 yearling smolts (average total length 170-190 mm) annually into Lake Superior (Anonymous 1988-1991). Based on findings from Lake Michigan, as well as from Oregon and Washington (see Seelbach 1987a), these yearling smolts are expected to successfully imprint to and migrate from the stream of release, show relatively high lake survival, and provide abundant adult returns. However, the performance of smolts stocked into Lake Superior has not been fully evaluated.

Returns of hatchery smolts to the creel were estimated in the 1960s (when the parasitic sea lamprey *Petromyzon marinus* was extremely abundant and thought to be impacting steelhead; Hansen and Stauffer 1971) and concurrent to this study (Peck 1992). In both cases returns were surprisingly low (0-2%). It was not clear whether poor returns were caused by poor survival to smolting, poor survival in Lake Superior, poor homing back to the study stream, or simply by low rates of exploitation. Exploitation rates in Lake Superior tributaries are typically about 20% (Kwain 1981; Scholl et al. 1984; Swanson 1985), suggesting that total returns to the stocked river were indeed low (1-5%) and that a problem existed with either survival or homing for steelhead in Lake Superior. Poor survival to smolting due to long transportation times and an abrupt change from hard (truck) water to soft (river) water was postulated by Wagner and Stauffer (1978). Survival in Lake Superior is not well understood, however, returns (a lower bound on survival) as high as 3-8% have been documented for rainbow trout stocked in Minnesota waters (Hassinger et al. 1974; Close and Hassinger 1981). Straying by returning hatchery adults to neighboring streams was observed by Hansen and Stauffer (1971) and Peck (1992), however no estimates of the magnitude of straying are available.

Hatchery steelhead are stocked based on the premise that recruitment of wild stocks is limited. Several studies in Lake Superior tributaries have revealed fairly low densities of age-1 steelhead parr (indicating poor instream survival), and modest numbers of returning adults (100-1,000 fish in most runs; Hassinger et al. 1974; Stauffer 1977; Kwain 1981, 1983; Swanson 1985). However, estimates of actual emigrant yields and subsequent survival rates are lacking.

To be successful, stocked fish should mimic the life history characteristics of wild populations. Wild population traits represent a successful response to local selection pressures and are optimal for survival. Many diverse life-history characteristics are seen among Great Lakes steelhead populations (Biette et al. 1981; Seelbach 1993). Notable among most Lake Superior populations is a predominance of age-1 emigrant parr that migrate somewhat late in the season (Hassinger et al. 1974; Biette et al. 1981; Kwain 1981, 1983; Swanson 1985). These are thought to be emigrating due to habitat limits (variable flows, harsh winters), rather than smolt transition (Kwain 1983; Seelbach 1993). Matching traits of hatchery and wild stocks would also minimize negative effects of stocking on wild populations (such as a loss of fitness through hybridization; Steward and Bjornn 1990).

The objectives of this study were to compile information needed for the management of hatchery steelhead in Michigan waters of Lake Superior. For hatchery-raised steelhead stocked into the Huron River, we sought to: (1) estimate mortality from stocking to smolting; (2) experimentally test the effects of transportation time and differential water hardness on pre-smolt mortality; (3) estimate total returns to the river and document age at maturity; (4) examine the effects of smolt size on survival; and (5) document straying of adult fish, both into and out of the river. For the wild steelhead population in the Huron River, we sought to: (1) estimate emigrant yields, numbers of returning adults, and survival rates (comparing the dynamics of emigrant parr and smolts); (2) describe life-history characteristics; and (3) estimate exploitation by the river sportfishery.

Study Site

This study was conducted on the Huron River in eastern Baraga County about 40 km northeast of the village of L'Anse (Figure 1). The Huron system drains about 24,365 hectares of forested land. Upstream from Lake Superior about 12 km, the Huron splits into East and West branches at Big Eric's Bridge. Another 22 km upstream, the East Branch divides again into the Little East and Little West branches. The Little West Branch originates in Curwood Lake (elevation 552 m). The Little East Branch originates from Summit Lake in the McCormick Wilderness Area (elevation 533 m). Both of these lakes lie approximately 20.9 km due south of the Lake Superior shoreline. The West Branch roughly parallels the East Branch and has its origin near High Lake (elevation 564 m). Since Lake Superior's elevation is about 183 m, the total fall of the river is about 366 m over about 34 km, for a steep mean gradient of 10.8 m/km (55.8 ft/mi).

There are seven waterfalls on the Huron River. The lowermost falls is immediately below Big Eric's Bridge and is not a barrier for potamodromous fishes. A barrier falls is located about 5 km upstream on the West Branch. On the East Branch a passable falls is found 2.6 km upstream from Big Eric's, with a barrier falls located another 2.7 km upstream. Thus approximately 22 river km are accessible to potamodromous fishes. Chink's Creek feeds into the East Branch below the barrier falls and provides an additional 3.7 km of accessible stream habitat. Upstream from the barrier falls on the West Branch are three additional falls (two are barriers).

Annual discharge patterns are typical of many Lake Superior tributaries that fall abruptly from high country. Headwater regions are perched, wetland aquifers that store some runoff, but little storage occurs as the river falls to the lake over impermeable Precambrian bedrock. As a result, spring thaws and rains produce high runoff peaks. Based on mean yields per hectare of nearby gaged streams (data from U.S. Geological Survey, Lansing, MI), mean discharge on the Huron River during April is about 13.2 cms (470 cfs). By August mean flows shrink to about 0.8 cms (30 cfs). During this study we experienced drought conditions in 1987 and 1988, and summer flows dropped to 0-0.3 cms (0-10 cfs). Severe high flows often occur again in September and October from extended rainfall events. Such severe flow variations create difficult stream habitat conditions. High peak flows limit the production of juvenile fishes and invertebrates, and low base flows limit summer rearing habitat (Poff and Ward 1992).

The mixed hardwood and conifer forests of the basin are actively logged by both state and private interests. Most logging involves selective cutting of hardwoods. Clearcutting of conifers occurs only in a small area (<10% of the basin area) near the river mouth. No significant residential or industrial development exists within the basin.

Headwater channels are generally less than 3 m in width. The East and West branches maintain a width of 5-7 m for most of their length. The river is about 13 m wide below Big Eric's Bridge, widening to nearly 35 m near the mouth. In the upper river the channel is characterized by long riffles and runs with broken bedrock and gravel substrates. Large woody debris is scarce. Below Big Eric's Bridge the channel has alternating deep pools and riffles, again with broken bedrock and gravel substrates. Towards the river mouth, sand becomes the predominant substrate. Occasional large jams of woody debris are found below Big Eric's.

The Huron River is relatively unproductive. Alkalinity is low, about 20-60 mg/L $CaCO_3$ (Hendrickson et al. 1973). Water temperatures range from freezing in winter (with some areas of the stream forming anchor ice) to about 21° C in the lower river during July and August (temperature data were collected occasionally during this study; Hendrickson et al. (1973) reported similar temperatures for nearby streams). Most of the mainstream, and the East and West branches remain below 15° C through the summer.

The Huron River supports a diverse fish community including with river-resident and potamodromous species, and cold-water and cool-water species. Thirty-seven species have been recorded from the Huron River (Appendix 1; data from this study and Moore and Braem 1965). The principal game fish in the upper river is brook trout *Salvelinus fontinalis;* while steelhead, coho salmon *Oncorhynchus kisutch*, and northern pike *Esox lucius* predominate in the lower river. Coho salmon flourish in rivers with low baseflows characterized by pool habitats (Hassler 1987) and are abundant in the study river. Data we collected on coho salmon emigrants and returning adults are presented in Appendix 2.

Methods

Stocking and assessing short-term survival of hatchery fish

In 1987-1989 we stocked steelhead smolts into the Huron River about 5.5 km upstream from its mouth. These smolts were first-generation progeny of wild parents from the Little Manistee River (a southern Michigan tributary to Lake Michigan). The MDNR raises steelhead to yearling smolts at Wolf Lake Fish Hatchery, located in southern Michigan near Kalamazoo. Groundwater sources and a fairly long growing season at this hatchery allow for accelerated growth needed to produce yearling smolts. We stocked these yearling smolts on 16 April 1987 (17,000; mean total length 193 mm), 2 May 1988 (17,000; mean total length 192 mm), and 15 May 1989 (17,500; mean total length 199 mm). To test an alternative, slower-growth rearing schedule, on 16 April 1987 we also stocked age-2 smolts (also Little Manistee strain) from the Marquette Hatchery, located near the study river (17,500; mean total length 195 mm).

Each stocked group was marked with an adipose fin clip signifying presence of a coded-wire tag in the fish's snout. Marquette hatchery fish were also marked with a caudal-tip fin clip to distinguish between hatchery groups for the first few weeks after stocking. Prior to stocking we measured 200 fish of each group to determine mean total length and length-frequency distribution.

We studied effects of long transportation distance, and differential hardness of rearing and receiving waters on mortality of stocked fish in two ways. First we held 150 of each stocking group in 3 live cages at the stocking site for 2 weeks to measure short-term mortality due to stresses of transportation and stocking. Second we conducted 5 controlled experiments testing the effects of transportation time and differential water hardness on short-term mortality of Wolf Lake Hatchery yearlings. In each experiment, 4 groups of 200 yearlings each were given unique experimental treatments and then held for 2 weeks in laboratory tanks at Wolf Lake Hatchery to assess short-term mortality. The treatments used a 2 x 2 experimental design (long and short transportation times x high and low hardness). Fish were transported for 12-13 and 0 hrs under the long and short transportation treatments, respectively. Hard water came from the Wolf Lake Hatchery supply and ranged from 189-255 mg/L $CaCO_3$. Soft water was trucked from the Huron River and ranged from 31-128 mg/L $CaCO_3$. Within each experiment we tested for significant differences in mortalities among treatments using a cross tabulation test.

Assessment of emigrants

We estimated yields of juvenile steelhead emigrating from the river from mid-April through June, 1987-1988. We employed a lead and box trap similar to the design of Hare (1973) about 4.2 km upstream from the river mouth. The lead was 2.5-mm mesh hardware cloth. The downstream end of the lead had a 1.3-mm mesh liner. The opening of the box trap faced downstream, capturing fish that moved back upstream after being trapped by the lead. This downstream opening prevented clogging of the throat of the box. We sampled 5 days per week. Each morning, captured juvenile steelhead were examined for fin clips, measured (total length in mm), scale sampled, and released downstream of the traps. Trap efficiency was estimated each season by marking a sample of emigrants with a slight caudal-tip fin clip (N=400), releasing them 150 m upstream of the traps, and determining the percent recaptured. Variance of the trap efficiency estimate was calculated as the variance of a binomial. Efficiency was 16.9±4.0% in 1987 and 19.5±4.0% in 1988.

Sampled emigrants were assigned to origin (hatchery or wild), age, and type (parr or smolt) groups. Hatchery fish were identified by fin clips. Stream annuli were identified based on a change from narrowly-spaced to widely-spaced circuli (signifying the change from winter to spring growth), and presence of anterior or posterior cutting over of circuli. Age-2 and age-3 fish were classified as smolts. Age-1 fish were assigned as smolts based on the criteria of having either a total length >125 mm or a back-calculated length at annulus 1 >95 mm. All backcalculation in this study was done using the Disbcal program with a length at scale formation of 32 mm (Anonymous 1989). We used the lower 95% confidence bound of the distribution of total lengths for age-2 smolts (125 mm) as the minimum threshold total length for an age-1 smolt in this population. This corresponds well with the thresholds of 130 mm used by Lirette et al. (1985) for a British Columbia population and 120 mm described by Leider et al. (1986). Steelhead that grow fastest during their first year become age-1 smolts, while slower-growing fish of the same cohort become age-2 or older smolts (Thorpe et al. 1980 showed this for the similar Atlantic salmon *Salmo salar*). We used the upper 95% confidence bound of the distribution of back-calculated lengths at annulus 1 for the age-2 smolts (95 mm) as the minimum threshold length at annulus 1 for an age-1 smolt (this corresponds well with data presented by Thorpe et al. 1980).

For each day, total emigrant catch was partitioned into hatchery smolts, wild age-1 smolts, wild age-2 smolts, and wild age-1 parr according to sample percentages for that day. For days not sampled, data were estimated as the mean of catches several days before and after the day in question. Estimated data made up about 40% of the total catch estimates each year. Daily catch figures were summed to give a seasonal total catch for each emigrant group. This total was expanded by trap efficiency estimates to give estimates of the total number of emigrants for each group.

For each emigrant group, we calculated yield per hectare of potential stream habitat upstream of the smolt traps (total potential habitat was 23 hectares). We also calculated mean total length and developed a length-frequency histogram. We then developed linear regressions relating Julian day of migration to back-calculated, pre-emigrant spring growth increment.

Assessment of adults

We estimated the number of adult steelhead ascending the river to spawn each spring, 1988-1992. A portion of the ascending fish were captured near the river mouth in trap nets, 5 days per week during April, May, and early June. These fish were measured, scale sampled, tagged with a Floy tag (fish >250 mm total length), and released. Fall-run fish were tagged in 1987-1988, but not thereafter. Fall-run fish represented a only small portion (<5%) of the annual catch of lake age-2+ fish and presumably their inclusion in 1988-1989 did not significantly bias estimates of the spring adult population. We assumed that tagged fish continued upstream and mixed with untagged fish. We collected data on angler-harvested fish and also trapped post-spawning downstream migrants as our recapture sample. We estimated total spring spawning populations using the Peterson-Bailey mark and recapture formula, and the associated variance as described by Ricker (1975; example 3.1). Anglers typically did not harvest smaller, lake age-1 fish, so we split our recapture data into two groups for analyses: lake age-1 fish and those older.

We assigned sampled adults to origin, age, and emigrant-type groups. Hatchery or wild origin was determined based on criteria for first-year scale circuli patterns developed by Seelbach and Whelan (1988). Stream annuli were identified as for emigrants. An emigrant check was identified as the point where more rapid lake growth began, frequently marked by the pinching together of 2-3 circuli. Lake annuli were identified according to criteria developed from known-age samples, and focused on a change from narrow to wide circuli spacing, as well as crossing-over of circuli at either posterior or anterior margins. Spawning checks were identified according to descriptions of Swanson (1985) and Myers and Hutchings (1987). For maiden-spawners we back-calculated total lengths at each stream annulus, at the smolt check, and at each lake annulus. Emigrant types were assigned using back-calculated lengths at annulus 1 and at the smolt check, with the criteria described above. The pre-emigrant spring growth increment increased significantly with Julian day for parr and smolts. We used the following regression equations to estimate Julian date of emigration: for parr - Julian day = 1.52 * spring growth increment (mm) + 94.57 ($P < 0.0000$; $R^2 = 0.76$); and for smolts (ages combined) - Julian day = 0.88 * spring growth increment (mm) + 113.30 ($P < 0.0000$; $R^2 = 0.85$).

Each year, for each unique emigrant group, we estimated the total number of adults returning by lake age, calculated mean lengths at each age, and developed frequency distributions for length at, and date of, emigration.

We calculated survival rates in Lake Superior as the number of emigrants in a group divided by the number of maiden-spawning adults returning from that emigrant cohort. We evaluated effects of emigrant length and migration date on survival by testing for differences between measured frequency distributions of emigrants and those back-calculated from adult scales (cross-tabulation test). All statistical tests were run using an α of 0.05. Survival rates to repeat spawn were calculated as the number of repeat spawners present in one year divided by the number of the same cohort estimated to have been spawning the previous year.

We calculated mean lengths at lake age for each group and tested for differences among emigrant groups and between maiden and repeat spawners (overlapping 95% confidence limits test). Mean back-calculated lengths at previous lake annuli were used to develop growth trajectories for each emigrant group. We tested for differences among these means using an overlapping 95% confidence limits test.

A measure of straying tendencies in hatchery fish was obtained by comparing the proportion of marked hatchery fish in the study river sample with the proportion in samples from other stretches of the Michigan shoreline. Straying of individual hatchery and wild fish was identified by returns of coded-wire tags and Floy tags (respectively) from distant sites. The contribution to the study river of hatchery fish stocked elsewhere in Lake Superior was determined as the component of the hatchery-origin adults that were unmarked or "otherwise"-marked.

Total angling catch in the Huron River was estimated each spring 1988-1992 and each fall 1987-1988 using an on-site creel survey. Anglers were counted and interviewed according to a stratified, random design (Ryckman and Lockwood 1985). Exploitation rates were calculated as the total catch of steelhead divided by the total adult population of fish >lake-age 1.

Results

Survival, returns, and growth of hatchery fish

Hatchery-raised smolts survived transportation and stocking well, and migrated quickly from the river. In 4 of 5 experimental tests there was high survival and no negative effects of either long transportation distance or differential water hardness (Figure 2). High and significant mortalities due to differential water hardness were observed in the 5th test; however, this result appeared to be related to the mid-May testing date, when fish were actively smolting and most sensitive to stress. No short-term mortality was observed in hatchery fish held in cages at the stocking site, supporting the experimental results.

Emigrant trap estimates for 1987 and 1988 indicated that 13,994±1,628 and 15,585±3,165 (respectively) yearling smolts stocked from Wolf Lake Hatchery left the river (80-89% of the number stocked). Only 10,574±1,190 of the age-2 smolts stocked in 1987 from Marquette Hatchery were estimated to have emigrated. This was only 60% of the number stocked and significantly lower than the percentage for Wolf Lake fish (cross-tabulation test). In each instance fish began migrating the day of stocking and 50% had migrated within 8 days (Figure 3). Hatchery smolts were much larger than wild smolts. Mean total length for Wolf Lake yearling migrants was 193±36 mm in 1987 and 192±50 mm in 1988, while mean total length for Marquette age-2 migrants was 195±49 mm.

Returns of these fish to the Huron River were very low and comprised only about 3% of returning adults in the 1987 and 1988 emigrant cohorts (Figure 4 and Appendix 3). Survival from emigrant to returning adult was 0.03-0.05% for the three hatchery groups stocked in 1987 and 1988. Age-2 Marquette smolts had no apparent survival advantage over Wolf Lake yearlings (5 and 15 coded-wire tags were returned from the 1987 stocking, respectively). Larger smolts (total length >210 mm) had relatively higher survival than smaller fish (Figure 5). The distribution of back-calculated length at smolting was significantly different than actual lengths at smolting.

Survival from previous spawning was quite high and similar to wild fish. Age-3 and Age-4 fish of both sexes averaged 82% survival. Survival for age-5 fish was 23% and for age-2 fish, only 4%. This latter, low value appears unrealistic and may indicate a difficulty in detecting a lake-age-1 spawning check on adult scales.

Non-returning fish could have either died or strayed to other rivers. One could assume that straying losses to other streams might be replaced by hatchery fish straying to the Huron River from these other sources. Indeed, based on scale analyses, hatchery fish of all origins made up 14% of the adults returning from 1987 and 1988 emigrant cohorts (Figure 4 and Appendix 3). These included some marked Kamloops-strain rainbow trout stocked in Minnesota (1.2% of the entire study sample).

Huron River hatchery fish also strayed widely. Coded-wire tags were returned from streams nearby (N=2), distant in Lake Superior (N=2), and even in Lake Michigan (N=3). Data collected by the roving clerks provided a basis for assessing abundance of marked fish per unit of collecting effort (total number of fish sampled). Proportions of adipose fin-clipped fish found in other nearby and distant streams (0.098 and 0.093) were similar to the proportion found in the Huron River (0.070), indicating a lack of homing.

Proportions of returning hatchery adults maturing at lake-ages 1, 2, and 3 (respectively) were 0.18, 0.37,and 0.45 for males and 0.00, 0.29, and 0.71 for females (Appendix 3). Growth of hatchery fish in Lake Superior was quite similar to wild fish (see below). Mean lengths at lake ages 1, 2, 3, and 4 (respectively), were 378, 546, 637, and 671 mm. Lengths were similar between sexes. The length-weight relationship was:

$$\text{Weight(g)} = 0.000040 * \text{Length(mm)}^{2.7709}$$

Recruitment, survival and returns, and growth of wild fish

The yield of emigrant steelhead was low and variable between years. A total of 9,141 emigrants was estimated in 1987 and only 1,031 in 1988. Yield, as mean number per hectare, ranged from 46 to 262 for smolts, and from 52 to 398 for all emigrants combined (Table 1). Age structure of emigrant populations also varied greatly between years (Table 1). Age-2 smolts made up 34-79% of annual emigrant populations; age-1 smolts and parr equally split the remainder each year.

Emigration occurred between mid-April and late June. Age-2 smolts migrated earlier than age-1 smolts and parr (Figures 6 and 7). Mean total lengths were similar for both age-1 smolts and age-2 smolts (160-187 mm range), and less for age-1 parr (122-113 mm;Table1).

Adult steelhead migrated upstream each spring from early April until early June. Peak movements were during late April and early May. Estimated wild adult runs during 1988-1992 varied from 864 to 3,690 fish (Table 3). The 1987 emigrant cohort produced about 2,450 maiden spawners, and the 1988 cohort about 1,364 maidens (Table 3, Figure 4).

Survival from emigrant to maiden adult was surprisingly high (11-51%; Table 3). Age-1 smolts had the highest survival, followed in turn by age-1 parr and age-2 smolts. Supportive of these relative survival rates, proportions of each of the emigrant types in the population changed between emigration and return (Table 1 and Appendix 3) . This change averaged +0.36 for age-1 smolts, +0.06 for age-1 parr, and -0.42 for age-2 smolts. Survival estimates for the 1988 age-1 emigrant groups were unrealistically high (>100%). Our trapping effort possibly missed some of the latest-migrating emigrants in 1988 (see arguments below), and thus our estimates for these groups may have been low.

Frequency distributions of smolt lengths back-calculated from scales of adults were similar to lengths of actual smolts, indicating no size-dependent survival. In 6 of 6 comparisons (3 emigrant types x 2 years), no significant differences were found between distributions. In contrast, large pre-emigrant, spring growth increments were more prevalent in returning populations than in emigrant populations, indicating that survival was higher for fish with this trait. For example, for the 1987 age-1 smolt cohort, the spring growth increment averaged 49 mm (95% confidence range 20-70 mm) for emigrants and 72 mm (range 40-115 mm) for returning adults. We found significant differences in 6 of 6 comparisons between the frequency distributions for Julian day of emigration back-calculated from spring growth increments and distributions of actual emigration patterns. In each case, back-calculated distributions favored later dates of migration (Figure 8). In addition, comparisons for age-1 smolts (both years) suggested that some of these fish migrated after we ceased trapping in late June. Lake survival appeared to increase dramatically for all types that emigrated after about the third week of May. This may explain the higher survivals measured for age-1 smolts and parr, which show a second migration peak in June (Figure 6). Age-2 smolts, which had the poorest survival, migrated primarily in May.

Repeat spawners were common, making up about 54% of adult populations (excluding age-1 males). Survival from previous spawning was only 4% for age-2 males, but averaged about 75% for age-3 and age-4 males and females. Survival declined to about 20% for age-5 fish of both sexes.

Most tag returns came from the Huron River, however, 24% were from other streams (which were not sampled intensively). Of these returns, 42% were from nearby streams and 58% from more distant streams.

Age at maturity differed between sexes. Proportions maturing at lake ages 1, 2, 3, and 4 were 0.78, 0.10, 0.10, and 0.02 (respectively) for males; mean lake age at maturity was 1.4. Proportions for females were 0, 0.19, 0.67, and 0.14 (respectively); mean lake age at maturity was 3.0. No differences in growth trajectories were present for back-calculated lengths at lake ages, indicating earlier age at maturity was not related to faster growth rate (Figure 9). Mean lengths of maiden spawners at lake ages 1, 2, 3, and 4 were 362, 509, 617, and 678 mm; and were not consistently different between fish that emigrated as parr or smolts (although length at emigration varied among these groups; Figure 10). Mean lengths at age did not differ between sexes; for example, maiden lake age-2 males averaged 511±12 mm while females averaged 522±16 mm. Mean lengths and weights at lake age generally declined with number of repeat spawnings, though differences were not significant (Figure 11).

Estimated spring angler catches of steelhead in the Huron River averaged about 225 and ranged from 178 to 344 (Table 4). Anglers fished about 3,300 hours each spring and catch per hour averaged about 0.07. Assuming that 14% of the catch was hatchery fish, the average catch of wild fish would be 193. Anglers kept very few lake-age-1 fish, so based on a typical returning population of 1,238 fish of lake age-2+ (Appendix 3), the exploitation rate was about 16%.

Discussion

Dynamics of hatchery fish

Survival of hatchery fish to smolting was excellent. Neither long transportation time nor differential water hardness caused short-term mortality. As expected for large-sized yearlings, a high proportion emigrated from the river. Long transportation time may not be a significant stressor, as Barton et al. (1980) found that rainbow trout acclimated to conditions within the hatchery truck. However, stocking fish abruptly from hard water into soft water certainly requires the expenditure of energy for osmoregulation (Parker 1986) and may stress fish. Such stress may be lethal when steelhead are actively smolting (and most sensitive; Wedemeyer et al. 1980), as demonstrated by our mid-May experiment. Although such stress was not evident in our study as short-term mortality, the unusually early, late-April emigration pattern displayed by fish stocked in 1987 (immediately after stocking) may have been a reflection of post-stocking stress. In contrast, steelhead stocked in southern Michigan consistently remained for several weeks in the river before emigrating in mid-May (Seelbach 1987a; Anonymous 1991b).

Returns of adult fish were very poor in this as in other studies (Hansen and Stauffer 1971; Peck 1992), suggesting that survival of rainbow trout smolts in Lake Superior may be very poor. Wagner and Stauffer (1978) and Peck (1992) both recommended termination of stocking programs in this light. However, good survival rates in Lake Superior have been documented for steelhead and other rainbow trout strains. In this study, survival of wild smolts was estimated to be at least 11%. Hassinger et al. (1974) reported minimum survival and return of 3% for large yearlings in Minnesota and Close and Hassinger (1981) found minimum return rates of 8% for Kamloops-strain rainbow trout. In addition, stray hatchery fish made up 14% of the Huron River run, indicating some potential for good survival.

Early migration may have placed our study fish in Lake Superior when conditions for survival were poor. We found that survival of wild adults was highest for fish that had entered Lake Superior after the third week of May. Poor survival of early emigrants could be related to coincident presence of predators or absence of food. The higher survival of large hatchery smolts that we observed is supportive of either hypothesis. Larger size would enhance predator avoidance (Walters et al. 1978; Ward et al. 1989). Conversely, where certain food resources are limited, larger size might permit switching to alternative (larger) foods, a greater searching area (due to greater swimming speed), or a longer time until feeding (due to greater fat reserves). Juvenile salmonids in the Great Lakes rely heavily on terrestrial insects as food (Jude et al. 1987; Connor et al. 1993) and these are likely scarce on Lake Superior until late spring or early summer. R. Elliott (Michigan State University, personal communication) found that food availability (terrestrial insects) on Lake Michigan increased dramatically in late April and that many chinook salmon *Oncorhynchus tshawytscha* sampled during late March and early April had empty stomachs. Significant increases in survival might be realized by understanding the timing of predator distributions and food availability in Lake Superior and tailoring stocking programs accordingly.

Extensive straying of hatchery fish was apparent. Stocked fish in this study and others (Hansen and Stauffer 1971) clearly did not imprint well to the stocked river. It is possible for steelhead to imprint to such soft-water rivers, as Hassinger et al. (1974) and Swanson (1985) found strong homing in wild populations. Imprinting occurs during the downstream migration of smolts and successful imprinting of hatchery smolts has been documented in southern Michigan rivers (Seelbach 1993; unpublished data). The unusually early emigration seen in this study may not have represented a fully-developed smolting process, and thus imprinting may have been impaired. Development of techniques for improving imprinting could significantly increase returns.

Traits of supplemental stocked fish should mimic traits of the wild population. Our hatchery fish were of the Little Manistee River-Lake Michigan stock, which is adapted to an extremely benign stream environment and a productive lake environment (Seelbach 1993). This stock (1) emigrates at 160+ mm at age-2, (2) emigrates in mid-May, and (3) matures after 2-3 years in the lake. These traits may be maladaptive in harsh stream and unproductive lake environments such as the Huron River and Lake Superior, where wild steelhead tend to (1) emigrate at 125+ mm at age-1, (2) emigrate in June, and (3) mature after 1-2 years if male or 3 years if female. Indeed, C. C. Krueger and B. May (Cornell University, personal communication), found that the Little Manistee stock was quite different genetically from wild Lake Superior populations. We observed the following example of a genetically-based, differential life-history response between wild and Little Manistee hatchery stocks: the 1987 cohort of 9,000 wild emigrants returned 1,305 age-1 males in 1988 (53% of the cohort return); concurrently the 1987 cohort of 34,000 hatchery smolts returned 0 age-1 males.

Use of a more appropriate, local (or regional) genetic stock of steelhead for supplementing Lake Superior populations offers many advantages. First, this would minimize negative effects (such as loss of fitness through hybridization) of hatchery supplementation on wild stocks (Steward and Bjornn 1990). The current Little Manistee hatchery stock is believed to have hybridized with wild stocks in several Minnesota streams, causing a decrease in the genetic distinctness of these populations (C. C. Krueger and B. May, Cornell University, personal communication). Second, the Huron River stock appeared to have a shorter length threshold for smolting (about 125 mm) than the Little Manistee Stock (about 160 mm). Thorpe et al. (1980) found similar among-stock variations in length at smolting for Atlantic salmon (90 mm and 140 mm in different populations). Steelhead could be easily grown to 125+ mm smolts at most Michigan hatcheries, including those in the Upper Peninsula. Finally, use of an appropriate stock would increase the feasibility of the hatchery program mimicking wild growth rates, dates of smolting (June), and imprinting; thus maximizing survival and returns.

Dynamics of wild fish

Yield of wild emigrants from the Huron River appeared quite variable, ranging from low to good (52-398 emigrants per hectare). The yield of age-2 smolts was low; 40-133 fish per hectare. Seelbach (1993) listed the range of published steelhead smolt yields as 200-730 smolts per hectare. The Little Manistee River, considered a top Great Lakes rearing stream, produced an average of 425 smolts per hectare. Stauffer (1977) surveyed fall steelhead parr populations in Chink's Creek (a tributary of the Huron River) and found fairly high densities of 7500 age-0 parr per hectare and 500 age-1 parr per hectare. These densities, however, may not be representative of the entire river system. Also, overwinter mortality is probably severe (90% or higher; Hassinger et al. 1974; Seelbach 1987b).

Juvenile steelhead rearing in the Huron River face several strong challenges to survival: severe spring floods that threaten early survival, summer drought flows that limit rearing habitat, and frigid winters equivalent to those at the northern edge of the steelhead's native range (Seelbach 1987b). The poor yields observed in 1988 were probably related to drought conditions present in 1987.

Due to limited stream production, recruitment of new fish to the returning adult population was fairly low. We estimated that about 2,046 adults returned each year, but 1,353 of these were maiden spawners, and only 544 of these were lake-age 2 and older. Miller (1974) reported spring steelhead runs during 1957-1970 at an electric sea lamprey barrier. Counts of fish >305 mm during this period averaged 328 fish (this is roughly comparable to our >lake-age 1 category that averaged about 1,237 fish). Runs may have increased since 1970; although comparisons are difficult as counts at lamprey barriers were not indicative of total run size (some migrants were probably discouraged by the barriers; Dahl and MacDonald 1980) and our population estimates were not precise. Nevertheless, such low annual production cannot sustain a high rate of angling harvest and exploitation should not be allowed to increase much beyond current levels. Similar concerns of potential overharvest have led to recent restrictive catch regulations in Wisconsin and Minnesota waters. In each state the limit is 1 fish over some minimum length (Anonymous 1991a, 1993).

Our estimates of adult run size had fairly wide confidence limits, a result of only handling small numbers of adults; however, they were in line with estimates for other Lake Superior populations (Krueger and May 1987). For future studies we recommend use of a more intensive sampling scheme for adult steelhead, preferably a counting fence.

Survival of wild steelhead emigrants in Lake Superior appeared quite high (stray fish not included). Four of our estimates ranged from 11% to 51%. Previous studies support this idea that survival is fairly high. Hassinger et al. (1974) calculated a minimum survival of 3% for wild emigrants. Swanson (1985) estimated survival from age-1 parr to returning adult to be about 4%; this figure included mortality during the presmolt winter (this can be >90%; Hassinger et al. 1974; Seelbach 1987b), implying that actual survival in Lake Superior could have been fairly high. Close and Hassinger (1981) reported 8% minimum returns for hatchery Kamloops rainbow trout. In Lake Michigan, survival of one steelhead population averaged 24% (Seelbach 1993). Likewise, survival of previous spawners was very high: 75% for fish of lake-ages 3 and 4. Many fairly old (5-7 lake years) fish were present in the population. No Great Lakes populations reported by Biette et al. (1981) had higher proportions of older fish, indicating minimal total adult mortality in the Huron River population.

Tagging returns suggested that many Huron River fish showed fidelity to the river. The more distant returns did not represent conclusive proof of straying. First, 14% of the adult fish we tagged were likely stray hatchery fish, unlikely to home again to the Huron River. Second, salmonids have been shown to explore several rivers before selecting a spawning site (Winter 1976). Finally, strong homing has been demonstrated in other Lake Superior populations (Hassinger et al. 1974; Swanson 1985).

The critical period for ocean salmonids, where mortality is highest and most variable, is believed to be the first months after smolting (Walters et al. 1978). This concept is applicable to naturalized populations in the Great Lakes, however, little is known about the behavior or dynamics of salmonids during this period. In testing for size- and timing-dependent mortalities, we were exploring hypotheses relating to this period of early lake life. We found no evidence of size-dependent survival for wild fish in Lake Superior, however, these fish did not reach the larger sizes (>210 mm) where positive effects were seen for hatchery fish. Size-dependent survival has not been demonstrated for Pacific salmonids in the Great Lakes, as it has for several populations on the Pacific Coast (Ward et al. 1989; Holtby et al. 1990). We did see strong evidence that survival was positively related to later times of entry into Lake Superior. Some returning adults showed dates of emigration as late as late June and early July. Although our traps did not capture emigrants during this period (see discrepancy between emigrants and adults in Figure 8), such late emigrants may have been present. Miller (1975) reported that emigrants were captured during late June and early July at an electric sea lamprey barrier operated on the Huron River during 1967-1970. Seelbach (1993) also found that later-migrating, age-1 smolts in the Little Manistee River had higher (3-7 times) survival rates in Lake Michigan than earlier-migrating age-2 smolts. Possible mechanisms relating timing to survival were discussed earlier.

The differences in migration timing patterns seen between emigrants and surviving adults could have arisen in two ways. Emigrants could have migrated directly into the lake, with the earlier ones suffering higher mortalities (in this case the smolt check on adult scales corresponds exactly with the date of emigration past our traps). Alternatively, emigrants may have paused in the lower river for a period of time, before moving out to the lake. Small salmonids have been observed in the lower river through early summer (observation by B. Miller). In this case it would not be clear whether the smolt check on adult scales corresponds to emigration past our traps or to actual date of lake entry--this would depend on growth patterns during this period, which are unknown. Shapovalov and Taft (1954) observed that some post-smolt steelhead remained for some time in the estuary of an Oregon river before going to sea. Further studies of the movements, diets, growth, and potential predators of post-emigrants are necessary to clarify the lake ecology and dynamics of this population.

Huron River steelhead displayed a life history strategy that emphasizes emigrating early (at age 1) from the river. This strategy is widespread in variable-flow tributaries found along the more rocky shorelines of the Great Lakes; particularly tributaries of Lake Superior and northern Lake Huron (Biette et al. 1981; E. Heuvel, Ontario Ministry of Natural Resources, personal communication). An extreme example of this strategy was observed in naturalized steelhead populations in certain tributaries of New York's Finger Lakes that have extremely low summer flows and high temperatures. In these streams (but not in neighboring, stable-flow streams), most young emigrated to the lake shortly after emergence (Northcote 1969). As a parallel from the Pacific Coast, pink salmon *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* have adapted to severe conditions in more northern spawning streams by evolving life histories that minimize the stream life phase; these spawn in lower river reaches and emigrate soon after emergence (Stearley 1992).

Ages at maturity differed between the sexes, apparently reflecting differential selection pressures. Males tended to return very early, indicating that the benefits of larger size (more gametes, competition for mates) did not outweigh the costs (mortality; Gross 1991). The equation apparently favored larger size (more gametes, competition for nest sites) for females. Both stream and lake growth rates were typical for Lake Superior populations (Hassinger et al. 1974; Kwain 1981, 1983; Peck 1992). Surprisingly, no differential growth trajectories were found among fishes of differing maturity schedules. Typically, age at maturity in salmonids is inversely related to growth rates (Thorpe 1986). Rand et al. (1993) identified distinct growth trajectories in Lake Michigan relating to maturity for steelhead from the Little Manistee River.

Implications

1. Stocked steelhead smolts (Little Manistee stock) failed to supplement the existing wild population in the Huron River; a typical stocking of 10,000 smolts would return 4 adults. Some supplementation occurs on a regional basis, as stray hatchery fish comprised 14% of returns to the Huron River. Stocked smolts emigrated but then either failed to survive or to home accurately.

2. A local, wild steelhead stock, adapted to variable-flow river conditions, should be used for hatchery supplementation in variable-flow streams of Michigan's Upper Peninsula (Lake Superior shoreline). This would minimize negative effects of stocking on the fitness of existing wild populations; and maximize opportunities to successfully mimic wild populations in growth rate, date of smolting, and imprinting.

3. The recruitment of wild juvenile steelhead to Lake Superior is limited primarily by hydrologic constraints (variable, low summer base flows). Research is needed to document whether degradation of the hydraulic functions of the Huron River has occurred, and if so, whether restoration is feasible.

4. Survival in Lake Superior was positively linked to the date of juvenile emigration. Research is needed to describe the movements, diets, growth

and potential predators of post-emigrants, and thus define the dynamics of this critical period.

5. The wild steelhead population in the Huron River is fairly unproductive and can support only limited harvests. About 54% of the run are repeat spawners and many of these are spawning for the third or fourth time. Exploitation should be limited to current levels.

Acknowledgements

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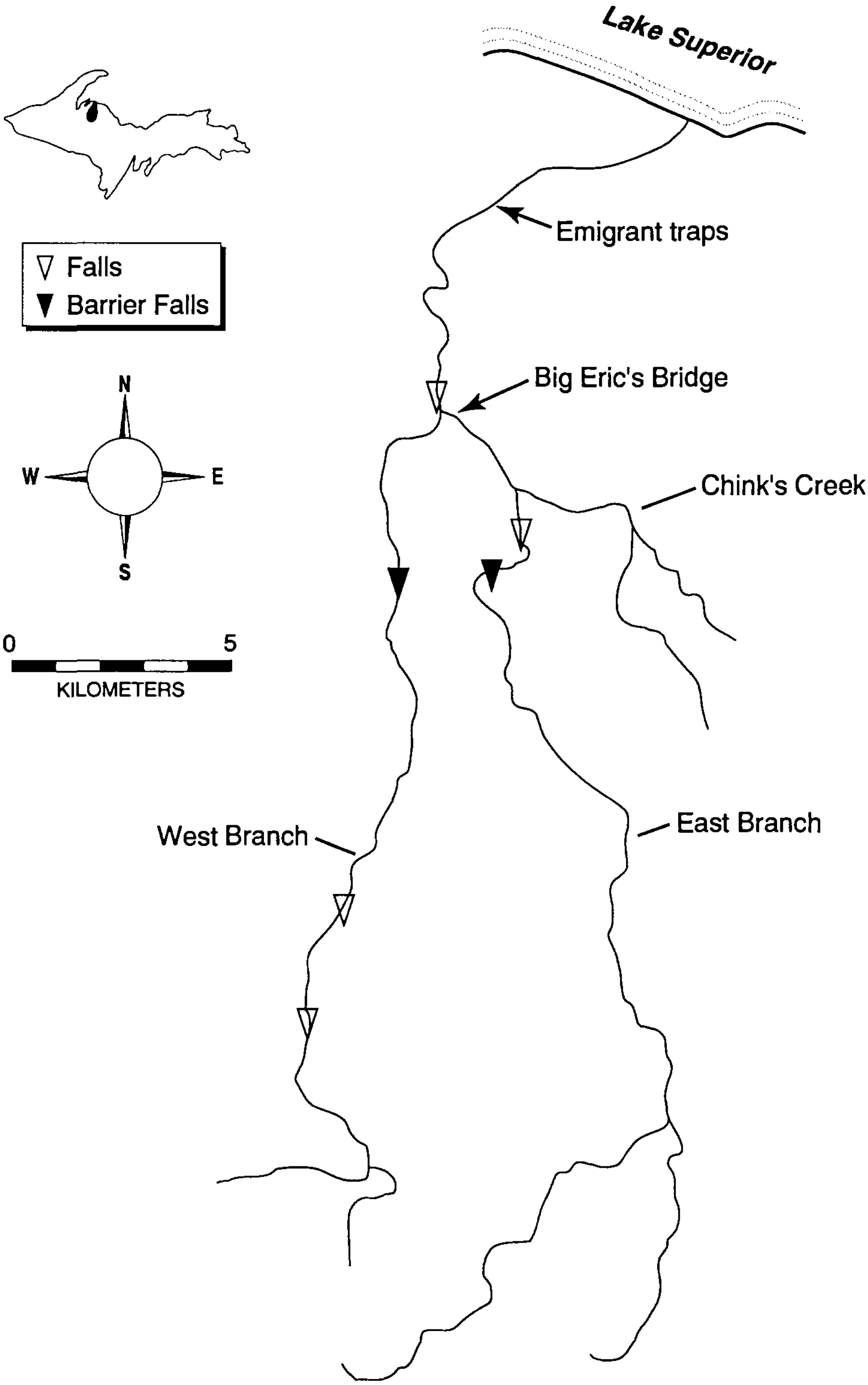

Figure 1.—Map of the Huron River. Inset shows location of the Huron River watershed within Michigan's Upper Peninsula.

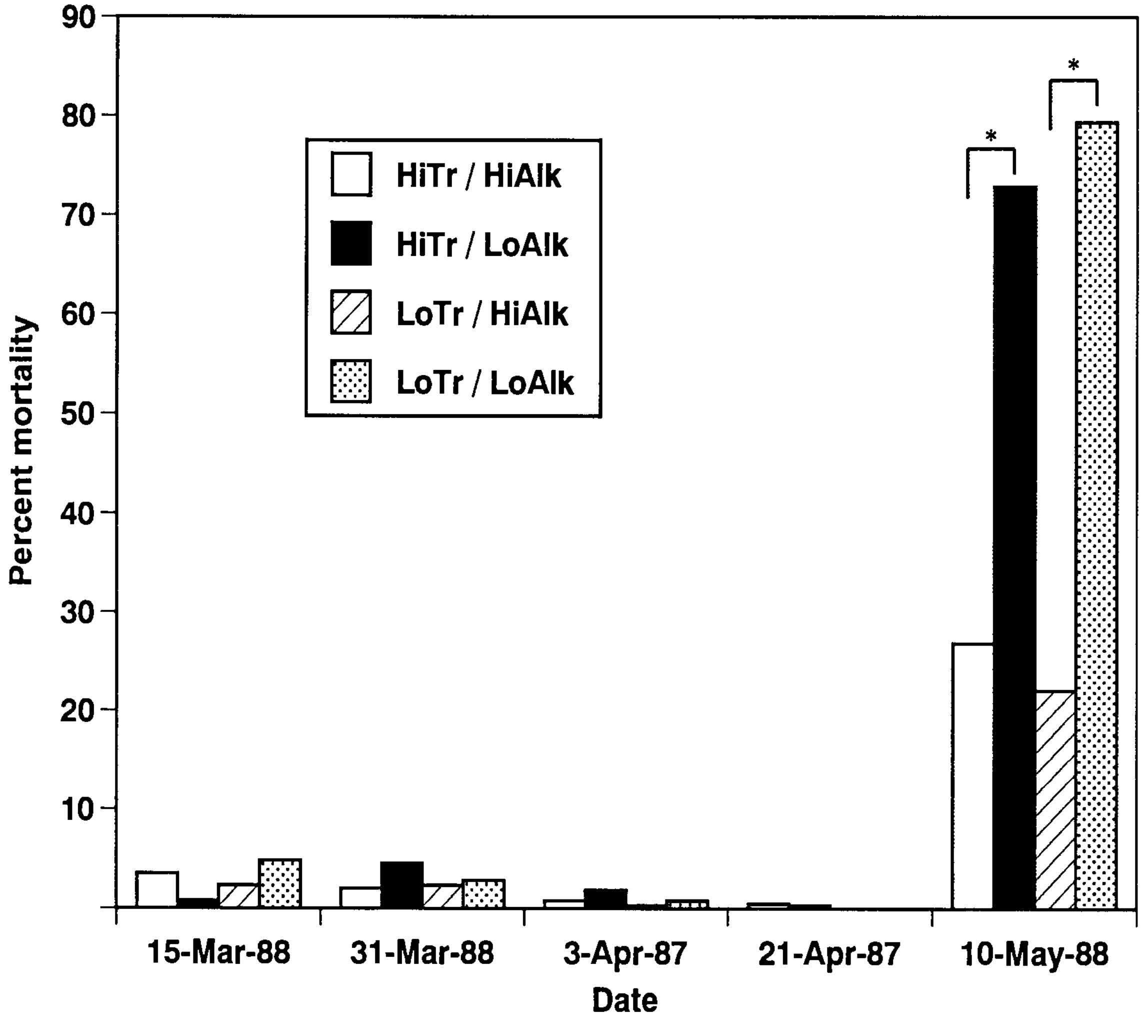

Figure 2.—Percent mortalities of hatchery steelhead smolts due to experimental treatments. Treatments are noted as: High Trucking + High Alkalinity = HiTr/HiAlk, etc. Comparisons that showed significant differences are shown with an "*".

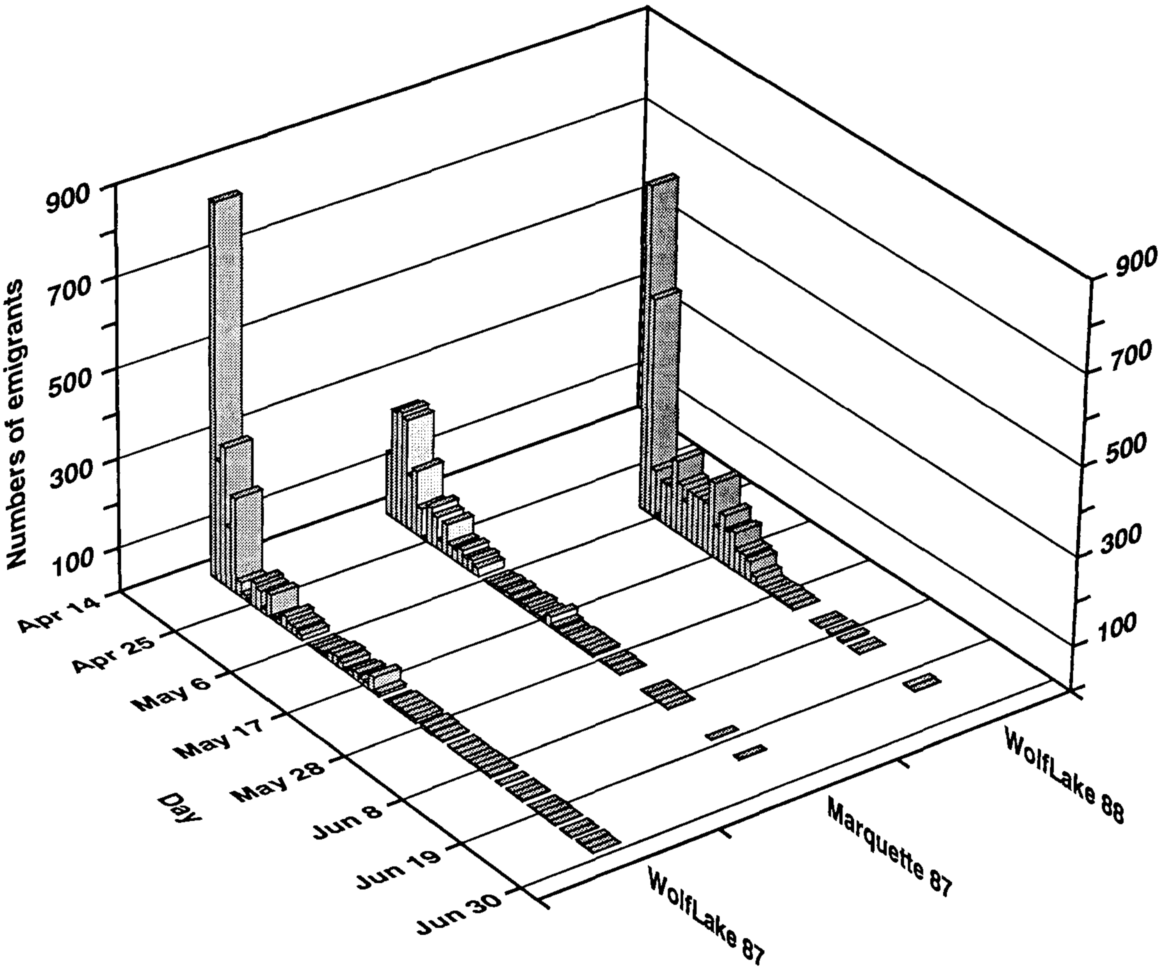

Figure 3.—Timing of emigration for groups of hatchery steelhead smolts stocked in the Huron River. Groups are Wolf Lake Hatchery yearling smolts in 1987 and 1988, and Marquette Hatchery Age-2 smolts stocked in 1987. In each case, emigration began on the day of stocking.

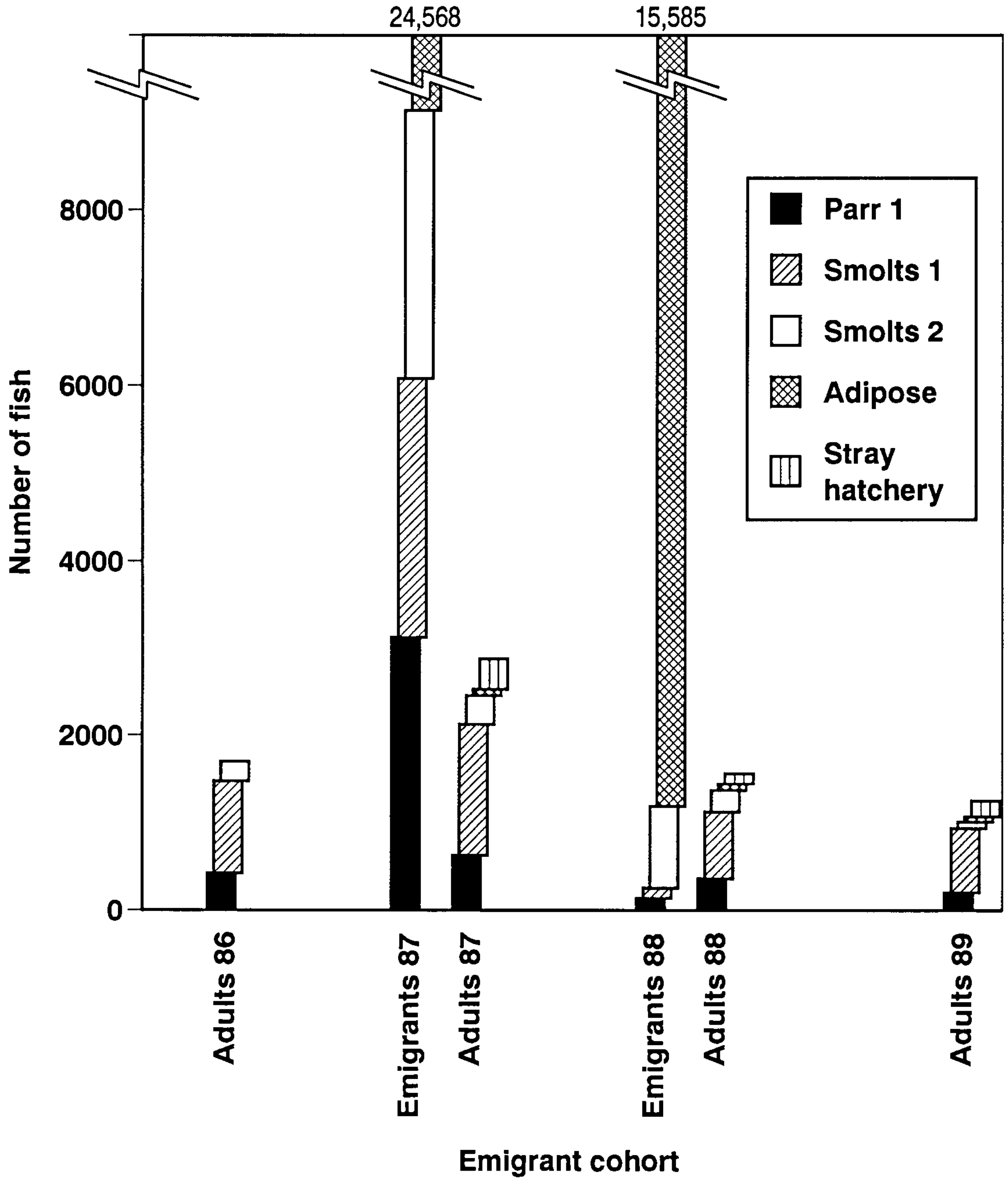

Figure 4.—Numbers of individuals in various emigrant groups comprising emigrant and returning maiden-spawning adult steelhead populations in the Huron River. Data are presented for the 1986-1987 emigrant cohorts. Number of emigrants of the adipose group is shown above the bar.

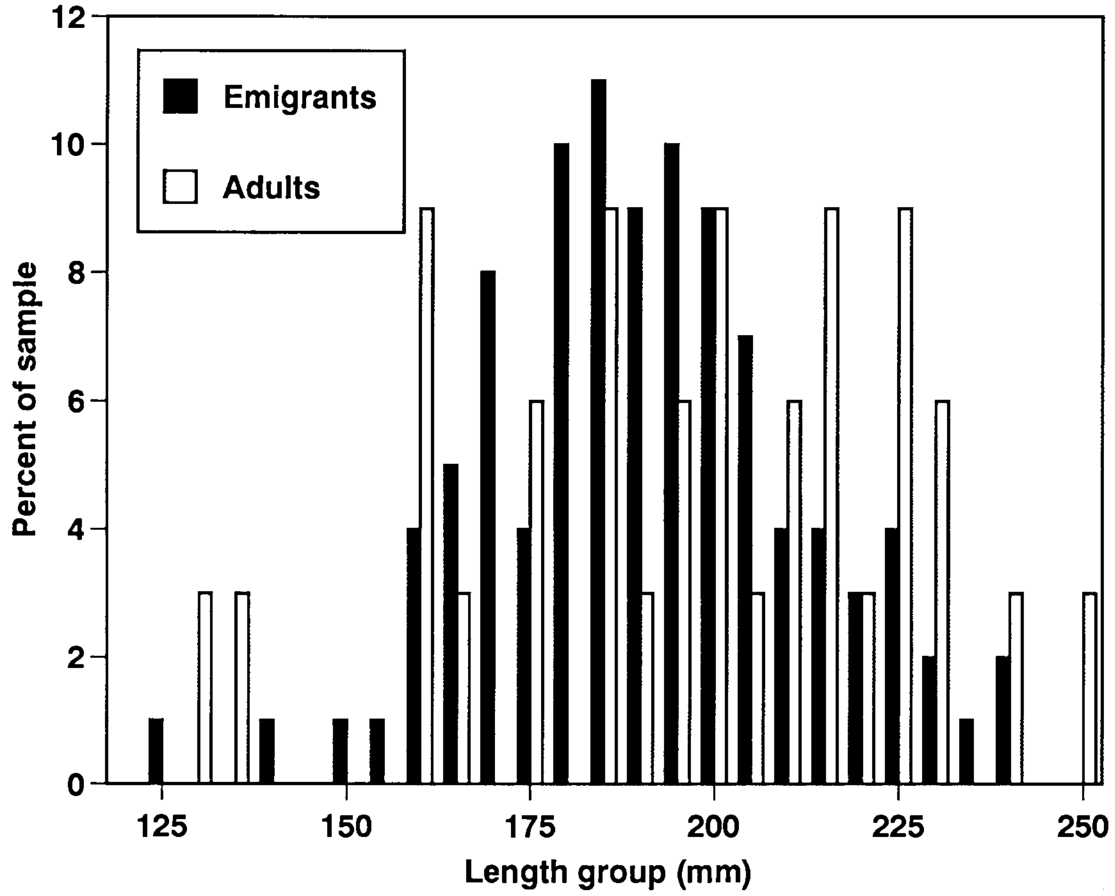

Figure 5.—Comparison between frequency distributions of hatchery smolt lengths (1987-1989) and smolt lengths back-calculated from scales of subsequent returning adults.

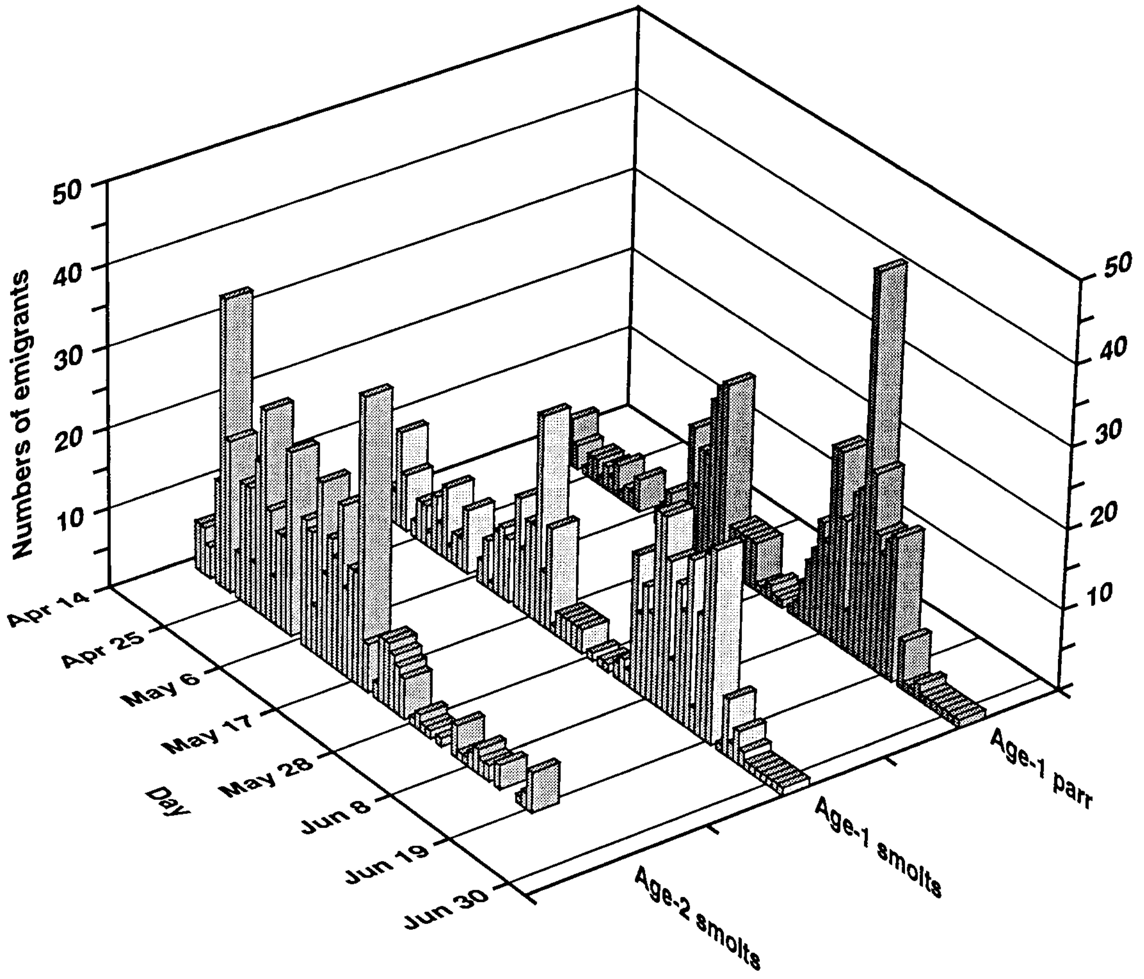

Figure 6.—Timing of emigration of wild steelhead from the Huron River in spring 1987.

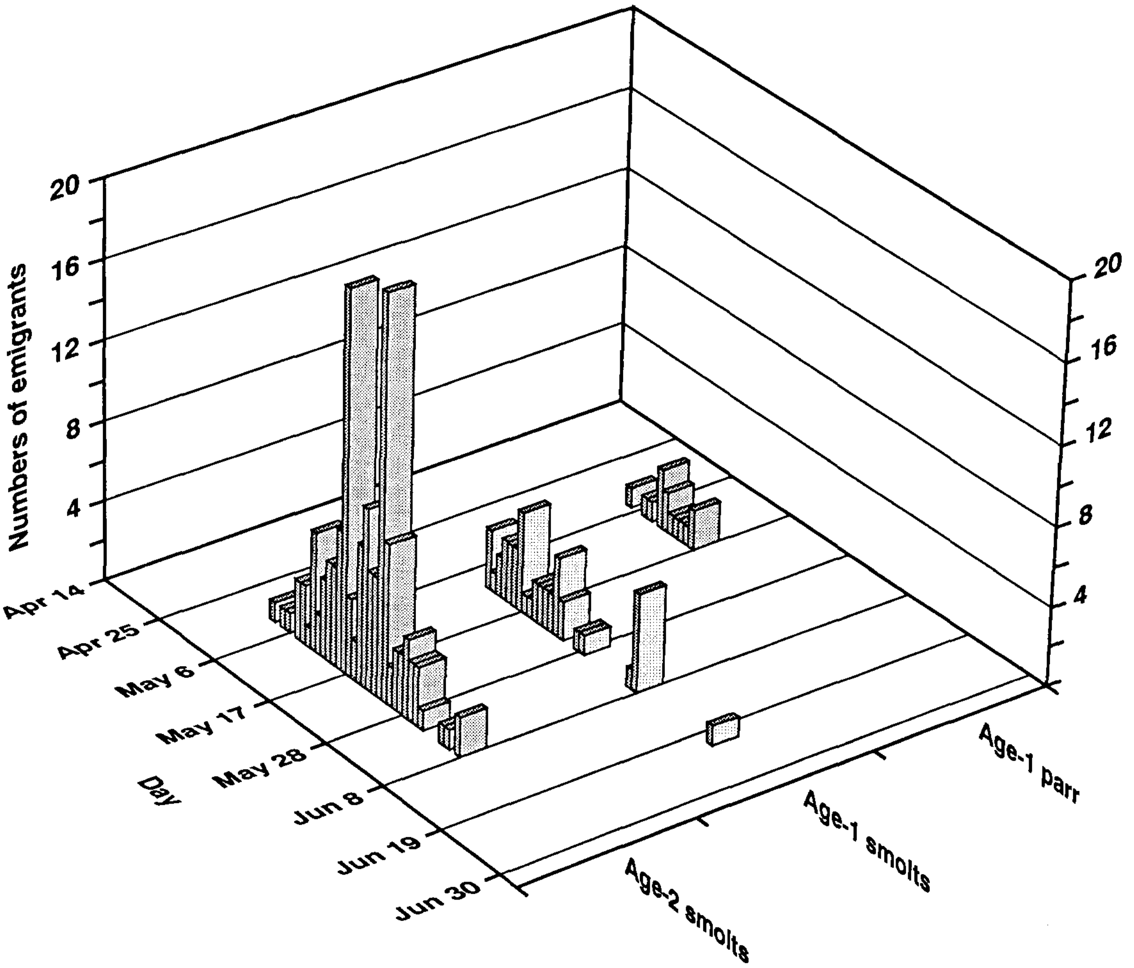

Figure 7.—Timing of emigration of wild steelhead from the Huron River in spring 1988.

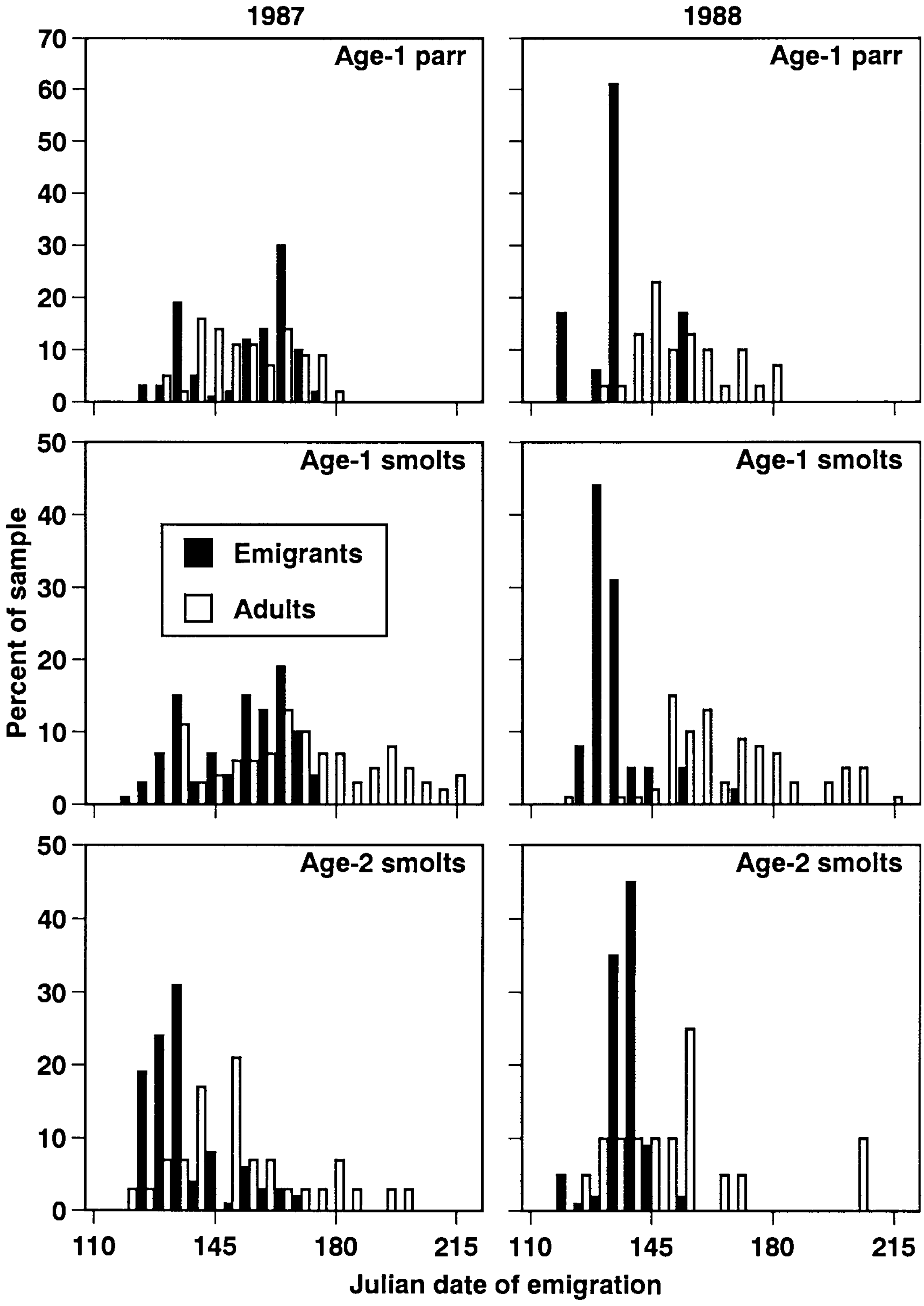

Figure 8.—Comparisons between frequency distributions of Julian date of emigration and this value back-calculated from scales of subsequent returning adults. Comparisons are shown for age-1 parr, age-1 smolt, and age-2 smolt groups of the 1987 and 1988 emigrant cohorts.

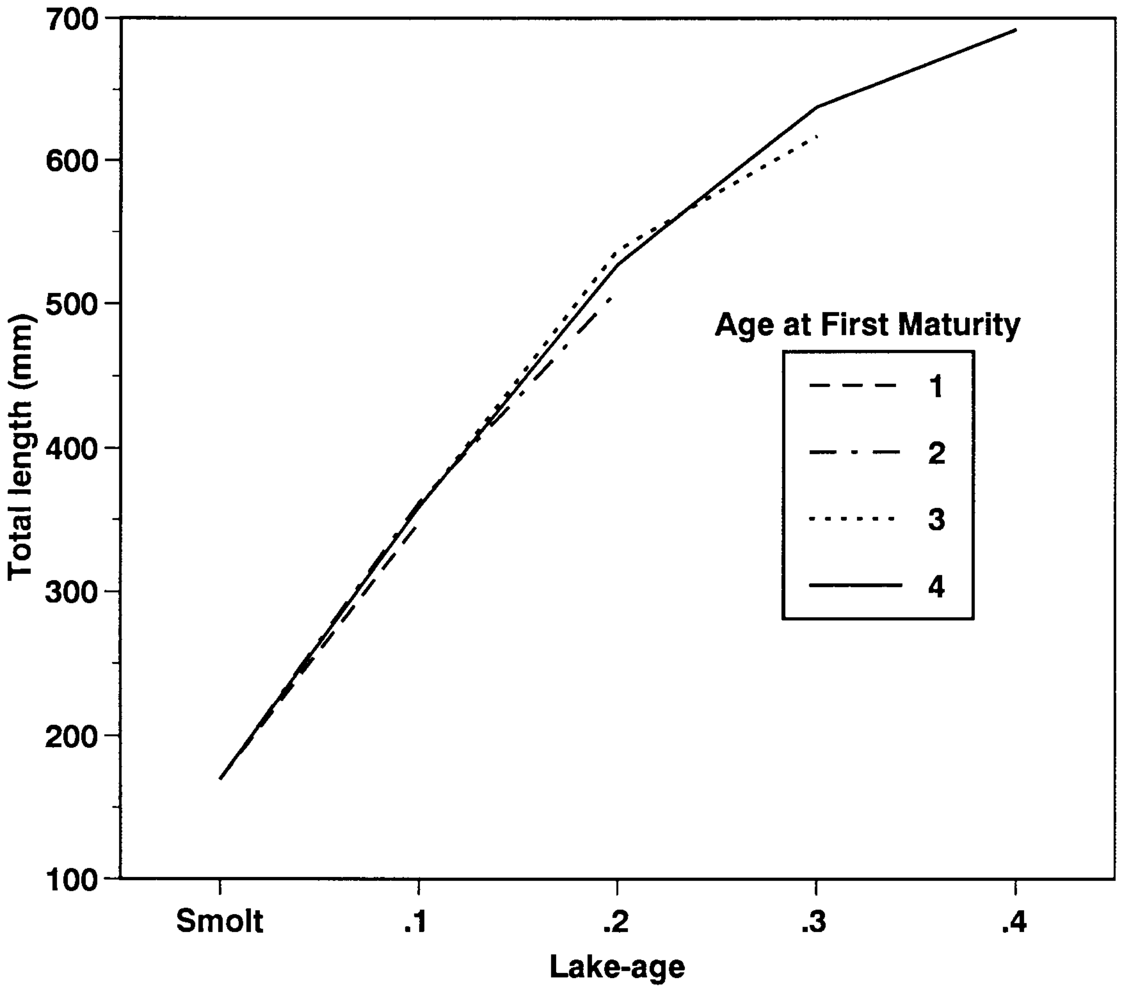

Figure 9.—Growth trajectories for steelhead in the Huron River maturing after 1, 2, 3, and 4 years in Lake Superior.

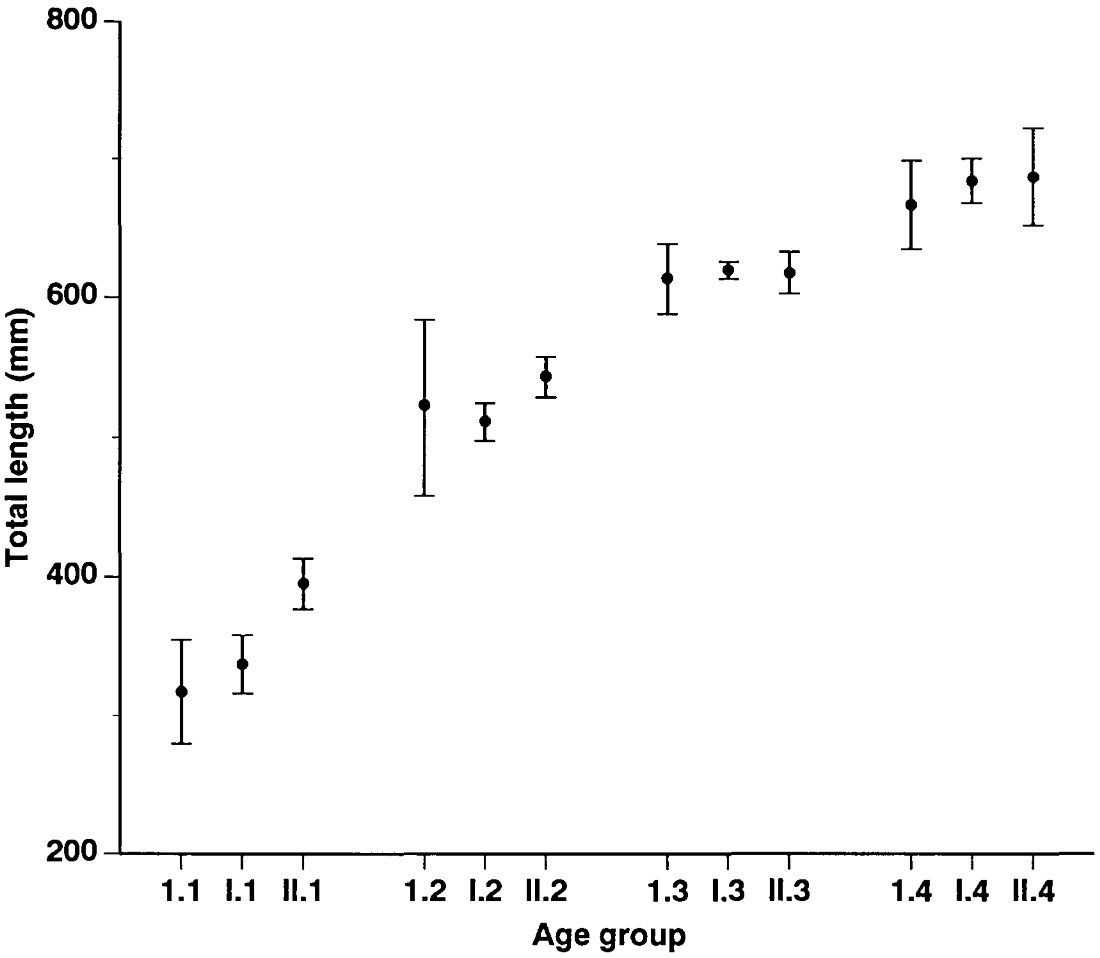

Figure 10.—Comparison of mean lengths at lake ages 1, 2, 3, and 4 for maiden spawning steelhead of differing emigrant types [age-1 parr (1), age-1 smolts (I), and age-2 smolts (II)]. Means are shown with two standard errors.

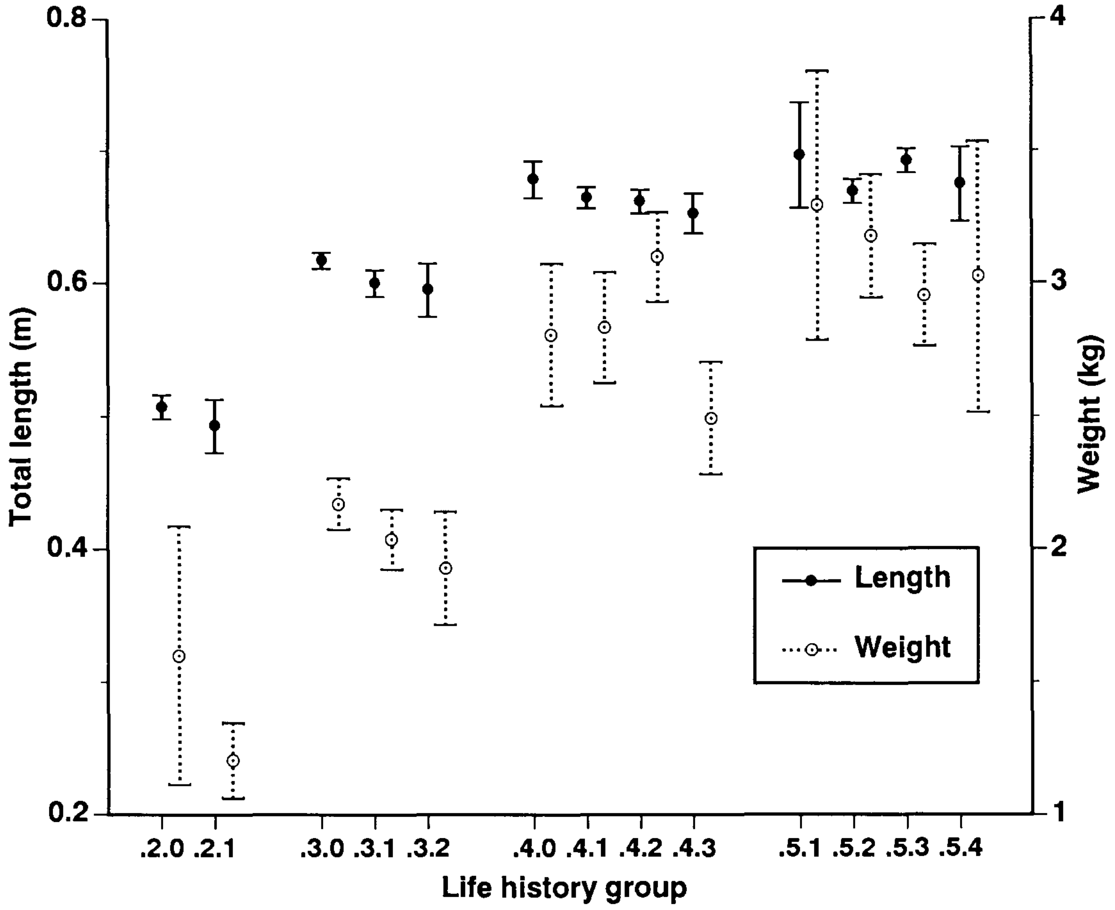

Figure 11.—Comparison of mean lengths and weights (with two standard errors) for adult steelhead returning to the Huron River with differing spawning histories [number of repeat spawners is designated by ".1 (1 repeat)" following lake age].

Table 1.–Characteristics of wild juvenile steelhead emigrating from the Huron River in 1987 and 1988. Shown are the mean with two standard errors (in parentheses).

Emigrant group	Age-1 parr	Age-1 smolts	Age-2 smolts
Number			
1987	3118	2964	3059
	(733)	(696)	(719)
1988	133	118	933
	(27)	(24)	(190)
Yield per hectare			
1987	136	129	133
1988	6	5	41
Percent of total			
1987	34	32	34
1988	11	10	79
Mean total length (mm)			
1987	112	160	183
	(18)	(59)	(51)
1988	113	187	164
	(21)	(58)	(45)

Table 2.-Mark-recapture data and population sizes for spawning steelhead in the Huron River, spring 1988-1992.

Year and lake age	Number marked	Number in recapture sample	Number recaptured	Population estimate	95% Confidence interval
1988					
1	107	46	5	838	492-2,829
2+	184	30	1	2,852	1,438-2,852
1989					
1	62	11	2	248	134-372
2+	52	130	4	1,362	762-6,414
1990					
1	9	1	0	301[1]	177-853[1]
2+	239	115	9	2,772	1,759-6,539
1991					
1	22	6	3	39	24-99
2+	117	133	18	825	583-1,411
1992					
1	19	11	1	114	58-114
2+	88	103	9	915	582-2,144

[1] No estimate made. Numbers presented are means of other years.

Table 3.-Survival rates in Lake Superior for various emigrant groups representing the 1987 and 1988 emigrant cohorts from the Huron River.

Year and emigrant group	Number of emigrants	Number of returning adults	Percent survival
1987			
parr	3,118	627	20
smolt 1	2,964	1,499	51
smolt 2	3,059	324	11
hatchery	24,588	7	<1
1988			
parr	133	359	>100
smolt 1	118	762	>100
smolt 2	933	243	26
hatchery	15,585	75	<1

Table 4.–Characteristics of the Huron River steelhead fishery, spring 1988-92. Shown are the mean and two standard errors.

Year	Number caught	Hours fished	Catch per hour
1988	184 ±132	3,950±1,143	0.05±0.00
1989	344 ± 33	2,093± 299	0.16±0.00
1990	191 ± 89	3,101± 730	0.06±0.00
1991	227 ± 88	4,602±1,233	0.05±0.02
1992	178 ± 76	2,907± 638	0.06±0.00

References

Anonymous. 1988-1991. Fish stocking records. Michigan Department of Natural Resources, Lansing.

Anonymous. 1989. Fishery analysis tools. Missouri Department of Conservation, Fisheries Division, Jefferson City.

Anonymous. 1991a. North Shore steelhead plan. Minnesota Department of Natural Resources, Fisheries Section, St. Paul.

Anonymous. 1991b. Buchanan Hydropower Project 2551, Application for License (Appendix E-2) to the Federal Energy Regulatory Commission. American Electric Power Service Corporation, Columbus, Ohio.

Anonymous. 1993. Wisconsin trout fishing regulations and guidelines. Wisconsin Department of Natural Resources, Madison.

Barton, B. A., R. E. Peter, and C. R. Paulencu. 1980. Plasma cortisol levels of fingerling rainbow trout (*Salmo gairdneri*) at rest, and subjected to handling, confinement, transport, and stocking. Canadian Journal of Fisheries and Aquatic Sciences 37:805-811.

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

Close, T., and R. Hassinger. 1981. Evaluation of Madison, Donaldson, and Kamloops strains of rainbow trout *Salmo gairdneri* in Lake Superior. Minnesota Department of Natural Resources, Fisheries Investigational Report 372, St. Paul.

Conner, D. J., C. R. Bronte, J. H. Selgeby, and H. L. Collings. 1993. Food of salmonine predators in Lake Superior, 1981-87. Great Lakes Fishery Commission, Technical Report 59, Ann Arbor, Michigan.

Dahl, F. H., and R. B. McDonald. 1980. Effects of control of the sea lamprey (*Petromyzon marinus*) on migratory and resident fish populations. Canadian Journal of Fisheries and Aquatic Sciences 37:1886-1894.

Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology 72:1180-1186.

Hansen, M. J., and T. M. Stauffer. 1971. Comparative recovery to the creel, movement and growth of rainbow trout stocked in the Great Lakes. Transactions of the American Fisheries Society 100:336-349.

Hare, G. M. 1973. A modified stake net for collecting migrating smolts of Atlantic salmon (*Salmo salar*). Journal of the Fisheries Research Board of Canada 30:128-129.

Hassinger, R. L., J. G. Hale, and D. E. Woods. 1974. Steelhead of the Minnesota North Shore. Minnesota Department of Natural Resources, Fisheries Technical Bulletin 11, St. Paul.

Hassler, T. J. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest): coho salmon. U.S. Fish and Wildlife Service, National Wetlands Research Center, Biological Report 82(11.70), Slidell, Louisianna.

Hendrickson, G. E., R. L. Knutilla, and C. J. Doonan. 1973. Hydrology and recreation on the cold-water rivers of Michigan's Upper Peninsula. U. S. Geological Survey, Water Information Report Series 4, Lansing, Michigan.

Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early-ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181-2194.

Jude, D. J., F. J. Tesar, S. F. Deboe,and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973-1982. Transactions of the American Fisheries Society 116:677-691.

Krueger, C. C., and B. May. 1987. Stock identification of naturalized brown trout in Lake Superior tributaries: differentiation based on allozyme data. Transactions of the American Fisheries Society 116:785-795.

Kwain, W.-H. 1981. Population dynamics and exploitation of rainbow trout in Stokely Creek, Eastern Lake Superior. Transactions of the American Fisheries Society 110:210-215.

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

Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Movement and survival of presmolt steelhead in a tributary and the main stem of a Washington river. North American Journal of Fisheries Management 6:526-531.

Lirette, M. G., R. S. Hooton, and W. R. Olmstead. 1985. A summary of wild steelhead smolt enumeration and habitat productivity studies at Quinsam River, 1976-1984. British Columbia Ministry of the Environment, Fish and Wildlife Branch, Fisheries Technical Circular 67, Nanaimo.

Miller, B. R. 1974. The spawning migration and growth studies of steelhead in the Huron River, Baraga County, Michigan 1966-1970. Michigan Department of Natural Resources, Fisheries Technical Report 74-10, Ann Arbor.

Miller, B. R. 1975. Results of transferring adult steelhead above migration barriers to spawn in the Huron River, Baraga County 1967-1970. Michigan Department of Natural Resources, Fisheries Technical Report 75-2, Ann Arbor.

Moore, H. H., and R. A. Braem. 1965. Distribution of fishes in U. S. streams tributary to Lake Superior. U. S. Fish and Wildlife Service, Special Scientific Report--Fisheries 516.

Myers, R. A., and J. A. Hutchings. 1987. Sea age at maturity for Atlantic salmon, *Salmo salar*, in North America. Canadian Technical Report of Fisheries and Aquatic Sciences 1566.

Northcote, T. G. 1969. Patterns and mechanisms in the lakeward migratory behavior of juvenile trout. Pages 183-204 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, The University of British Columbia, Vancouver.

Parker, N. C. 1986. Physical and biological factors influencing growth and survival of stocked fish. Pages 235-242 *in* R. H. Stroud, Editor. Fish culture in fisheries management. American Fisheries Society Symposium, Bethesda, Maryland.

Peck, J. W. 1992. The sport fishery and contribution of hatchery trout and salmon in Lake Superior and tributaries at Marquette, Michigan, 1984-87. Michigan Department of Natural Resources, Fisheries Research Report 1975, Ann Arbor.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818.

Rand, P. S., D. J. Stewart, P. W. Seelbach, M. L. Jones, and L. R. Wedge. 1993. Modeling steelhead trout population energetics in Lakes Michigan and Ontario. American Fisheries Society 122:977-1001.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin 191.

Ryckman, J. R., and R. N. Lockwood. 1985. On-site creel surveys in Michigan 1975-82. Michigan Department of Natural Resources, Fisheries Research Report 1922, Ann Arbor.

Scholl, D. K., P. J. Peeters, and S. T. Schram. 1984. Migratory brown trout and rainbow trout populations of the Brule River, Wisconsin. Wisconsin Department of Natural Resources, Fish Management Report 123, Madison.

Seelbach, P. W. 1987a. Smolting success of hatchery-raised steelhead planted in a Michigan tributary of Lake Michigan. North American Journal of Fisheries Management 7:223-231.

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

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

Seelbach, P. W., and G. E. Whelan. 1988. Identification and contribution of wild and hatchery steelhead stocks in Lake Michigan tributaries. Transactions of the American Fisheries Society 117:444-451.

Shapovalov, L., and A. C. Taft. 1954. Life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*), with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game, Fish Bulletin 98, Sacramento.

Stauffer, T. M. 1977. Numbers of juvenile salmonids produced in five Lake Superior tributaries and the effect of juvenile coho salmon on their numbers and growth, 1967-1974. Michigan Department of Natural Resources, Fisheries Research Report 1946, Ann Arbor.

Stearley, R. F. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus*. Pages 622-658 *in* R. L. Mayden, Editor. Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Palo Alto, California.

Steward, C. R., and T. C. Bjornn. 1990. Supplementation of salmon and steelhead stocks with hatchery fish: a synthesis of published literature. U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, Technical Report 90-1, Portland.

Swanson, B. L. 1985. Pikes Creek/Lake Superior steelhead population: population dynamics, fishery, and management alternatives. Wisconsin Department of Natural Resources, Fish Management Report 125, Madison.

Thorpe, J. E. 1986. Age at first maturity in Atlantic salmon *Salmo salar*: freshwater period influences and conflicts with smolting. Pages 7-14 *in* D. J. Meerburg, Editor. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89.

Thorpe, J. E., R. I. G. Morgan, E. M. Ottaway, and M. S. Miles. 1980. Time of divergence of growth groups between potential 1+ and 2+ smolts among sibling Atlantic salmon. Journal of Fish Biology 17:13-21.

Wagner, W. C., and T. M. Stauffer. 1978. Survival of rainbow trout stocked in a Lake Superior tributary, 1971-1973. Michigan Department of Natural Resources, Fisheries Research Report 1859, Ann Arbor.

Walters, C. J., R. Hilborn, R. M. Peterman, and M. Staley. 1978. A model for examining early ocean limitations of Pacific salmon production. Journal of the Fisheries Research Board of Canada 35:1303-1315.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853-1858.

Wedemeyer, G. H., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Marine Fisheries Review 42:1-14.

Winter, J. D. 1976. Movements and behavior of largemouth bass (Micropterus salmoides) and steelhead (Salmo gairdneri) determined by radio telemetry. Doctoral Dissertation, University of Minnesota, St. Paul.

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Appendix 1.-Fish species found in the Huron River by Moore and Braem (1965) and observed in this study. Collections in this study were not exhaustive.

Common name	Scientific name	Present in 1965	Observed in this study
Northern brook lamprey	Ichthyomyzon fossor	x	
Silver lamprey	*Ichthyomyzon unicuspis*	x	
Sea lamprey	*Petromyzon marinus*	x	x
Lake chub	*Couesius plumbeus*	x	
Common carp	*Cyprinus carpio*		x
Brassy minnow	*Hybognathus hankinsoni*	x	
Common shiner	*Luxilus cornutus*	x	x
Pearl dace	*Margariscus margarita*	x	
Hornyhead chub	*Nocomis biguttatus*		x
Blacknose shiner	*Notropis heterolepis*	x	
Spottail shiner	*Notropis hudsonius*	x	x
Northern redbelly dace	*Phoxinus eos*	x	x
Blacknose dace	*Rhinichthys atratulus*	x	x
Longnose dace	*Rhinichthys cataractae*	x	x
Creek chub	*Semotilus atromaculatus*	x	x
White sucker	*Catostomus commersoni*	x	x
Longnose sucker	*Catostomus catostomus*	x	x
Yellow bullhead	*Ameiurus natalis*		x
Northern pike	*Esox lucius*	x	x
Central mudminnow	*Umbra limi*	x	x
Rainbow smelt	*Osmerus mordax*	x	x
Lake whitefish	*Coregonus clupeaformis*		x
Pink salmon	*Oncorhynchus gorbuscha*		x
Coho salmon	*Oncorhynchus kisutch*		x
Rainbow trout	*Oncorhynchus mykiss*	x	x
Chinook salmon	*Oncorhynchus tshawytscha*	x	
Round whitefish	*Prosopium cylindraceum*		x
Brown trout	*Salmo trutta*		x
Brook trout	*Salvelinus fontinalis*	x	x
Troutperch	*Percopsis omiscomaycus*	x	x
Burbot	*Lota lota*	x	x
Brook stickleback	*Eucalia inconstans*	x	
Mottled sculpin	*Cottus bairdi*	x	x
Rock bass	*Ambloplites rupestris*	x	x
Smallmouth bass	*Micropterus dolomieu*	x	x
Johnny darter	*Etheostoma nigrum*	x	
Yellow perch	*Perca flavescens*	x	x
Logperch	*Percina caprodes*	x	

Appendix 2.-Population characteristics of wild coho salmon in the Huron River, 1987-1988.

	1987	1988
Smolts		
Total number	13,154 ± 3,090	7,744 ± 1,572
Mean length (mm)	121 ± 12	112 ± 21
Mean date of migration	May 17 (95% of migration: 5/3 - 5/31)	May 18 (95% of migration: 5/7 - 5/29)
Adults		
Population size		
Number handled	56	89
Number per net day	2.8	3.7
Mean length (mm)		
Jacks	313 ± 40	---
Adults	539 ± 91	535 ± 74
Migration period	September 3 - November 11	September 19 - October 28

Appendix 3.-Estimated numbers of maiden-spawning adult steelhead returning to the Huron River during spring 1988-1992. Age is shown as "stream years.lake years". For 1 stream year-fish, parr and smolts are designated as "I" and "1", respectively.

Origin, sex Emigrant cohort and age	1986	1987	1988	1989
Wild				
Male				
I.1	282	522	270	55
1.1	571	661	576	475
2.1	86	122	126	11
I.2	17	0	0	0
1.2	35	198	44	10
2.2	0	108	33	0
I.3	36	11	10	17
1.3	144	110	10	51
2.3	36	11	21	0
I.4	0	0	17	6
1.4	44	10	0	18
2.4	11	0	0	4
Female				
I.2	0	72	0	10
1.2	70	90	22	10
2.2	0	18	22	0
I.3	54	22	62	103
1.3	144	409	41	120
2.3	90	44	41	51
I.4	33	0	0	11
1.4	44	21	69	11
2.4	0	21	0	7
All Hatchery				
Male				
1.1	-	244	90	44
1.2	-	54	22	21
1.3	-	11	41	34
1.4	-	0	0	0
Female				
1.2	-	36	0	10
1.3	-	66	41	69
1.4	-	10	0	3
Adipose Hatchery				
Male				
1.1	-	0	17	0
1.2	-	17	8	10
1.3	-	8	35	0
1.4	-	0	0	0
Female				
1.2	-	34	0	0
1.3	-	16	15	52
1.4	-	0	0	0