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Life-history Characteristics, Population Structure, and Contribution of Hatchery and Wild Steelhead in a Lake Huron Tributary

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ABSTRACT. *Life-history characteristics, size structure, and relative composition of hatchery-reared and wild-produced steelhead* Oncorhynchus mykiss *in the Carp River, Michigan, were examined to determine if population attributes were similar between origins. Quantitative scale analyses were used to determine the origin and life-history attributes of adult fish captured during their spring spawning migration from 1995–1998. Hatchery males and females comprised 40% and 23%, respectively, of the spawning migration, while wild males and females comprised 19% and 18%, respectively. Male and female hatchery steelhead had shorter stream-residence durations (1 year) than wild fish (2 years). Both genders of hatchery individuals also reached reproductive maturity at younger ages (males, 3 years; females, 4 years) than wild fish (5 years). The number of years between repeat-spawning events was the same (1 year), irrespective of gender or origin. However, the number of fish captured during repeat-spawning events differed between origins (hatchery males: 42%; wild males: 9%; hatchery females: 23%; and wild females: 26%). The median number of years in lake residence prior to maiden spawning did not differ between hatchery and wild fish (males, 2 years; females, 3 years). Median length-at-age estimates differed between hatchery and wild male steelhead at age 4 (66 cm and 58 cm, respectively), while the median length-at-age for all other age classes did not differ, irrespective of gender and origin. Our results suggest that differences in life-history characteristics exist between hatchery-reared and wild-produced Carp River steelhead, and that system-specific management objectives should be considered prior to the initiation of stocking efforts.*

INDEX WORDS: *Carp River, Lake Huron, life history,* Oncorhynchus mykiss, *potamodromous, scale analysis.*

INTRODUCTION

Steelhead *Oncorhynchus mykiss*, the potamodromous (i.e., migratory) life-history variant of the rainbow trout, were introduced throughout the Laurentian Great Lakes in the late 1800s (MacCrimmon and Gots 1972, Seelbach 1987). Over the past century, this species has established naturally-reproducing populations in all five Great Lakes (Biette *et al*. 1981, Seelbach 1993). Steelhead have become an important and intensely-managed sport fish throughout the region, supporting a popular recreational fishery (Kocik and Jones 1999). To enhance and sustain naturalized populations, state fisheries management agencies utilize hatchery-stocking programs. Fish are stocked into Great Lakes tributaries as smolts, with the intent that these individuals will emigrate to the lakes proper shortly after release and return to their tributary of introduction to spawn as adults.

Despite its importance as a recreational species, knowledge regarding the life-history attributes and relative contribution of hatchery-reared and natu-

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rally-produced (hereafter referred to as hatchery and wild, respectively) steelhead in the Great Lakes is limited (Seelbach and Whelan 1988, Seelbach 1993). Stocking programs are evaluated based on the number of introduced fish that survive and return to the river in which they were stocked as adults (Ward and Slaney 1990), their occurrence in the creel, and the degree to which stocked fish resemble the behavior, growth, and life history of wild individuals. The Great Lakes Fishery Commission (GLFC) has recommended that management practices should be focused on the production of naturally sustainable fisheries and the preservation of wild stocks (GLFC 1992), and that hatchery-stocking programs used to maintain such fisheries should be tailored to avoid erosion of wild-stock integrity (Harbeck 1999). Because the characteristics of wild populations are a result of local environmental pressures and genetics, the characteristics of hatchery fish should resemble those of the wild population in order for stocking efforts to be successful (Steward and Bjornn 1990, Harbeck 1999). Therefore, information regarding life-history characteristics of hatchery and wild fish are vital for the optimal management of steelhead within a given system (i.e., enhancement or protection of wild populations versus supplementation with hatchery fish), and for the development of scientifically-sound Great Lakes management policies (Seelbach and Whelan 1988).

In recent years, considerable attention has been focused on the potential effects of hatchery steelhead on wild populations of this species. Artificial selection pressures in the hatchery may result in the stocking of fish that are different from wild individuals, rendering them less fit than wild conspecifics with which they may interact or spawn (Campton *et al.* 1991). Numerous studies have also examined differences in the physical attributes, behavior, and genetic contributions of wild and hatchery steelhead (Reisenbichler and McIntyre 1977; Chilcote *et al.* 1986; Leider *et al.* 1986, 1990; Seelbach and Whelan 1988; Campton *et al.* 1991; Seelbach and Miller 1993; McMichael *et al.* 1999, 2000). However, differences in life-history traits between hatchery and wild fish have received little attention. Leider *et al.* (1986) observed fewer age categories, younger ages-at-reproductive maturity, and a lower incidence of repeat spawners for hatchery steelhead relative to wild fish in the Kalama River, Washington. Harbeck (1999) reported shorter stream-residence durations and fewer repeat-spawning hatchery fish compared to wild individuals in the Betsie River, Michigan. In addition, other studies have reported that hatchery steelhead may fail to become migratory due to inappropriate sizes at stocking (i.e., too large or too small) and precocious sexual development, thereby contributing little to the spawning population and fishery (Wagner *et al.* 1963, Slaney and Harrower 1981, Rempel *et al.* 1984, Ward and Slaney 1990).

The objective of this study was to compare the life-history attributes, size structure, and relative composition of hatchery and wild adult steelhead in the Carp River, Michigan, during the 1995 -1998 spring spawning migration. Quantified scale analyses were used to determine life-history traits and capture rates to compare relative compositions of each origin type and gender. Our null hypothesis was that there were no significant differences between hatchery and wild fish of either gender for each life-history characteristic examined.

STUDY SITE

The Carp River, a fourth-order tributary of northern Lake Huron, is located within Chippewa and Mackinaw counties in the Upper Peninsula of Michigan. From its origin at Trout Lake, the river flows 58-km southeast, draining an area of approximately 45,000 ha. The Carp River is shallow and wide, with a mean water depth and wetted width of 0.5 m and 15 m, respectively, and exhibits a highly dynamic flow regime with seasonal fluctuations in discharge ranging from 4 to 40 m^3/s over an average gradient of 6 m/km. Bottom substrates are comprised primarily of sand, although long stretches of the river contain cobble and gravel. The channel morphology is highly unstable, which can be attributed to the extensive sand bedload caused by timber-harvest practices in the early 1900s (Klingler 1997).

The Carp River is managed as a trout stream by the Michigan Department of Natural Resources (MDNR) as self-sustaining populations of native brook trout *Salvelinus fontinalis* and naturalized brown trout *Salmo trutta* exist in this system. Over the past decade, efforts have been undertaken by the MDNR and the USDA Forest Service to improve salmonid habitat through re-establishment of a deeper, narrower channel that is more representative of the system prior to historical timber harvest (S. Scott, MDNR, unpublished data). A steelhead stocking program was initiated in 1980 by the MDNR to improve angling opportunities in the Carp River. Since 1980, a total of 211,674 Michigan

TABLE 1. Date of stocking, number stocked, and mean length of hatchery-reared steelhead released in the Carp River, Michigan, 1980–1998.

Date stocked	Number stocked	Mean length (cm)
June 1980	10,000	10.6
June 1981	10,000	12.0
June 1982	10,003	8.2
May 1983	10,000	10.5
May 1984	7,000	13.2
April 1985	10,000	14.6
May 1986	20,000	16.9
April 1987	15,000	18.5
May 1988	11,500	16.7
May 1989	10,900	19.7
May 1990	9,610	17.5
May 1991	9,600	18.2
May 1992	10,000	18.9
May 1993	10,574	17.4
June 1994	16,650	16.5
May 1995	10,250	18.5
May 1996	9,180	18.5
June 1996	2,340	19.3
May 1997	9,840	16.2
May 1998	9,200	19.4

winter-strain steelhead smolts have been stocked in the system approximately 150 m upstream from the river mouth (Table 1).

METHODS

Two passive gear types were used to capture adult steelhead from the Carp River during spring spawning migrations that occurred from March through June 1995–1998. Four fyke nets (1.2-m wide × 1.2-m high square frame and 15-m wings; 2.0-cm stretch mesh) and one trap net (1.8-m wide × 1.8-m high mouth and 45-m lead; 6.4-cm stretch mesh) were set parallel to the river current, with the mouth of each net oriented in a downstream direction to capture steelhead migrating upriver. Nets were deployed immediately downstream of known spawning sites, which were located 0.3 km, 1.9 km, and 4.5 km upstream from the river mouth at Lake Huron. Fyke nets were set at water depths ranging from 0.5 to 1.0 m on gravel substrates (water-velocity range, 0.3–1.0 m/s), while the trap net was set at water depths ranging from 1.0 to 1.25 m on sand substrates (water-velocity range, 0.1–0.5 m/s). Paired sets were used when water depth was greater than 1.25 m to increase the percentage of the stream sampled and to improve capture rates. All nets were checked daily during each annual sampling period.

All captured steelhead were measured for total length (TL) to the nearest 1 cm, gender was recorded, and scale samples were collected posterior to the dorsal fin and anterior to the anal fin above the lateral line (Scarnecchia 1979, Knudsen and Davis 1985). Fish were not anesthetized during processing. Gender for each individual was assigned based on the presence of milt or eggs, which was determined by exerting light pressure to the abdomen of the fish. All fish were marked with a serially-coded, T-bar anchor tag (Floy Tag, Seattle, Washington) to prevent resampling of the same individual. Steelhead were released 200 m upstream of their capture location to prevent recapture in the same net.

In the laboratory, scales were separated, cleaned of debris and mucus, and retained for age and life-history analyses if there were no signs of damage or regeneration. In the event that scales collected from a fish did not meet these requirements, the individual was omitted from further analyses. Impressions of four scales from each steelhead were made on cellulose acetate slides using a roller press and examined at 100× magnification using a microfiche projector. Two readers analyzed each scale sample independently. Discrepancies between readers led to re-analysis of the scale sample in question until agreement was reached.

Characteristics of the circuli and annuli, as described by Edinger (1987), were used to estimate age and life-history traits. Age was recorded as "stream years.lake years," and an "s" noted the occurrence of a spawning event (Shapovalov and Taft 1954, Withler 1966, Seelbach 1993). A stream year was defined as a year of life in which an individual resided in the stream environment, while a lake year was defined as a year spent in the Great Lakes following emigration from the stream. Scale analyses and resulting life-history notations for hatchery and wild fish were handled identically. We acknowledged that the first stream-residence year for hatchery individuals was spent in the hatchery environment during the interpretation of the results. Smolt checks were used to determine the age at which an individual emigrated to the lake environment, while spawning checks were used to determine the age-at-reproductive maturity, lake-residence years prior to maiden spawning (i.e., the first spawning event experienced by an individual), and the number of years between repeat-spawning events. We assumed that the first year an individual

TABLE 2. Percent composition (numbers) of adult steelhead captured during spring spawning migrations in the Carp River, Michigan, 1995–1998.

	Fish origin				
Sampling year	Hatchery male	Wild male	Hatchery female	Wild female	Total captured
1995	54 (40)	18 (13)	18 (13)	10 (8)	74
1996	34 (26)	26 (20)	15 (11)	25 (19)	76
1997	14 (4)	10 (3)	43 (13)	33 (10)	30
1998	43 (17)	15 (6)	35 (14)	7 (3)	40
Total	40 (87)	19 (42)	23 (51)	18 (40)	220

spawned was the age at which it reached reproductive maturity, and that spawning was to occur during the year of capture.

Fish origin (hatchery or wild) was derived from ratio 23, which was defined by Seelbach and Whelan (1988) as the ratio between the width of the five intercircular spaces immediately prior to formation of the first annulus (scale-band 2) to that of the five intercircular spaces immediately after that annulus (scale-band 3). Fish were considered to be of hatchery origin if the calculated ratio was greater than 0.7, while fish were designated as wild origin with a ratio less than that value (Seelbach and Whelan 1988).

Steelhead were classified based on origin (hatchery or wild) and gender (male or female). Data from all 4 years of the study were pooled to increase sample sizes and statistical power. To detect differences between origins for each life-history characteristic, data were analyzed using a Wilcoxon two-sample test for each gender. For length-at-age analyses, individuals were further categorized based on their age-at-capture and each cohort was tested independently. Analysis of the spawning migration composition (hatchery, wild; male, female) was accomplished using a chi-square goodness-of-fit test. A Kolmogorov-Smirnov test was used to compare the length-frequency distributions of hatchery and wild fish of each gender (Zar 1999). All statistical analyses were conducted at an $\alpha = 0.05$ level of significance.

RESULTS

A total of 220 steelhead was captured during the 4-year study period. Hatchery males and females accounted for 40% and 23%, respectively, of the total spawning run composition, while wild males and females comprised 19% and 18%, respectively (Table 2). Gender ratios (male:female) for hatchery and wild fish (1.7:1 and 1.3:1, respectively) were not significantly different ($\chi^2 = 2.59$, $P = 0.11$).

Hatchery steelhead, regardless of gender, exhibited a shorter stream-residence duration than wild fish (males, $W = 4{,}252$, $P < 0.001$; females, $W = 2{,}492$, $P < 0.001$; Table 3). Eighty-six percent of hatchery males left the stream after 1 year of residence, whereas 81% of wild males left the stream after 2 years (range, 1 to 3 years). For females, 77% of the hatchery steelhead left the stream after 1 year, compared to 13% for wild fish (range, 1 to 2 years).

The number of lake-residence years prior to maiden spawning events did not differ for either gender of steelhead (males, $W = 2{,}906$, $P = 0.99$; females, $W = 1{,}669$, $P = 0.09$; Fig. 1). For males,

TABLE 3. Percent composition (numbers) based on stream-residence duration of adult steelhead captured during spring spawning migrations in the Carp River, Michigan, 1995–1998.

	Fish origin				
Stream years	Hatchery male	Wild male	Hatchery female	Wild female	Total number
1	86 (75)	17 (7)	77 (39)	13 (5)	126
2	13 (12)	81 (34)	23 (12)	87 (35)	93
3	0 (0)	2 (1)	0 (0)	0 (0)	1

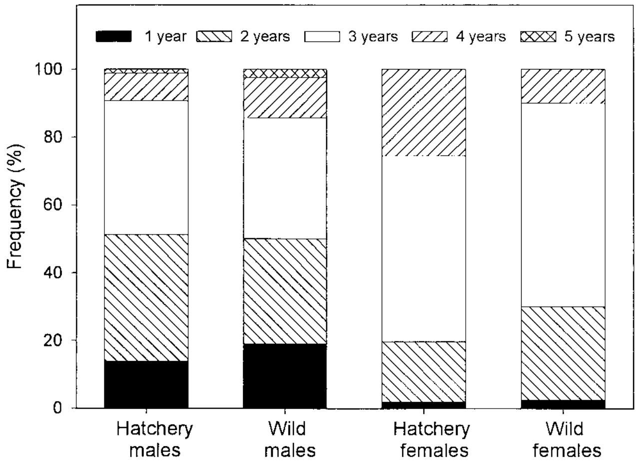

FIG. 1. Number of lake-residence years prior to maiden spawning events for hatchery and wild male and female steelhead captured during spring spawning migrations in the Carp River, Michigan, 1995–1998.

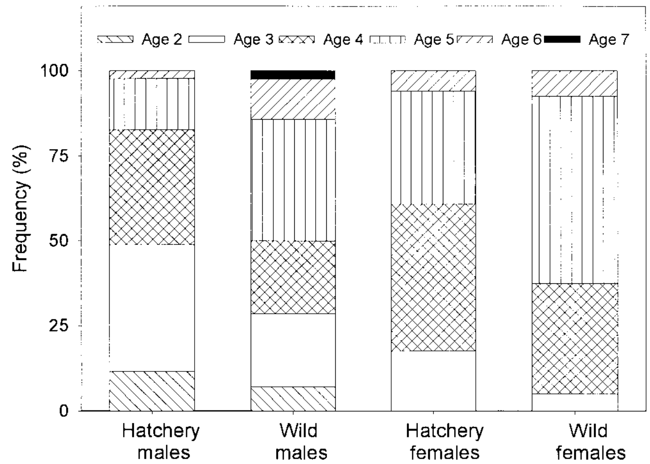

FIG. 2. Age-at-reproductive maturity of hatchery and wild male and female steelhead captured during spring spawning migrations in the Carp River, Michigan, 1995–1998.

37% and 34%, respectively, of the hatchery and wild fish captured during the spawning migration returned to spawn after 2 years of lake residence, while 34% and 37% of hatchery and wild males, respectively, returned to spawn after 3 years (range, 1 to 5 years). Of females, 45% of the hatchery fish captured returned to spawn after 3 years of lake residence, while 73% of wild fish returned after 3 years (range, 1 to 4 years).

The number of years between repeat-spawning events was not significantly different between hatchery and wild steelhead for either gender (males, $W = 83.5$, $P = 0.21$; females, $W = 165.0$, $P = 0.83$; Table 4). Fish captured during their second or third spawning event typically spawned again in consecutive years. For males, 86% of hatchery and 50% of wild repeat-spawning fish captured during the spring spawning migration spawned in consecutive years (range, 1 to 3 years), while the same was observed for 83% and 71% of hatchery and wild females, respectively (range, 1 to 2 years). The number of individuals captured during a repeat-spawning event was significantly different between hatchery and wild fish ($\chi^2 = 7.19$, $P = 0.007$; Table 4). Hatchery males comprised 42%, wild males 9%, hatchery females 23%, and wild females 26% of fish captured during a repeat-spawning event. During spawning migrations, 24% and 14% of hatchery males and females, respectively, and 24% and 38% of wild males and females, respectively, were captured during a repeat spawning event.

Age-at-reproductive maturity was significantly different between hatchery and wild steelhead (males, $W = 3{,}577$, $P < 0.001$; females, $W = 2{,}146$, $P = 0.015$; Fig. 2). For males, 37% of hatchery fish reached reproductive maturity at age 3, while 33% of wild males reached reproductive maturity at age 5 (range, 2–7 years). Hatchery females also

TABLE 4. Percent composition (numbers) of repeat spawning steelhead based on the number of years between spawning events in the Carp River, Michigan, 1995–1998.

	Fish origin				
Years between spawning events	Hatchery male	Wild male	Hatchery female	Wild female	Total number
1	86 (19)	50 (3)	83 (10)	71 (10)	42
2	9 (2)	50 (3)	17 (2)	29 (4)	11
3	5 (1)	0 (0)	0 (0)	0 (0)	1

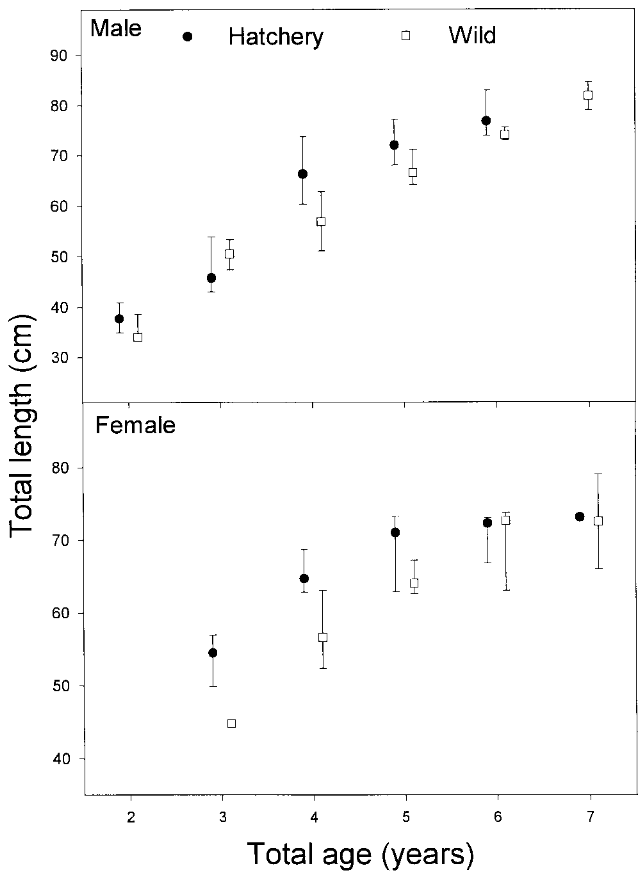

FIG. 3. Median length-at-total age estimates for hatchery and wild male and female steelhead captured during spring spawning migrations in the Carp River, Michigan, 1995–1998. Error bars indicate 25th and 75th percentiles.

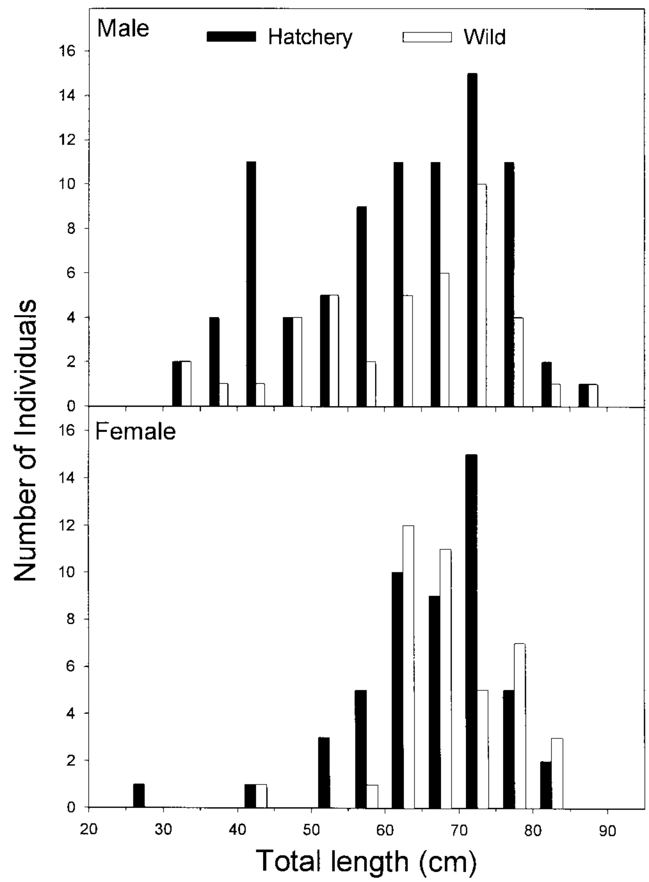

FIG. 4. Length-frequency distributions for hatchery and wild male and female steelhead captured during spring spawning migrations in the Carp River, Michigan, 1995–1998.

reached reproductive maturity at a younger age, with 43% reaching reproductive maturity at age 4, while a majority of wild females (55%) reached reproductive maturity at age 5 (range, 3–6 years).

Hatchery male steelhead at age 4 had a significantly-greater length-at-age than wild fish (W =121, P = 0.005; Fig. 3). The median value of male hatchery fish at age 4 was 9.2 cm larger than their wild counterparts. All other age classes of hatchery and wild fish, irrespective of gender, did not differ significantly in length (all $W \geq 11$, all $P \geq 0.08$). Neither hatchery nor wild male or female fish were consistently larger throughout the age ranges observed in annual spawning returns. Length-frequency distributions of hatchery and wild fish were not significantly different for either gender (males, Z = 0.85, P = 0.47; females, Z = 0.72, P = 0.67; Fig. 4).

DISCUSSION

Since the age at which salmonids smolt is affected by their growth rate (Hoar 1976, Randall *et al.* 1987, Peven *et al.* 1994), the shorter stream-residence duration observed for stocked steelhead in the Carp River could be attributed to enhanced growth conditions maintained in the hatchery. Steelhead within a cohort which reach a minimum size of approximately 15 to 16 cm during the first year of life typically smolt, while smaller individuals will remain in the river for additional periods of time (Wagner *et al.* 1963, Wallis 1968, Chrisp and Bjornn 1978). Since juvenile steelhead are stocked in the Carp River at a mean length of 16.1 cm, the 1 year of stream residence observed for hatchery individuals is actually the year spent in the hatchery prior to stocking. Wagner (1968) suggested that an ideal stocking program involves rapid imprinting and emigration shortly after introduction. Wallis (1968) and Chrisp and Bjornn (1978) reported that hatchery fish are typically subjected to high mortality when individuals remain in the river for extended periods of time after stocking due to competition with wild individuals. The results of this study suggest a majority of hatchery fish leave the system shortly after stocking.

Among other Great Lakes populations, Thompson and Ferreri (2002) found that based on scale analyses, greater than 98% of male and female adult steelhead captured during the spawning run spent 1 year in stream residence in three Lake Erie tributaries with populations dominated by hatchery fish stocked as smolts. Conversely, Seelbach (1993) found that 77% of wild steelhead resided in the stream for 2 years in the Little Manistee River, Michigan. Harbeck (1999), examining the life-history characteristics of hatchery and wild steelhead in the Betsie River, Michigan, found that nearly all hatchery fish left the stream after 1 year of residence, while most wild individuals smolted after 2 years. Studies by Kwain (1971) and Stauffer (1972) reported similar results in other Great Lakes tributaries. The results of these studies indicate that stream-residence durations observed for hatchery and wild steelhead in the Carp River are similar to other Great Lakes populations.

The different ages-at-reproductive maturity observed between hatchery and wild steelhead may be due to the shorter stream-residence durations observed for hatchery individuals. The larger size and earlier emigration of hatchery smolts may result in continued enhanced growth in the lake and increase the probability of returning to the river to spawn at a younger age. Wagner (1967) and Ward *et al.* (1989) identified inverse relationships between smolt length and age-at-maturity for hatchery and wild steelhead. In addition, studies of Pacific coast populations have shown that smolts stocked at a large size (> 45 g) had greater survival rates than smaller individuals, resulting in a higher rate of return (Larson and Ward 1955, Wagner 1967, Royal 1972, Tipping 1991). Seelbach (1987) reported that large (mean length = 20 cm) steelhead stocked in the Little Manistee River, Michigan, had a higher rate of smolting relative to smaller (mean length = 19 cm or less) hatchery individuals. These results suggest that stocking of larger hatchery fish reduces interactions with wild individuals, improves survival, and produces adults which return to spawn at a younger age. As a result, these relationships may necessitate the stocking of larger individuals when primary management objectives are to increase population size and returns to the creel of hatchery fish.

Although a difference in length-at-age was observed for age-4 hatchery and wild male steelhead, neither origin nor gender had a consistently larger length at a given age. Harbeck (1999) reported no significant differences in length between hatchery and wild steelhead. Leider *et al.* (1986) reported that hatchery fish were significantly longer than wild cohorts after 1 year in the ocean, while hatchery fish were significantly shorter than wild fish when returning to spawn after 2 or 3 years. The authors also noted that significant inter-year variations in fish length existed for all but one age category of wild fish. Mackey *et al.* (2001) reported that wild female steelhead were larger than hatchery females, although wild fish had greater variation in length than those of hatchery origin. Our results are in agreement with these studies, suggesting that individual growth rates are highly variable among steelhead, particuliarly following emigration to the lake or ocean. However, the gender-specific length-frequency distributions observed in our study are similar to those reported by Harbeck (1999) and Thompson and Ferreri (2002), suggesting that the size structure of steelhead in the Carp River is comparable to that of other steelhead populations in the Great Lakes.

Our observation that most repeat-spawning steelhead in the Carp River spawned in consecutive years is similar to that of other Great Lakes populations (Seelbach 1993, Thompson and Ferreri 2002). However, the greater abundance of hatchery males captured during repeat-spawning events observed in the Carp River contradicts the results of similar studies. Harbeck (1999) reported that 18% of wild and 10% of hatchery steelhead were captured during repeat-spawning events, and that the incidence of repeat spawning was more prevalent among females than males. Rosentreter (1977) and Leider *et al.* (1986) reported lower numbers of hatchery steelhead captured during repeat-spawning events when compared to wild fish. Cederholm (1984) observed that hatchery steelhead began their spawning migrations earlier in the year than wild fish, increasing the likelihood of experiencing adverse environmental conditions (i.e., freshets and high turbidity). As a result, these fish exhibited lower survival relative to wild fish. The greater abundance of hatchery males relative to wild males captured during our study may account for the greater number of those individuals observed during repeat-spawning events.

The abundance of hatchery steelhead in the annual spawning migrations increased the returning adult stock by 214% in the Carp River. Although the potential does exist for hatchery fish to contribute to spawning, the reproductive success of hatchery fish has been shown to be much lower than wild steelhead in other systems. Leider *et al.* (1990) reported lower survival of offspring produced from hatchery steelhead, suggesting that long-term artificial selection and domestication in broodstock fish may cause differential mortality between offspring of hatchery and wild individuals. Chilcote *et al.* (1986) reported that the reproductive success of hatchery steelhead was substantially less than that of wild fish. These results suggest that increasing the size of the spawning stock with hatchery fish may not result in a greater reproductive output. Future studies should be undertaken to determine if wild spawning stocks of steelhead in Great Lakes tributaries enhanced with hatchery fish produce greater numbers of offspring with similar survival rates.

The stocking of steelhead in the Carp River has increased adult returns with hatchery fish that are similar to the wild stock in both size and abundance. However, differences exist in the life-history traits of hatchery and wild fish. Since many of these characteristics are affected by the size-at-stocking of hatchery individuals, heritability, or a combination of these factors, the life-history characteristics of wild fish may be altered when interbreeding occurs with hatchery steelhead (Ricker 1972, Ayerst 1977, Crawford 1979, Garrison and Rosentreter 1980, Gall *et al.* 1988, Tipping 1991). Differences in life-history attributes may also negatively affect the growth and survival of naturally-produced juveniles, as well as the spawning success of wild adults (Chilcote *et al.* 1986, Woodward and Strange 1987, Campton *et al.* 1991, Gresswell 1997, McMichael *et al.* 1999). If management objectives are to increase angling opportunities or population abundance, the stocking of hatchery steelhead may be a useful approach. However, objectives based on conserving wild steelhead populations through maintenance stocking may fail to preserve the life-history traits of wild fish. As a result, steelhead hatchery practices should minimize utilization of fish with attributes which are different from wild fish. To retain these life-history characteristics, the creation of a system-specific broodstock with life-history traits that resemble wild fish may be necessary (Chilcote *et al.* 1986, Leider *et al.* 1986). To minimize differences in early life-history traits, the earlier release of hatchery fish may minimize artificial selection pressures and differential growth rates. However, the survival of hatchery fish released at a smaller size may be significantly lower. Therefore, management objectives for steelhead populations should be addressed before considering the stocking of hatchery-reared fish.

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REFERENCES

Ayerst, J.D. 1977. The role of hatcheries in rebuilding steelhead runs of the Columbia River system. In *Columbia River salmon and steelhead,* Schweibert, E., ed. pp. 84–88. Bethesda, Maryland: American Fisheries Society Special Publication Number 10.

Biette, R.M., Dodge, D.P., Hassinger, R.L., and Stauffer, T.M. 1981. Life history and timing of migrations and spawning behavior of rainbow trout (*Salmo gairdneri*) populations of the Great Lakes. *Can. J. Fish. Aquat. Sci.* 38:1759–1771.

Campton, D.E., Allendorf, F.W., Behnke, R.J., and Utter, F.M. 1991. Reproductive success of hatchery and wild steelhead. *Trans. Am. Fish. Soc.* 120: 816–827.

Cederholm, C.J. 1984. Clearwater River wild steelhead spawning timing. In *Proceedings of the Olympic wild fish conference,* pp. 257–268. Peninsula College, Port Angeles, Washington.

Chilcote, M.W., Leider, S.A., and Loch, J.J. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Trans. Am. Fish. Soc.* 115:726–735.

Chrisp, E.Y., and Bjornn, T.C. 1978. *Parr-smolt transformation and seaward migration of wild and hatchery steelhead trout in Idaho. Idaho* Cooperative Fishery Research Unit, Federal Aid in Fish Restoration, Moscow. Project F-49-12.

Crawford, B.A. 1979. *The origin and history of the trout brood stocks of the Washington Department of Game.* Washington Game Department, Olympia.

Edinger, S.A. 1987. Age, growth patterns, abundance, and survival rates of adult rainbow trout (*Salmo* *gairdneri*) of the Little Garlic River, Marquette County, Michigan. M.S. thesis, Northern Michigan University, Marquette.

Gall, G.A., Baltodano, J., and Huang, N. 1988. Heritability of age at spawning for rainbow trout. *Aquaculture* 68:93–102.

Garrison, R.L., and Rosentreter, N.M. 1980. *Stock assessment and genetic studies of anadromous salmonids.* Oregon Department of Fish and Wildlife, Fisheries Division Annual Progress Report Number AFS 73–3.

GLFC (Great Lakes Fishery Commission). 1992. *Strategic vision of the Great Lakes Fishery Commission for the decade of the 1990s.* GLFC, Ann Arbor, Michigan.

Gresswell, R.E. 1997. Introduction to ecology and management of potamodromous salmonids. *N. Am. J. Fish. Manage.* 17:1027–1028.

Harbeck, J.R. 1999. Relative contribution and comparative life history characteristics of hatchery and wild steelhead trout in the Betsie River, Michigan. M.S. thesis, Michigan State University, East Lansing.

Hoar, W.S. 1976. Smolt transformation: evolution, behavior, and physiology. *J. Fish. Res. Board Can.* 33:1234–1252.

Klingler, G.L. 1997. The effect of a graduated electric field barrier on the upstream migration of steelhead (*Oncorhynchus mykiss*). M.S. thesis, Northern Michigan University, Marquette.

Knudsen, C.M., and Davis, N.D. 1985. *Variation in salmon scale characters due to body area sampled.* Document submitted to the annual meeting of the International North Pacific Fisheries Commission, Tokyo, Japan, November, 1985. FRI-UW-8504, Fisheries Research Institute, University of Washington, Seattle.

Kocik, J.F., and Jones, M.L. 1999. Pacific salmonines in the Great Lakes basin. In *Great Lakes fisheries policy and management: a binational perspective,* eds. W.W. Taylor and C.P. Ferreri, pp. 455–488. East Lansing, Michigan: Michigan State University Press.

Kwain, W.H. 1971. Life history of rainbow trout (*Salmo gairdneri*) in Batchawana Bay, eastern Lake Superior. *J. Fish. Res. Board Can.* 28:771–775.

Larson, R.W., and Ward, J.M. 1955. Management of steelhead trout in the state of Washington. *Trans. Am. Fish. Soc.* 84:261–274.

Leider, S.A., Chilcote, M.W., and Loch, J.J. 1986. Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. *Can. J. Fish. Aquat. Sci.* 43:1398–1409.

_____, Hulett, P.L., Loch, J.J., and Chilcote, M.W. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. *Aquaculture* 88:239–252.

MacCrimmon, H.R., and Gots, B.L. 1972. *Rainbow trout in the Great Lakes.* Ontario Ministry of Natural Resources, Toronto, Canada.

Mackey, G., McLean, J.E., and Quinn, T.P. 2001. Comparisons of run timing, spatial distribution, and length of wild and newly established hatchery populations of steelhead in Fork's Creek, Washington. *North Am. J. Fish. Manage.* 21:717–724.

McMichael, G.A., Pearsons, T.N., and Leider, S.A. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. *North Am. J. Fish. Manage.* 19: 948–956.

_____, Pearsons, T.N., and Leider, S.A. 2000. Minimizing ecological impacts of hatchery-reared juvenile steelhead trout on wild salmonids in a Yakima River basin watershed. In *Sustainable Fisheries Management: Pacific Salmon,* eds. E.E. Knudson, C.R. Steward, D.D. MacDonald, J.E. Williams, and D.W. Reiser, pp. 365–380. Boca Raton, Florida: CRC Press LCC.

Peven, C.M., Whitney, R.R., and Williams, K.R. 1994. Age and length of steelhead smolts from the mid-Columbia River basin, Washington. *North Am. J. Fish. Manage.* 14:77–86.

Randall, R.G., Healy, M.C., and Dempson, J.B. 1987. Variability in length of freshwater residence of salmon, trout, and char. *American Fisheries Society Symposium* 1:27–41.

Reisenbichler, R.R., and McIntyre, J.D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. *J. Fish. Res. Board Can.* 34:123–128.

Rempel, M.H., Land, R.W., Mitchell, L.W., and Ward, B.R. 1984. *Wild and hatchery steelhead and cutthroat trout populations of the Little Campbell River, B.C., 1983.* Victoria, British Columbia, Province of British Columbia Fisheries Technical Circular 62.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In *The stock concept in Pacific salmon,* eds. R. C. Simon and P. A. Larkin, pp.19–60. Vancouver, British Columbia: H. R. MacMillan Lectures in Fisheries.

Rosentreter, N.M. 1977. Characteristics of hatchery fish: angling, biology, and genetics. In *Columbia River salmon and steelhead,* Schweibert, E., ed. pp. 79–83. Bethesda, Maryland: American Fisheries Society Special Publication Number 10.

Royal, L.A. 1972. *An examination of the anadromous trout program of the Washington State Game Department.* Washington Department of Game, Olympia.

Scarnecchia, D.L. 1979. Variation in scale characters of coho salmon with sampling location on the body. *Prog. Fish-Culturist* 41:132–135.

Seelbach, P.W. 1987. Smolting success of hatchery-raised steelhead planted in a Michigan tributary of northern Lake Michigan. *North Am. J. Fish. Manage.* 7:223–231.

______. 1993. Population biology of steelhead in a stable-flow, low-gradient tributary of Lake Michigan. *Trans. Am. Fish. Soc.* 122:179–198.

______, and Miller, B.R. 1993. *Dynamics in Lake Superior of hatchery and wild steelhead emigrating from the Huron River, Michigan.* Michigan Department of Natural Resources, Ann Arbor, Michigan, Fisheries Research Report 1993.

______, and Whelan, G.E. 1988. Identification and contribution of wild and hatchery steelhead stocks in Lake Michigan tributaries. *Trans. Am. Fish. Soc.* 117:444–451.

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

Slaney, P.A., and Harrower, W.L. 1981. Experimental culture and release of steelhead trout reared in net-pens at O'Connor Lake in British Columbia. In *Proceedings: propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat symposium*, pp. 43–51. Humboldt State University, Arcata, California.

Stauffer, T.M. 1972. Age, growth, and downstream migration of juvenile rainbow trout in a Lake Michigan tributary. *Trans. Am. Fish. Soc.* 101:18–28.

Steward, C.R., and Bjornn, T.C. 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, Portland, Oregon. Technical Report 90-1.

Thompson, B.E., and Ferreri, C.P. 2002. Population biology of steelhead spawning runs in three Pennsylvania tributaries to Lake Erie. *J. Great Lakes Res.* 28: 264–275.

Tipping, J.M. 1991. Heritability of age at maturity in steelhead. *North Am. J. Fish. Manage.*11:105–108.

Wagner, H.H. 1967. *A summary of investigations of the use of hatchery-reared steelhead in the management of a sport fishery.* Oregon State Game Commission, Research Division, Portland, Oregon, Fishery Report Number 5.

______. 1968. Effect of stocking time on survival of steelhead trout, *Salmo gairdneri*, in Oregon. *Trans. Am. Fish. Soc.* 92:202–210.

______, Wallace, R.L., and Campbell, H.J. 1963. The seaward migration and return of hatchery-reared steelhead trout, *Salmo gairdneri* Richardson, in the Alsea River, Oregon. *Trans. Am. Fish. Soc.* 92:202–210.

Wallis, J. 1968. *Recommended time, size, and age for release of hatchery-reared salmon and steelhead trout.* Fish Commission of Oregon, Clackamas.

Ward, B.R., and Slaney, P.A. 1990. Returns of pen-reared steelhead from riverine, estuarine, and marine releases. *Trans. Am. Fish. Soc.* 119:492–499.

______, Slaney, P.A., Facchin, A.R., and Land, R.W. 1989. Sized-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. *Can. J. Fish. Aquat. Sci.* 46:1853–1858.

Withler, I.L. 1966. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. *J. Fish. Res. Board Can.* 23:365–392.

Woodward, C.C., and Strange, R.J. 1987. Physiological stress responses in wild and hatchery-reared rainbow trout. *Trans. Am. Fish. Soc.* 116:574–579.

Zar, H.H. 1999. *Biostatistical analysis.* 4th edition. Upper Saddle River, New Jersey: Prentice Hall.

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