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This is to certify that the

thesis entitled

Relative Contribution and Comparative Life History Characteristics of Hatchery and Wild Steelhead Trout in the Betsie River, Michigan

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RELATIVE CONTRIBUTION AND COMPARATIVE LIFE HISTORY CHARACTERISTICS OF HATCHERY AND WILD STEELHEAD TROUT IN THE BETSIE RIVER, MICHIGAN

By

James R. Harbeck

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ABSTRACT

RELATIVE CONTRIBUTION AND COMPARATIVE LIFE HISTORY CHARACTERISTICS OF HATCHERY AND WILD STEELHEAD TROUT IN THE BETSIE RIVER, MICHIGAN

By

James R. Harbeck

Spawning runs of wild, naturalized steelhead trout occur in northern tributaries of Lake Michigan including the Betsie River. Management of Betsie River steelhead has focused on supplementing wild stocks with hatchery fish though little is known about natural production. Scales from adult migrants were collected by volunteer anglers and river guides from 1994 through 1996. Relative contribution and life history characteristics were determined through scale pattern analysis. Management agencies surrounding Lake Michigan were contacted to determine the presence of uniquely marked Betsie River hatchery steelhead in their waters.

The spawning runs of 1994-1996 were composed of 46, 40, and 30 percent wild steelhead respectively. The most common life history pattern in the wild population was 2 years of growth in the stream followed by 3 years in the lake. Eighteen percent had spawned previously. The most common pattern in the hatchery population was 1 year in the hatchery/stream and 3 lake years. Ten percent had spawned previously. Wild and hatchery steelhead had similar sex ratios, length-at-age and migration timing. Betsie River hatchery steelhead were widely distributed in the southern two thirds of Lake Michigan. Straying was evident in rivers on both sides of the lake as far south as the St. Joseph River in Indiana and the Root River in Wisconsin.

To my wife Judy, for your patience, encouragement, and help throughout my graduate studies.

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I am indebted to the scale reading efforts and expertise of Steve Vanderlaan and Sally Markham, MDNR fisheries technicians and to Doug Workman, my fellow lab partner. I have also benefited from the friendships, discussions, and assistance of my other lab mates, Tammy Newcomb and John Skubinna.

A research project such as this would not be possible without the help of numerous Betsie River volunteer anglers and river guides. My special thanks to John Westley who not only provided the majority of the steelhead scales but also introduced me to the Betsie and her fishery via his drift boat.

I'm also grateful to the biologists of the Illinois Department of Natural Resources, the Illinois Natural History Survey, the Indiana Department of Natural Resources, the Michigan Department of Natural Resources, the Wisconsin Department of Natural

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INTRODUCTION

The steelhead trout, *Oncorhynchus mykiss*, is an anadromous form of the rainbow trout. It is also an iteroparous salmonid in contrast to the other species within the genus which are semelparous (Leider 1985). Life history traits vary considerably among populations of this species. Diverse age structure, growth, sex ratios, age at first maturity, percent repeat spawn, spawning and migration timing, and homing fidelity have been documented in discrete stocks of steelhead (Withler 1966; Shapovalov and Taft 1954).

Although native to the Pacific Coast, the steelhead has been introduced worldwide including into the Great Lakes (MacCrimmon 1971). Its successful adaptation is due, in part, to the steelhead's variable life history characteristics. Biette et al. (1981) believe that steelhead populations in the Great Lakes retained their variable characteristics from their native range that allowed for the development of discrete stocks peculiar to regions and perhaps specific watersheds. Krueger et al. (1994) found separate, genetically identifiable steelhead populations occurring in the tributaries along the Minnesota shoreline of Lake Superior. Ferguson et al. (1993) documented both life history and genetic differences among steelhead populations in Lake Ontario. This ecologically adaptive variation in life history minimizes impacts on a population by spreading risks to multiple year classes in an unpredictable environment. Successful colonization of different watersheds thus becomes a possibility.

The State of Michigan obtained its first rainbow trout eggs from California in 1880 and began stocking many of its Great Lakes tributaries (Latta 1974). Populations became wild and reproduced naturally. The steelhead trout now occupies a unique ecological niche in Michigan waters (Jude et al. 1987). Runs of naturalized steelhead presently occur in numerous northern tributaries of Lake Michigan including the Betsie River in northwest lower Michigan.

This introduction has also formed the basis of a popular and economically valuable sport fishery in Michigan. Recreational angling in Michigan accounts for an estimated 1.3 billion dollars in expenditures annually (Garling and Dann 1995). Michigan anglers spend more money per day trip pursuing steelhead than any other gamefish (Mahoney et al. 1991). Therefore, for both ecological and economical reasons, the state has a vested interested in the proper management of the steelhead trout.

Relevant Literature

According to Allendorf et al. (1997), the variation in salmonid life history traits helps to maintain genetic viability within a species. They recommend that stocks be managed as discrete identities and given priority when traits and the underlying genetics are unique. MacLean and Evans (1981) also advocate the identification and preservation of each individual stock and their characteristics as a primary management goal.

Various methods of stock identification from mixed samples were reviewed by Ihssen et al. (1981). They identified the analysis of scales as a valid technique for distinguishing stocks. Scale pattern analysis is currently used to discriminate commercially valuable stocks of fish originating from different environmental conditions. Stocks of Alaskan sockeye, *Oncorhynchus nerka*, are separated using techniques developed by Bethe and Krasnowski (1977). Pattern classification was also used to identify wild and hatchery stocks of Columbia River chinook salmon, *Oncorhynchus tshawytscha* (Schwartzberg and Fryer 1989) and wild and hatchery chinook from the Rakaia River, New Zealand (Unwin and Lucas 1993). Discrimination of Norwegian farmed, ranched and wild Atlantic salmon, *Salmo salar,* was successful using circuli spacing and scale texture data (Friedland et. al. 1994). Techniques that used life history information resulted in higher classification accuracy than those that did not (Davis 1987). Knudsen and Davis (1985) also found that classification models that compared circuli band widths (ratio data) had higher accuracy than models with no ratio data.

Seelbach and Whelan (1988) developed a scale analysis technique to identify wild and hatchery steellhead trout that relied on both life history and ratio information. The authors recognized a difference in circuli spacing between wild and hatchery steelhead from the Great Lakes. Circuli on scales from hatchery fish were evenly spaced across the portion of scale laid down during the time the fish resided in the hatchery. The pattern reflected the constant environmental conditions of the hatchery. Circuli from wild fish scales were closely spaced prior to the first stream annulus and widely spaced after the annulus. This pattern paralleled the slow growth of winter and faster growth of spring experienced by the wild fish. Based on these differences, the two researchers developed an objective assignment rule for distinguishing wild and hatchery steelhead.

Estimating smolt-to-adult survival rates of Vancouver Island steelhead was accomplished by Ward and Slaney (1988) and Ward et al. (1989) by using scale backcalculation procedures. Smolt lengths back calculated from adult scales were compared to observed smolt lengths. Survival based on smolt size was then determined. A similar scale technique was used by Seelbach et al. (1994) for steelhead from two Michigan rivers. Scale radii frequencies were compared between smolts and adults of the same cohort to determine the effect of smolt size on return.

Steelhead Life History

Steelhead generally make spawning runs in the spring to their stream of origin. Successful reproduction depends on suitable habitat. Redd sites with gravel diameters of 1.3 cm to 11.4 cm and well oxygenated flows with current velocities of 23-155 cm/sec are chosen by the female (Pauley et al. 1986).

The majority of steelhead live to spawn only once. Those fish that do spawn more than once are predominantly female, even though male/female ratios of maiden spawners are close to 1:1 (Leider 1985). The disproportionate survival of females after spawning is explained by McKeown (1984) as having a behavioral and hormonal basis. Male steelhead tend to enter the spawning stream earlier than females and remain longer. Defending the redd has its energy costs and little food is consumed once the males enter the stream (Shapovalov and Taft 1954).

Fecundity varies with size. Females lay and bury between 1,000-12,000 eggs (Moyle and Cech 1988; Pauley et al. 1986). Eggs hatch in 4-7 weeks depending on water temperature. When the yolk sac is absorbed, fry emerge from the gravel and develop bars or parr marks on their sides. The "parr" then spend 1-3 years in their natal stream (Biette et al. 1981; Seelbach 1993). In preparation for a change in habitat, parr begin a transformation in morphology, physiology, and behavior (Hoar 1976) until they become smolts. The new smolts are silvery, more elongated than parr, and are migratory in nature. Smoltification is size dependent and its timing is influenced by temperature, photoperiod, and discharge (Damsgard 1991; Seelbach 1987; Stauffer 1972). Upon smolting, steelhead emigrate out to a lake or ocean where they grow and mature for 2 or 3 years in preparation for their own spawning runs. Juveniles primarily select aquatic and terrestrial invertebrates as food items. In Lake Michigan adult steelhead prey on alewife *Alosa pseudoharengeus* and rainbow smelt *Osmerus mordax,* although not to the degree of other salmonids (Rand et al. 1993; Jude et al. 1987). Invertebrates are also a major diet component for adults.

Populations exhibit a wide range of variation within this general life history pattern. Biette et al. (1981) identified 18 different age categories in Great Lakes spawning populations. Withler (1966) also found high variability in traits of steelhead along the Pacific Coast. Percentage of repeat spawning and age at first maturity differ with strain and latitude of the natal stream. Kwian (1981), Seelbach (1993), and Biette et al. (1981) found the duration of stream residency to range from 0-4 years among populations. Migration tendency and homing accuracy vary between strains of both wild and hatchery steelhead (Steward and Bjornn 1990). In a Lake Superior stream Hansen and Stauffer (1971) found evidence of extensive straying of hatchery fish as did Seelbach and Miller

(1993). But when comparing hatchery strains stocked in southern Michigan streams, Seelbach et al. (1994) found good homing fidelity in both strains when stocked at upstream sites.

Steelhead in the Betsie River

As with many rivers in Michigan, management of steelhead in the Betsie River historically focused on supplementing naturalized stocks with hatchery fish (Wicklund and Dean 1958; Hansen and Stauffer 1971). According to contemporary researchers, the past contribution of hatchery fish to the fishery was probably negligible (Seelbach 1987). The adult steelhead run in the Betsie was sampled in 1984. From a sample of 58 specimens, 93 percent were judged to be wild, naturally produced fish. Only 7 percent of the run were thought to be from hatchery steelhead (Seelbach and Wheland 1988).

However, two major events with the potential to alter the relative contributions of both hatchery and wild fish, have occurred within the watershed. First, the stocking program for the Betsie has changed (Table 1). The location at which fish are stocked was moved from the mouth of the river near Frankfort to an upstream location. Initially the release site was moved upstream to River Road (1989-1991). Currently, fish are released directly from the Orsini Hatchery which is even further upstream. Stocking location has implications for smolt survival and homing ability. Steelhead smolts stocked at an upstream site develop higher homing fidelity than smolts planted lower in the watershed (Steward and Bjornn 1990), but they are exposed to river predators and other unfavorable environmental conditions (Ward and Slaney 1990). Therefore, smolts stocked

Table 1. Twenty year stocking record of steelhead in the Betsie River, 1975-1995.

Year	Planting Site	Strain	Number	Mean Total Length (mm)	Clip
1975	Frankfort	L.Manistee	10,044	(558 per #)	None
1976	Frankfort	L.Manistee	10,260	(540 per #)	None
1977	Frankfort	L.Manistee	12,170	(307 per #)	None
1978	Frankfort	L.Manistee	15,206	(1,152 per #)	None
1979	Frankfort	L.Manistee	0	-	-
1980	Frankfort	L.Manistee	20,000	104	None
1981	Frankfort	L.Manistee	20,004	145	None
1982	Frankfort	L.Manistee	15,000	81	None
1983	Frankfort	L.Manistee	23,359	112	None
1984	Frankfort	L. Manistee	15,000	154	None
	Frankfort	Rogue	8,000	166	LPRV
1985	Frankfort	L. Manistee	13,000	160	None
1986	Frankfort	L. Manistee	20,001	154	AD
1987	Frankfort	Skamania	17,500	196	DOAD
1988	Frankfort	Skamania	15,000	198	MTAD
1989	Black Bridge	L. Manistee	100,875 fry	24	None
	River Road	L. Manistee	15,000 YS	175	MTAD
	Black Bridge	L. Manistee	15,000 FF	81	None
1990	River Road	L. Manistee	10,000	175	None
	River Road	Skamania	10,000	199	None
1991	Orsini Hatchery	L. Manistee	29,171	174	None
	River Road	Skamania	10,000	195	None
1992	Orsini Hatchery	L. Manistee	32,141	204	None
1993	Orsini Hatchery	L. Manistee	44,125	152	RV
1994	Orsini Hatchery	L. Manistee	48,561	137	RV
1995	Orsini Hatchery	L. Manistee	50,036	150	RV

upstream experience lower riverine survival but return to the natal river with less straying (Seelbach et al. 1994). Numbers of steelhead stocked annually have increased from an average of 12,000 per year (1975- 1984) to 50,000 in 1995 (Anonymous 1975 - 1995). Intuitively, increased smolt numbers would contribute more to the adult population. Yearling smolts are now stocked instead of the formerly planted parr. In other systems, large sized hatchery smolts were proven to have greater survival rates and yield better adult returns than hatchery parr (Seelbach 1987).

The second factor affecting the steelhead population is a physical change within the watershed itself. In 1989, the Thompsonville Dam failed and was not rebuilt. This event opened additional spawning and rearing habitat for anadromous fish including a previously unavailable coldwater tributary, the Little Betsie River. However, some habitat downstream of Thompsonville was compromised by sediments from the washed out impoundment. Wicklund and Dean (1958) identified the Thompsonville Dam as a major cause of warm, summer temperatures found in the mainstream that exceed steelhead tolerances. Since 1989, therefore, the potential for production of wild, naturalized steelhead has increased in the Betsie watershed.

These two factors, one a habitat change, the other a change in hatchery inputs, probably changed the structure of Betsie River steelhead population. As a result the relative contributions of hatchery and wild steelhead to the fishery were unknown as were their respective life history traits.

Knowledge of steelhead run composition (hatchery/wild) is important information when determining proper stocking recommendations and prescriptions. Life history information is also invaluable. Because local wild population characteristics are a result of local environmental pressures and genetics, hatchery fish characteristics should resemble those of the wild population in order to be successful (Steward and Bjornn 1990). In addition, the more different the life histories of the two populations, the more likely the wild stock will suffer genetic loss of fitness when spawning conjointly with hatchery fish (Helle 1981).

As an important element of resource management, the Michigan Department of Natural Resources' Management Plan (1997) addressed the need for determining the contribution of naturally produced salmonids to the Great Lakes fisheries. Furthermore, the Great Lakes Fishery Commission (GLFC 1992) also recommends that management practices should be directed towards a naturally sustainable fishery and the preservation of wild populations. Hatchery programs should be tailored to avoid erosion of wild stock integrety. Field evaluation of hatchery stock performance is also an essential component of resource management (MDNR 1994). Therefore, these types of data are essential to the future management of the Betsie River steelhead population.

Goals and Objectives

The goal of this study was to evaluate the Betsie River adult steelhead population as it now exists in response to a major habitat change and a change in the hatchery stocking regime. The resulting information is intended to aid in the management of the steelhead and its fishery by providing evidence of population composition and structure.

The specific research objectives include:

1. Estimate the relative contribution of hatchery and wild adults to the spawning population from the 1994-1996 runs and compare this percentage with that of the 1984 study.

2. Describe and compare wild and hatchery stock characteristics (age structure, growth, sex ratios, age at first maturity, migration timing, and percent repeat spawners).

3. Evaluate smolt size influences on probability of adult return.

4. Document the lake distribution and river straying of hatchery fish.

For the purposes of this thesis, the term "wild" steelhead refers to those fish which have resulted from natural reproduction regardless of ancestry (i.e. hatchery, wild, or interbred). "Hatchery" steelhead refers to those fish which have been spawned and reared for some part of their life cycle in a hatchery regardless of lineage.

Study Site Description

The Watershed - The Betsie River is a Lake Michigan tributary located in northwestern Michigan (Figure 1). Originating in Duck and Green Lakes southwest of Traverse City, the Betsie flows in a westerly direction to its mouth in Lake Michigan at Frankfort. The river is approximately 82 km long and drains an area of 67,149 hectares in Grand Traverse, Manistee, and Benzie counties. Over fourteen thousand hectares within the watershed are state-owned as part of the Pere Marquette State Forest and the Betsie River State Game Area. In 1973 the Betsie River was listed in the state's Natural Rivers Program.

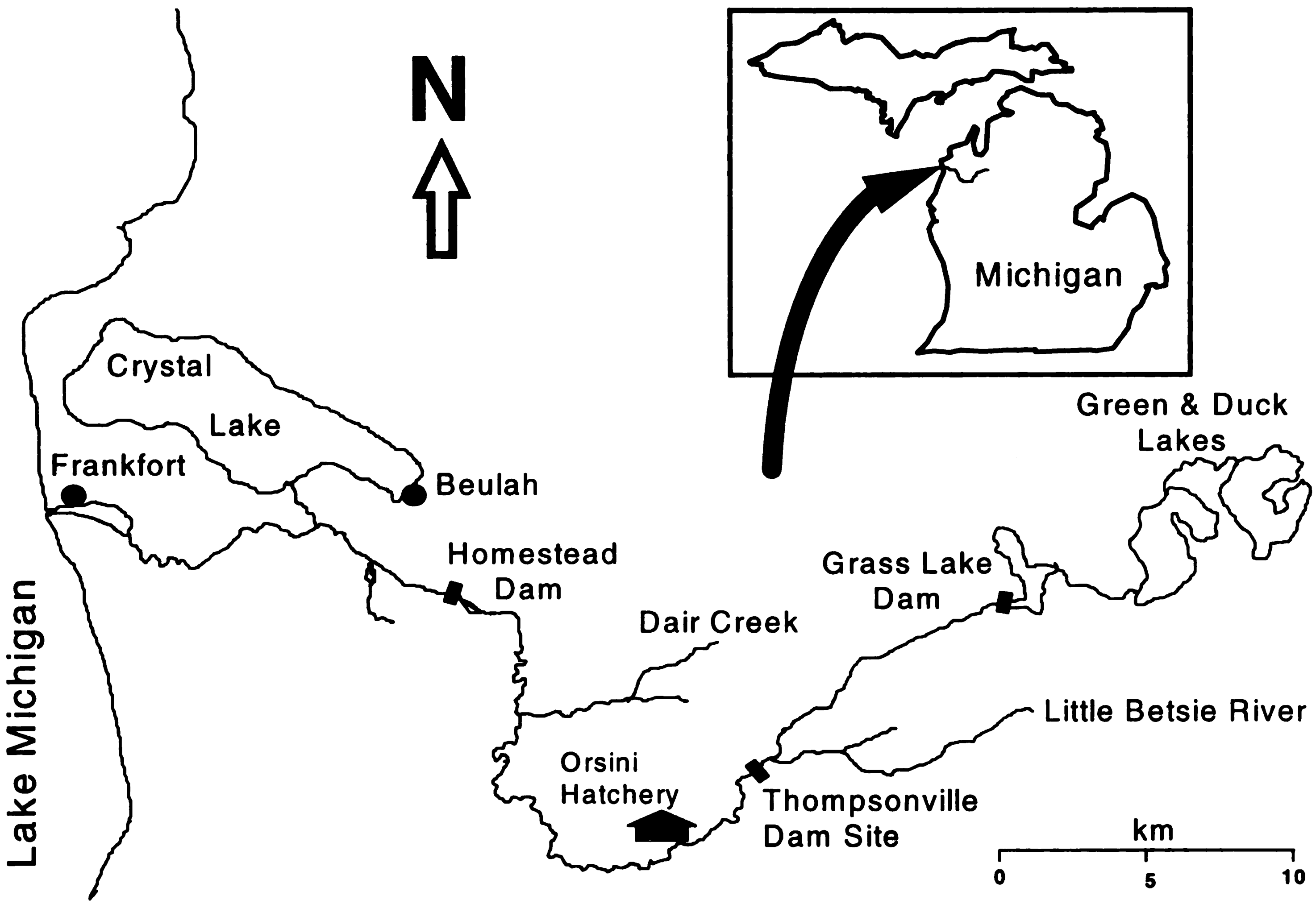


Figure 1. The Betsie River watershed located in the northwestern lower peninsula. Key cultural features are detailed in the text.

The river flows through the Highland, Newaygo, and Manistee regional landscape ecosystems which is reflected in a patchwork of geologic features (Albert et al. 1986). The watershed is characterized by a topography of gently rolling hills, several glacial moraines and outwash plains. Soils are primarily classified within the Rubicon-Grayling series. This association is dominated by sandy soils interspersed with loamy soils. Therefore the soil is very permeable and has low water holding capacity. Approximately 60% of the watershed is forested by northern hardwoods. Coniferous forests are restricted to poorly drained areas of outwash channels (Albert et al. 1986).

The Betsie River discharges an estimated 8.5 m^3/s at Thompsonville Road (Anonymous 1970) and between 4.0 m^3/s and 12.8 m^3/s at Homestead Dam throughout the year (Newcomb 1998). Water quality is considered good and is comparable to the Pere Marquette and Boardman Rivers (Hartig and Stifler 1978). Nutrient levels are low. Nitrate and phosphate concentrations are typically 0.10mg/L or less. River water sampled at Thompsonville had a pH of 8.2 and an alkalinity ($CaCO_3$) of 135mg/L (Anonymous 1970).

The river has been modified by the existence of three dams. The first upstream from Lake Michigan is the Homestead Dam, lying 20 km above the mouth. Prior to 1972, the dam prevented the passage of anadromous fish. Salmonids were trapped and physically carried over the barrier and allowed to continue their spawning migration (Wicklund and Dean 1958). In 1972, the dam was modified into a low head lamprey weir. Strong swimming fish like steelhead are now able to negotiate the weir on their own.

Thirty-six kilometers upstream from Homestead is the site of the former Thompsonville Dam. The dam maintained a head of 3 meters and prevented upstream fish passage. Since its failure in March, 1989, migratory fish are no longer excluded from the upstream portion of the watershed. The mouth of the Little Betsie River, the largest tributary in the system, is 0.5 km above this site.

Six kilometers below the outlet at Green Lake is the Grass Lake Dam. Originally established for logging operations, the Grass Lake Wildlife Flooding is now managed for waterfowl. The dam maintains a head of 1- 2 meters.

The Betsie is classified as a marginal trout stream by the Michigan Department of Natural Resources (Wicklund and Dean 1958). However, typical of a varied temperature regime, the watershed supports a diverse fish community including many game species. In addition to steelhead, coho salmon, *Oncorhynchus kisutch*, and chinook salmon make spawning runs and produce smolts annually. Resident salmonids, such as brook trout, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, are common in coldwater Dair Creek and the Little Betsie River. Walleye, *Stizostedion vitreum*, northern pike, *Esox lucius*, and white sucker, *Catostomus commersoni*, predominate in the lower river. Northern pike and centrarchids also inhabit Grass Lake (Carbine 1945).

The Hatchery - the Orsini Hatchery is dedicated solely to the production of steelhead smolts. The 2100 sq. ft. building is located on the river between Homestead Dam and the Thompsonville Dam site, 52 km upstream from Lake Michigan. An artesian well releases 600 liters per minute of 9 ^{0} C water through the hatchery. This privately owned facility is sponsored and maintained by the Manistee County Sport Fishing

Association with contributing funds donated by the Michigan Department of Natural Resources and other sport fishing groups.

Steelhead smolts are released directly into the river from the hatchery near highway M-115. Numbers released have increased from 29,000 in 1991 to 55,000 in 1996 and account for the dramatic rise in stocking levels (Figure 2).

The Orsini Hatchery fish are first generation offspring of wild parents from the Little Manistee River. Spawners are obtained by MDNR personnel at the Little Manistee River weir facility. The fertilized eggs are hatched at the state owned Wolf Lake Hatchery. Fingerlings are then transported to the Orsini Hatchery where they are reared to smolt size yearlings and released into the Betsie River.

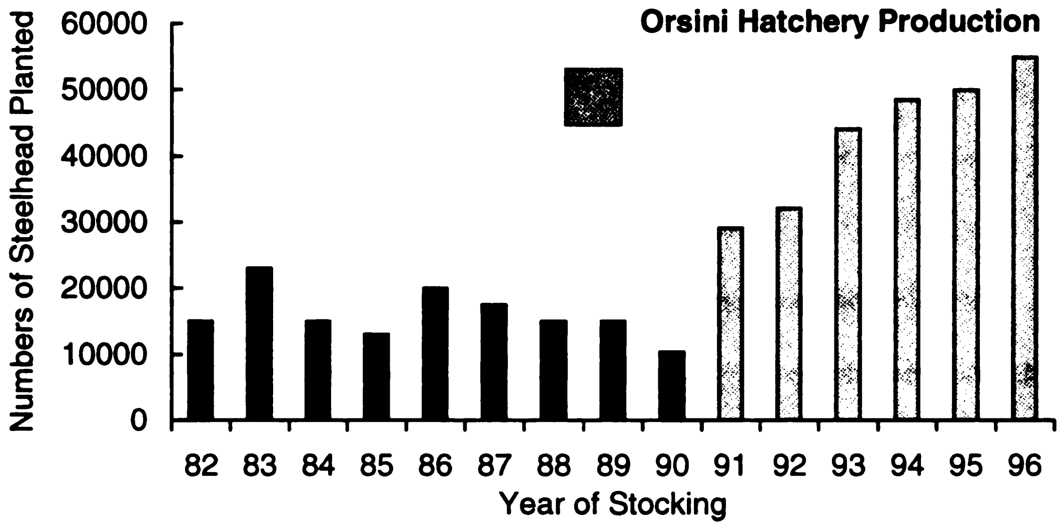


Figure 2. Stocking record for steelhead stocked in the Betsie River. Orsini Hatchery began operations in 1991.

METHODS

Data Collection

I assessed the adult steelhead population primarily through scale analysis along with other data collected from individual fish. Adult scale samples were obtained through a collection program by river guides and volunteer anglers fishing the Betsie River from 1994 - 1996. Guides and anglers were supplied with envelopes for the return of the scale samples. Scales were removed from the preferred area between the posterior edge of the dorsal fin and the anterior edge of the anal fin above the lateral line (Scarnecchia 1979; Knudsen and Davis 1985). Anglers were asked to record total length, sex, date, location of capture, and the presence of any fin clips (Appendix A).

In order to describe the distribution of sport caught steelhead, I divided the segment of the river open to fishing during the extented season into three sections. The section from Highway 31 down to the mouth at Frankfort was termed the lower section, the river from the Homestead weir to Highway 31was labeled as the middle section, and the area above the Homestead weir was considered the upper section.

In 1996 the number of scales collected by guides and volunteer anglers was supplemented by sampling emigrating kelts caught in a block net above Homestead Dam. As part of a concurrent smolt study (Newcomb 1998), the blocknet was designed to capture smolts but also captured adults. The constricted area of the block net was electrofished for three nights in May during the emigration of spent adults. In 1997 guides collected scales from marked hatchery fish only.

A target sample size for each year was set at 200. For scale pattern analysis on an "unknown" mixed stock, a sample size of 100 is recommended by Conrad (1985) when a sample of 200 "knowns" is obtained for each stock. The criteria for distinguishing between wild and hatchery stock of Lake Michigan steelhead was developed by Seelbach and Whelan (1988) with "known" wild and hatchery samples of 622 and 346 respectively. Therefore, a target of 200 "unknowns" per year assured an adequate number of readable scales for the analysis.

A percentage of yearling hatchery smolts released from the Orsini Hatchery during 1993-1995 were marked with a right pelvic fin clip (Ralph Hay, MDNR Personal Communication). I contacted management agencies around Lake Michigan to request their port creel surveys and lake catch records in order to document the lake distribution of right pelvic fin clipped steelhead. I also solicited river creel surveys and weir and ladder reports to assess straying by Betsie River marked fish.

Scale Analysis

Prior to examination I prepared the scales by soaking them in a mild detergent and manually cleaning them to remove epidermal tissue and dirt. The scales were then rinsed with distilled water and mounted between two glass microscope slides. Up to 10 scales were mounted per fish.

I acquired scale pattern data with a computerized imaging system. Images of each scale were captured through an Olympus dissecting microscope using a Cohu RS-170 video camera and displayed on a Sony Trinitron HR monitor. The monitor is interfaced with a microcomputer and Optimas image-processing software (Bioscan 1989). Measurements were obtained along a 360^0 axis line from the scale focus towards the anterior edge using a mouse and the menu driven Optimas program.

Origins - I determined origins of sampled fish from the Betsie River with the scale pattern criteria developed by Seelbach and Whelan (1988). After identifying the first stream/hatchery annulus, the width of the five circuli just inside the first annulus is compared to the width of the five circuli just outside of the annulus resulting in a numeral determination called "ratio 23" (Figure 3). Using ratio 23, I assigned fish to either hatchery or wild origin for each year's spawning run. Validation was possible by the presence of a fin clip on a hatchery fish.

Calculation of relative abundance required hatchery and wild assignment frequencies and classification error rates. I determined frequencies for my analysis from blind readings of known origin adult scales archived at the Institute of Fisheries Research, University of Michigan. The frequencies of origin assignment were as follows:

P_{hw} (0.06) = hatchery classified as wild
P_{wh} (0.102) = wild classified as hatchery
P_{ww} (0.898) = wild classified as wild
P_{hh} (0.94) = hatchery classified as hatchery

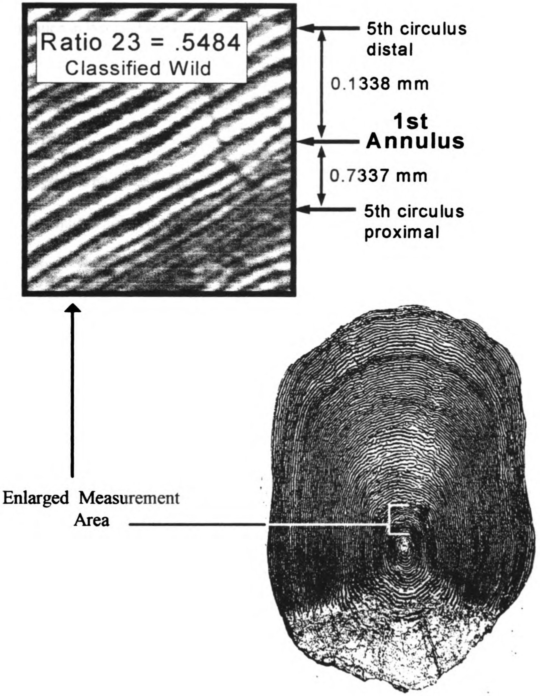


Figure 3. Scale from a wild steelhead showing measurement area for Ratio 23 determination.

I calculated the proportion of wild steelhead adjusted for classification error according to the equation in Worlund and Fredin (1962):

$$P_1 = (P_{ww} \times P_w) + P_{hw}(1 - P_w)$$

where P_w is the observed proportion of wild steelhead from ratio 23 determinations and P_1 is the adjusted proportion predicted by the above equation. An estimate of the true proportion of wild steelhead was then obtained through a maximum likelihood solution (Millar 1987, 1990). I used the following equation in a maximum likelihood scenario to determine the true relative contributions of wild steelhead:

$$\text{Log}(L) = n_1 \times \log(P_1) + n_2 \times \log(1 - P_1)$$

where Log(L) is the objective function to be maximized, n_1 is the of observed number of wild steelhead in a spawning run, and n_2 is the number of observed hatchery steelhead in the same run. I calculated the variance of each year's wild contribution estimate by the equation:

$$\text{Var} = \frac{-1}{(P_{hw} - P_{ww})^2 \left[-\frac{n_2}{1 + P_{hw}(-1 + P_w) - (P_w P_{ww})^2} - \frac{n_1}{(P_{hw} - P_{hw}P_w + P_w P_{ww})^2} \right]}$$

The variance equation was developed by using the maximum likelihood parameter estimate in the second derivative of the likelihood function. The inversion generates the the variance.

Life history characteristics - Scale reading is also a widely used method of aging fish and analyzing growth (Jearld 1983). The long history of using scales in age and growth studies was summarized by Carlander (1986).

I used steelhead scale aging methods described by Davis and Light (1985), Seelbach and Beyerle (1984), and Jones (*unpublished*). Previous spawning checks were identified according to descriptions by Seelbach and Beyerle (1984) and Hartman (1959). Stream and lake growth are distinguishable by circuli spacing and a smolting check. Circuli laid down during lake residency are much more widely spaced than during stream growth. Based on these criteria I estimated age structure and spawning history for both hatchery and wild fish.

I used the European nomenclature for fish age description as described by Schwartzberg and Fryer (1989). The number of stream annuli (number of winters a fish spent in the stream) is designated by an Arabic numeral followed by a period and the number of lake annuli. Thus, a steelhead that spent two years in the Betsie River watershed as a juvenile and two years in Lake Michigan would have a recorded age of 2.2 (Figure 4). A repeat spawner is indicated by an "S" after the lake age followed by the next lake year. If the above mentioned fish had spawned after its first lake year it would be recorded as 2.1S1.

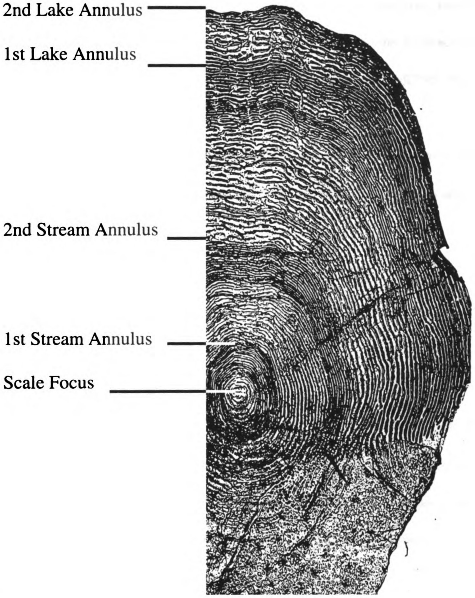


Figure 4. Image of a steelhead scale from a 4 year old fish (2.2) collected in the spring of 1995. The wild steelhead spent 2 years in a stream environment and 2 years in Lake Michigan.

Beamish and McFarlane (1983) stressed the need for age validation when using scales. Validation techniques include mark and recapture of known age fish, and length frequency analysis. Numerous studies by the MDNR have validated the accuracy of steelhead scale aging methodology in the Great Lakes (Paul Seelbach, MDNR Personal Communication).

The precision or repeatability of my age determinations was estimated by an average percent error (APE) index (Beamish and Fournier 1981) using the equation:

$$\text{APE (Average Percent Error)} = \frac{1}{\text{N}}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{\left|\text{X}_{ij}-\text{X}_j\right|}{\text{X}_j}\right] * 100\ ,$$

where N is the number of fish aged, R is the number of scale readers, X_{ij} is the ith age of the jth fish, and X_j is the average age of the jth fish. When multiplied by 100 the equation becomes the index of average percent error for a set of age determinations. The index ranges from 0 to 100, and indicates higher precision with smaller index values. Three readers independently aged a 50 scale subset from the Betsie River steelhead scale collection to obtain APE estimates of stream, lake, and total age.

The coefficient of variation (CV) is also a strong estimator of reproducibility according to Chang (1982). I calculated CV for each fish and averaged over all fish. The percent error contributed by each observation can be estimated by the following index of precision (Chang 1982):

$$D = \frac{CV}{\sqrt{R}},$$

where D is the index of precision value, CV is the coefficient of variation for each fish, and R is the number of scale readers. I calculated D for each fish and averaged over all fish aged.

I determined proportions of fish maturing at lake age for wild and hatchery populations. Mean age-at-maturity was calculated by sex and origin. I computed mean lengths at lake age and age-at-maturity by year, sex, and origin. Analysis of variance (ANOVA) and student's t-tests were used to compare group means. Mean lengths at lake age were used to develop growth trajectories with respect to sex and origin.

For each year, sex ratios were determined as percent male:female for an overall ratio and a ratio at each lake age by origin. I tested for differences between observed sex ratios and a 50:50 ratio with a chi-square test.

I compared spring migration timing based on the weekly catch at one location in the watershed. Although fishing effort may have been variable throughout the season due to weather and other factors, I assumed equal catchability between wild and hatchery fish. Median weekly dates of capture for wild and hatchery fish were compared each year. Distributions of migration timing were compared with chi-square tests. For all statistical tests, I used an $\alpha = 0.05$.

Smolt size influence - I tested for smolt size influence on eventual adult return by comparing mean scale radius from migrating smolts captured at the Homestead Dam during 1993-1994 , with mean smolt check radius from returning adults of the same cohort. I used a student's t-test to statistically compare mean smolt radius by cohort and origin.

To graph the relationship, I converted smolt check radius to smolt length using simple linear regression for both hatchery and wild smolts. The traditional Fraser-Lee equation was not used because of an apparent saltatory growth pattern in the scatter plot of scale radius and fish length. The residual plot also indicated a systematic error pattern which suggested the Fraser-Lee model would over predict length for smaller individuals and under predict length for larger fish. Therefore, wild and hatchery smolt length estimates were derived from back-calculations based on the following predictive regression equations relating smolt scale radius with smolt total length:

$$TL = 9.0697 \times SR + 11.491 ,$$

where TL is fish total length and SR is scale radius. The regression was highly significant with residuals normally distributed indicating no heterogeneity of variance ($P < 0.001$, $r^2 = 0.39$, $N = 283$). The regression for wild smolts also was highly significant ($P < 0.001$, $r^2 = 0.54$, $N = 165$). Residual variance was homogenous. Wild smolt lengths were estimated with the equation:

$$TL = 10.109 \times SR + 9.7239 .$$

Observed, measured smolt lengths from the 1993 and 1994 Newcomb (1998) data set were then plotted against smolt lengths back-calculated from returning adults of the same cohort.

RESULTS

River guides and anglers collected scale samples and data from 191, 131, and 157 steelhead during the years 1994, 1995, and 1996 respectively (479 total). Fish sampled in the fall were considered as part of the following spring spawning run. Sixty six kelts were sampled during three nights in May of 1996. An abbreviated and targeted collection program in 1997 produced 10 RV clipped fish. Steelhead were obtained throughout the three study sections of the watershed, but primarily from the middle study section of the river below the Homestead weir (Table 2).

Of the 555 steelhead sampled for the study, 48 had scales that were regenerated or otherwise unusable for analysis. Therefore, 507 samples were used to determine origin and life histories.

Origins

Relative proportions of wild steelhead in the spawning runs of 1994, 1995, and 1996 were estimated to be **0.457** (0.044 SE), **0.404** (0.054 SE), and **0.299** (0.046 SE) respectively. Wild fish made up **0.505** (0.077 SE) of the kelt population in 1996 (Figure 5). These estimates of wild steelhead are all much smaller than the estimate made by Seelbach and Whelan (1988). They represent a significant change in the relative contributions of wild and hatchery steelhead to the Betsie River fishery since 1984 (χ^2 = 58, df=1, P< 0.001).

Table 2. Distribution of sampled sport catch by river section, 1994 - 1996. The kelt sample is not included.

	STUDY SECTION [1]			
Return Year	Lower	Middle	Upper	*n*
1994	9%	78%	13%	*191*
1995	22%	58%	20%	*131*
1996	33%	54%	13%	*157*

[1] Sections defined in Methods

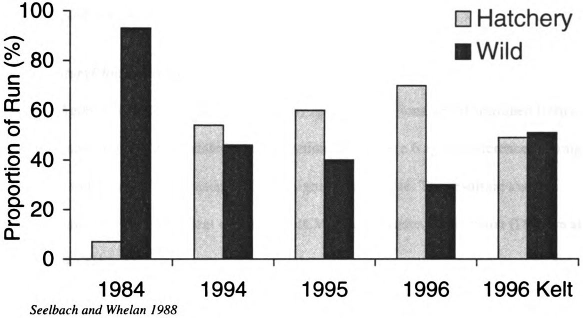


Figure 5. Relative contribution of hatchery and wild steelhead to the Betsie River fishery, 1994-1996. The 1996 kelt population was sampled with blocking nets and electrofishing gear. The 1984 sample is included for comparison.

Hatchery strays from other rivers identified by unique fin clips contributed up to 11% of the sampled fish (Appendix B).

Life HistoryCharacteristics

Aging Precision - The precision of my age classifications was determined from a 50 scale subsample of the Betsie River collection. There were 6 aging differences among the three independent scale readers when assigning stream age. The resulting average percent error (APE), coefficient of variation (CV), and the index of precision (D) were all under 5% (Table 3).

The scale readers produced only four discrepancies in estimating lake age. The index of APE, CV, and D were under 2% for lake age assignments (Table 4). The scale readers disagreed 10 times in total age determination. As a result, the APE, the CV, and D were all calculated to be under 3% (Table 5).

Age Structure and Composition - The overall age structure of wild steelhead varied between years but was dominated by either the 1.3, 2.2, or 2.3 age category during the spawning years 1994-1996. In contrast, the age structure of hatchery steelhead remained consistent throughout the study. The 1.2 and 1.3 age categories comprised over 70% of the returning hatchery steelhead in all three years. Eighteen age categories were identified among the sampled wild fish and 11 different age categories were identified in the hatchery sample (Figures 6, 7, and 8).

The majority of wild and hatchery steelhead returned at a lake age of 3 but ranged in age from 1 to 5 lake years. Wild and hatchery fish differed slightly in lake age patterns

Table 3. Estimated **stream** ages and associated APE[1] ,CV[2] , and D[3] from three independent readers. The fifty scale subsample taken from the 1994 -1996 Betsie River collection.

	Estimated **Stream** Age					
		Reader				
n	1	2	3	APE	CV	D
28	1	1	1	0	0	0
16	2	2	2	0	0	0
1	1	1	2	0.3333	0.4330	0.250
1	1	2	2	0.2667	0.3464	0.200
1	2	1	2	0.2667	0.3464	0.200
1	2	1	1	0.3333	0.4330	0..250
1	1	2	2	0.2667	0.3464	0.200
1	1	1	2	0.3333	0.4330	0.250
			Average	0.0360	0.0468	0.0270

[1] APE = Average Percent Error

[2] CV = Coefficient of Variation

[3] D = Index of Precision

Table 4. Estimated **lake** ages and associated APE[1], CV[2], and D[3] from three independent readers. The fifty scale subsample taken from the 1994-1996 Betsie River collection.

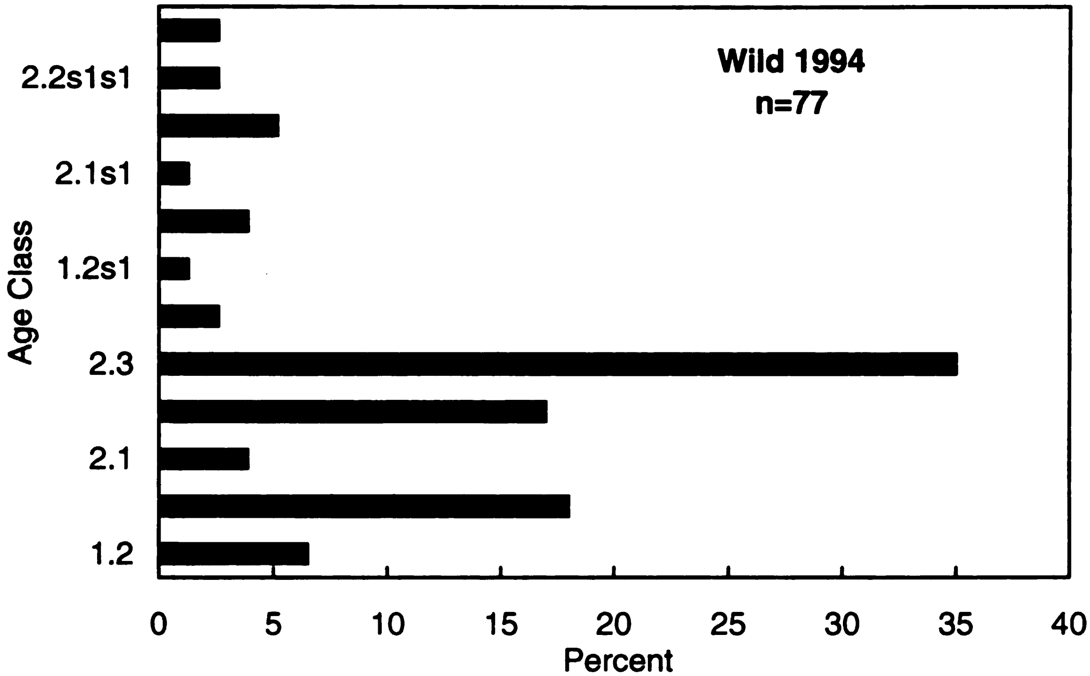
	Estimated **Lake** Age					
		Reader				
n	1	2	3	APE	CV	D
7	1	1	1	0	0	0
14	2	2	2	0	0	0
21	3	3	3	0	0	0
4	4	4	4	0	0	0
1	3	2	3	0.1667	0.2165	0.1250
1	4	4	3	0.1212	0.1575	0.0909
1	4	2	3	0.2222	0.3333	0.1925
1	4	3	4	0.1212	0.1575	0.0909
			Average	0.0126	0.0173	0.010

[1] APE = Average Percent Error
[2] CV = Coefficient of Variation
[3] D = Index of Precision

Table 5. Estimated **total** ages and associated APE[1], CV[2], and D[3] from three independent readers. The fifty scale subsample taken from the 1994-1996 Betsie River collection.

	Estimated **Total** Age					
		Reader				
n	1	2	3	APE	CV	D
5	2	2	2	0	0	0
7	3	3	3	0	0	0
18	4	4	4	0	0	0
10	5	5	5	0	0	0
1	5	4	5	0.0952	0.1237	0.0714
1	5	5	4	0.0952	0.1237	0.0714
1	5	3	4	0.1667	0.2500	0.1443
1	3	3	4	0.1333	0.1732	0.1000
1	5	6	6	0.0784	0.1019	0.0588
1	4	3	4	0.1212	0.1575	0.0909
1	3	3	4	0.1333	0.1732	0.1000
1	5	4	5	0.0952	0.1237	0.0714
1	5	4	4	0.1026	0.1332	0.0769
1	4	5	5	0.0952	0.1237	0.0714
			Average	0.0223	0.0297	0.0171

[1] APE = Average Percent Error
[2] CV = Coefficient of Variation
[3] D = Index of Precision



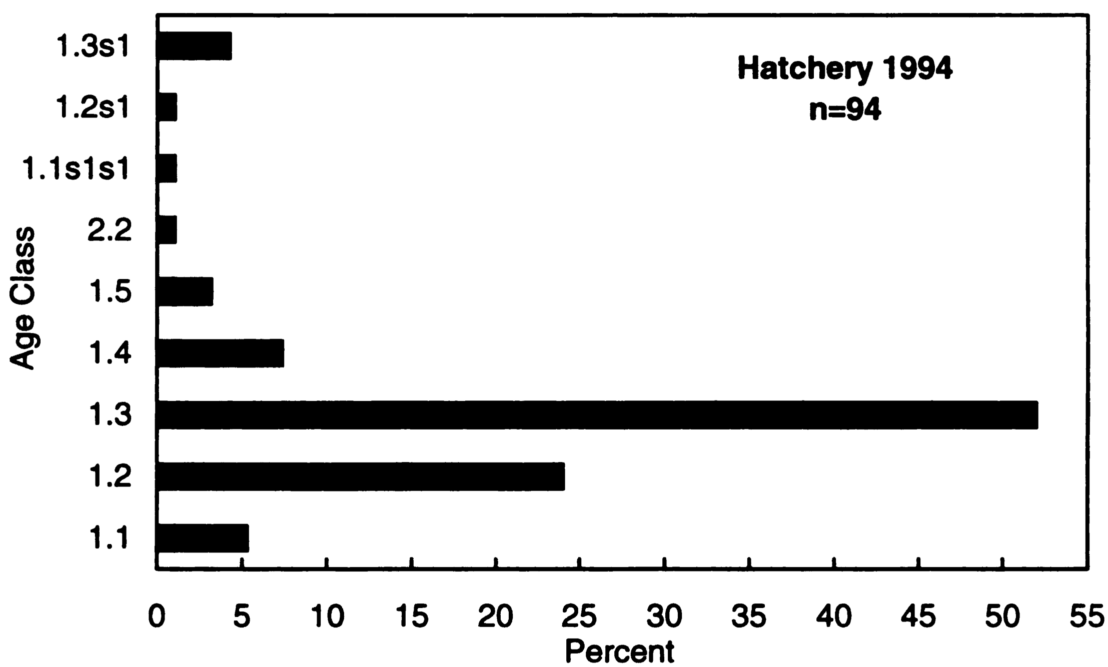


Figure 6. Age class structure of wild and hatchery steelhead from the Betsie River, 1994.

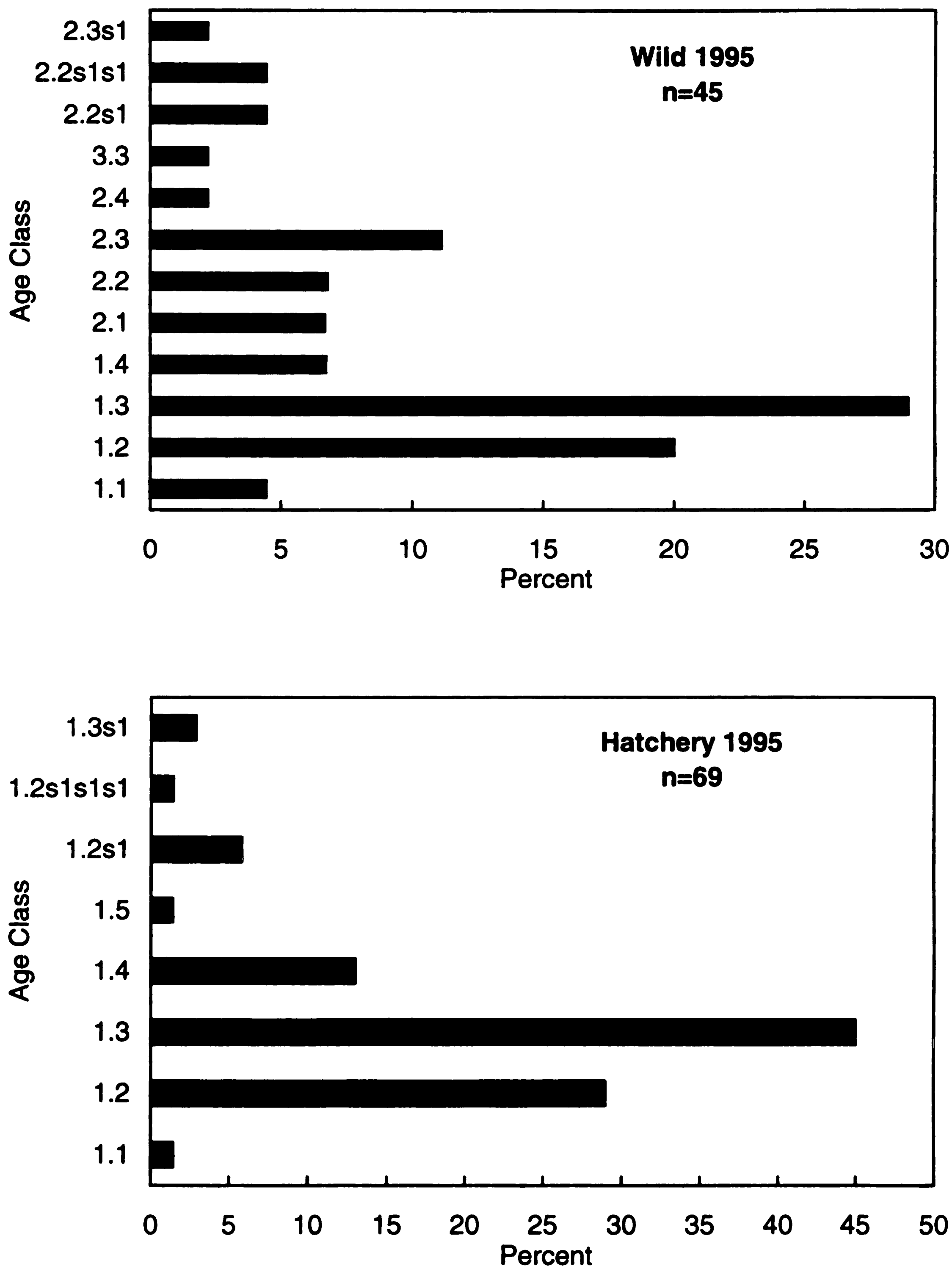


Figure 7. Age class structure of wild and hatchery steelhead from the Betsie River, 1995.

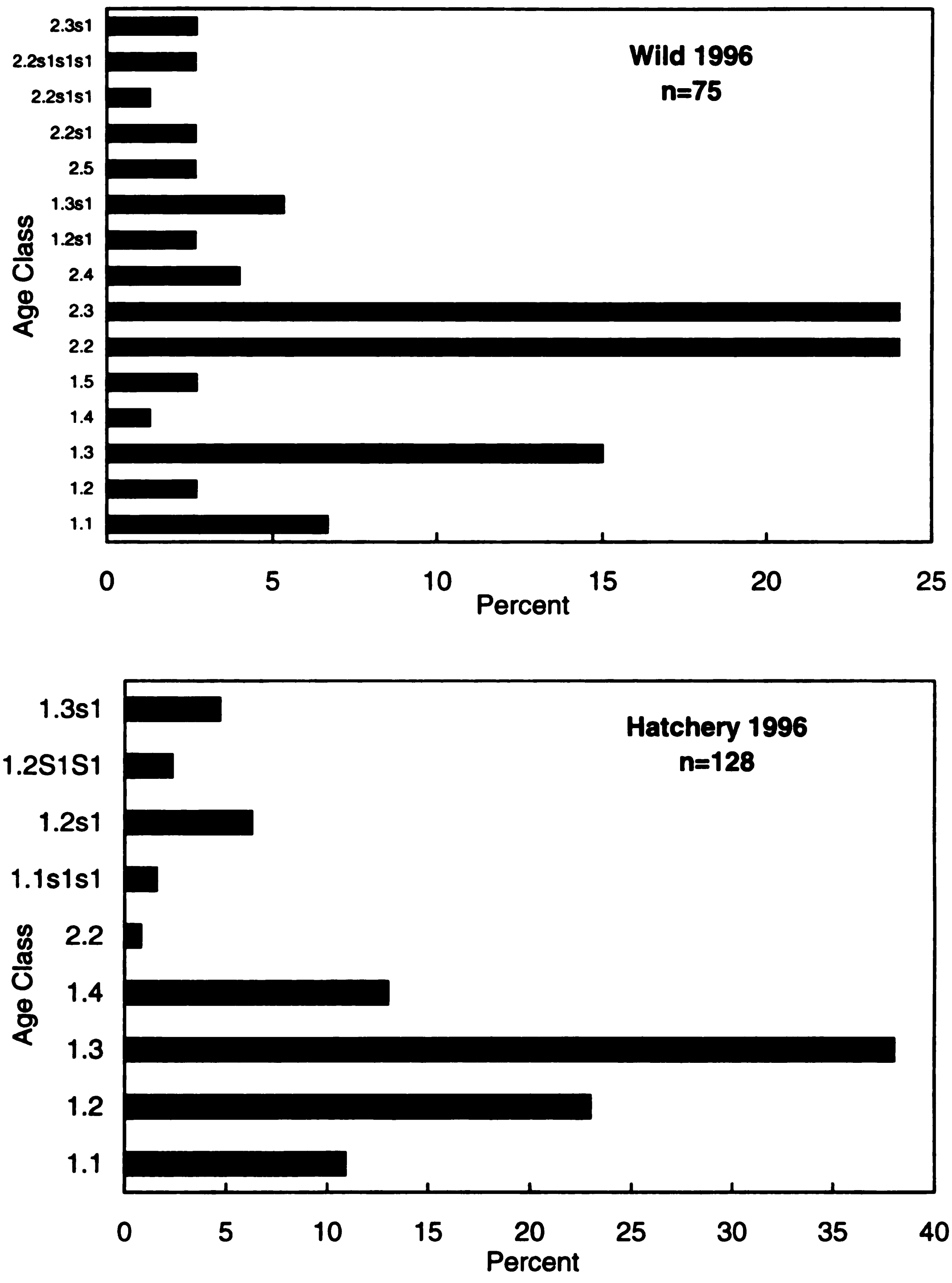


Figure 8. Age class structure of wild and hatchery steelhead from the Betsie River, 1996.

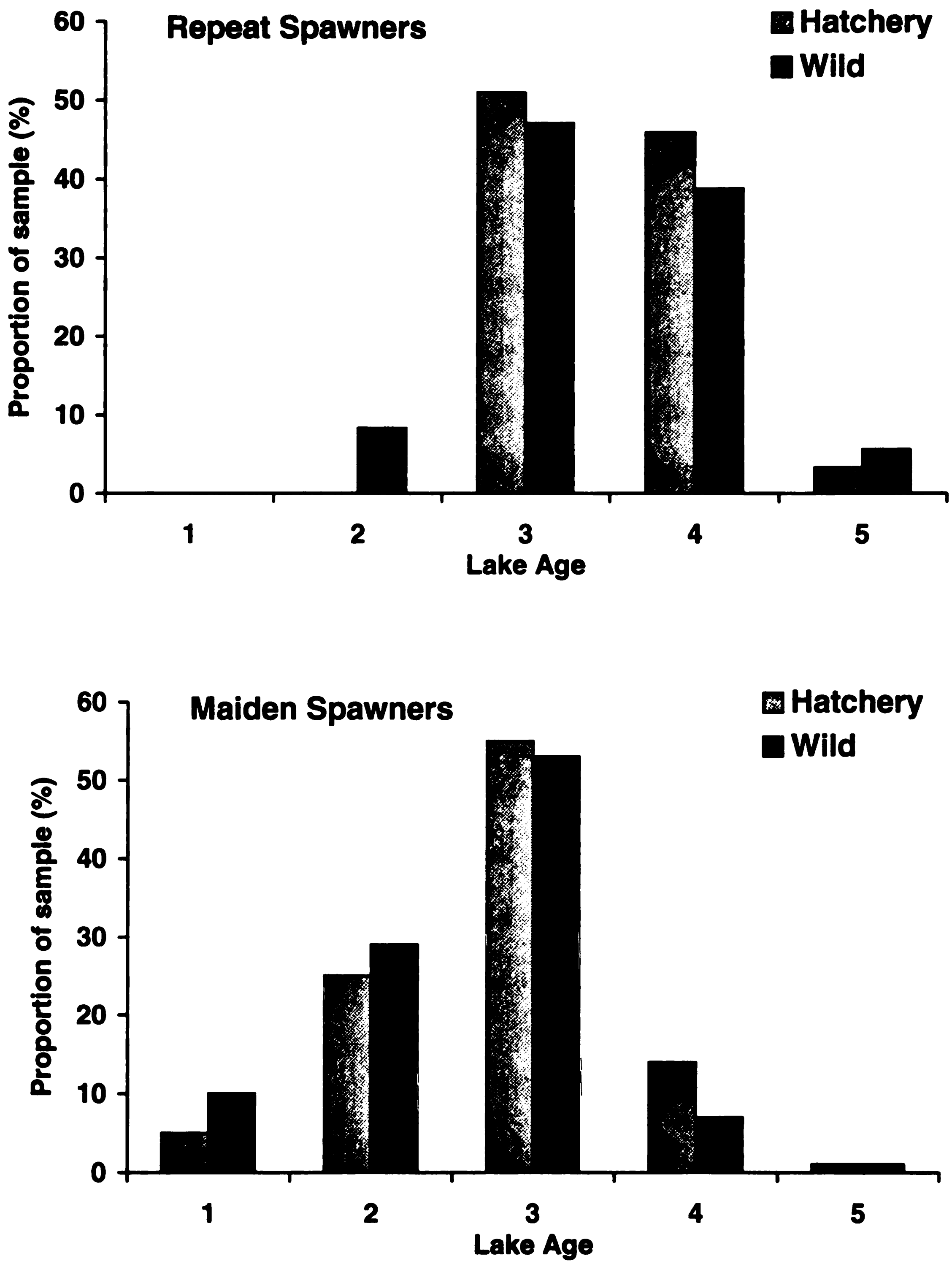


Figure 9. Proportions of hatchery and wild **maiden** and **repeat** spawners according to lake age, 1994-1996.

(Figure 9). Wild fish matured earlier than hatchery fish, with mean lake ages of 2.6 and 2.8 years respectively (*t*=2.66, *df*=164, *P*=0.009). Age at maturity also differed between the sexes. Both wild and hatchery males matured earlier than females (wild: *t*=2.40, *df*=81, *p*=0.0186; hatchery: *t*=2.74, *df*=134, *P*=0.007). Steelhead returning after 1 lake year were always precocious males in both the wild and hatchery samples (Table 6).

The wild adult population displayed an average composition of 38.5% stream age-1 fish, 61% stream age-2 fish, and 0.5% stream age-3 fish. Although most wild adults smolted at stream age-2, the age at smolting as inferred from adult scales varied between years. (Table 7). For example, in 1995 the 55% of returning wild adults entered Lake Michigan as smolts after 1 year in the watershed. Hatchery adults were virtually all age-1 smolts (99%).

Repeat Spawning Frequency - The majority of steelhead sampled, regardless of their origin or year of return, were on their maiden spawning run. Repeat spawning frequency was higher among wild steelhead than among hatchery steelhead. Eighteen percent of wild fish had spawned previously and 10% of hatchery fish were repeat spawners. A contingency table test indicated the difference between wild and hatchery repeat spawning frequency to be significant ($\chi^2 = 6.76$, $df = 1$, $P < 0.01$).

A variety of repeat spawner age categories were observed in the 3 year sample for both wild and hatchery populations (Figures 6, 7, and 8). As expected, the predominant repeat spawner groups were those that had spawned only once previously. The percentage of wild and hatchery repeat spawners progressively diminished with each successive

Table 6. Lake age structure of maiden adult steelhead returning to the Betsie River, 1994 - 1996.

			Percentage of maiden adults according to lake age					
Origin	Sex	*n*	1	2	3	4	5	Mean lake age at maturity
Wild	Male	*81*	18	28	45	6	3	2.5
	Female	*82*	0	37	56	6	1	2.7
	Combined	*163*	**9**	**32**	**51**	**6**	**1**	**2.6**
Hatchery	Male	*129*	10	29	46	12	2	2.6
	Female	*135*	0	24	60	15	1	2.9
	Combined	*264*	**5**	**27**	**53**	**14**	**1**	**2.8**

Table 7. Distribution of age at time of smolting for wild adult steelhead according to year of return.

		STREAM AGE	
Return Year	% Age-1	% Age-2	% Age-3
1994	30	70	0
1995	55	43	2
1996	37	63	0
Weighted Mean	38.5	61	0.5

Table 8. Frequency of repeat spawning incidence in wild and hatchery steelhead returning to the Betsie River, 1994-1996.

Spawning history	WILD *n*	Percent	SE	HATCHERY *n*	Percent	SE
Maiden	*163*	82	2.7	*269*	90	1.7
1 spawn	*26*	13	2.4	*23*	7.7	1.5
2 spawn	*8*	4	1.4	*6*	2	0.8
3 spawn	*2*	1	0.7	*1*	0.3	0.3
Total repeat	*36*	18		*30*	10	

spawning episode. No steelhead had spawned more than 3 times prior to its current spawning run (Table 8).

Incidence of repeat spawning was more prevalent among females than in males. Numbers of female repeat spawners outnumbered male repeat spawners in all three years for both wild and hatchery fish. Females represented 72% of wild repeat spawners and 63% of hatchery repeat spawners.

Sex Ratios - The overall sex ratio for wild steelhead was 1: 1.2 (male:female). Although the ratio slightly favors females, it was not significantly different from a 1:1 ratio ($\chi^2 = 2.020$, df=1, P= 0.155). The overall sex ratio for hatchery steelhead (1:1.1) also did not significantly depart from a uniform sex ratio ($\chi^2 = 1.215$, df=1, P= 0.270).

Male to female ratios varied according to return year. Number of males exceeded the number of females in 1994 for both wild and hatchery steelhead. Females predominated in

1995, 1996 and the wild and hatchery kelts sampled in 1996 (Table 9). These yearly differences where not significant except in 1996 for wild kelts ($\chi^2 = 4.172$, df=1, P=0.041). Seventy percent of male kelts (wild and hatchery) were infected with *Saprolegnia,* a fungus infection common in stressed or injured salmonids.

Sex ratios of returning steelhead also varied with lake age. Higher male proportions were related to earlier lake ages. Ratios for lake age-1 through age-5 were 1:0, 1:1.2, 1:1.2, 1:2, and 1:3 respectively for wild fish. Ratios for hatchery fish at each lake age were 1:0, 1:.89, 1:1.4, 1:1.9, and 1:1.5 (Figure 10).

Table 9. Sex ratios for adult wild and hatchery steelhead according to return year. Asterisk indicates a significant difference ($P < 0.05$) from a 1M:1F sex ratio

	WILD M:F			HATCHERY M:F		
Return Year	*n*	%	Ratio	*n*	%	Ratio
1994	39:37	51:49	1:.95	48:46	51:49	1:.96
1995	21:25	47:53	1:1.2	36:38	49:51	1:1.1
1996	20:27	43:57	1:1.4	55:74	43:57	1:1.3
1996 Kelt	9:20 *	31:69	1:2.2	12:18	40:60	1:1.5
Total	89:109	45:55	1:1.2	139:158	47:53	1:1.1

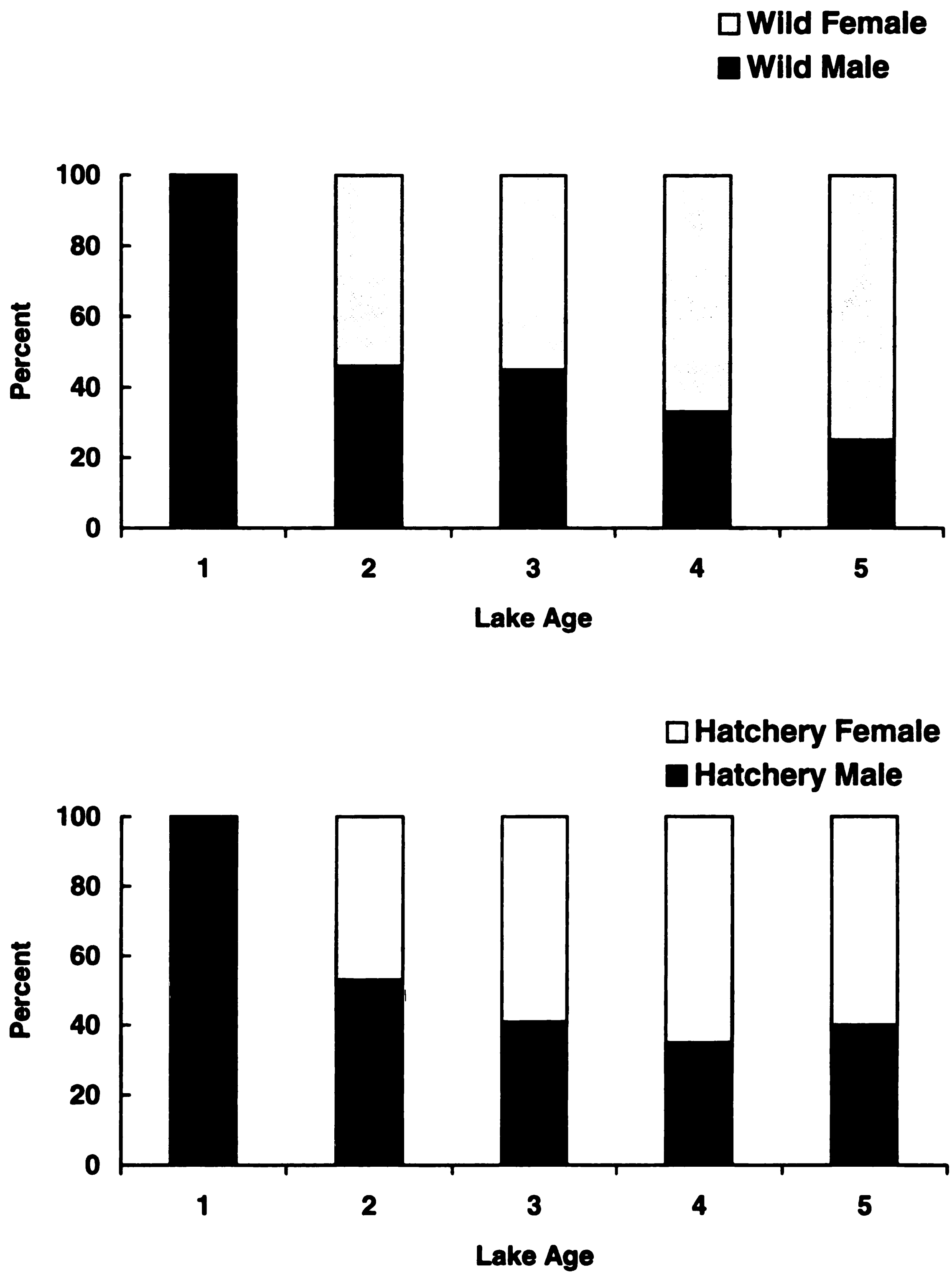


Figure 10. Gender composition by lake age in samples of wild and hatchery steelhead returning to the Betsie River during 1994-1996.

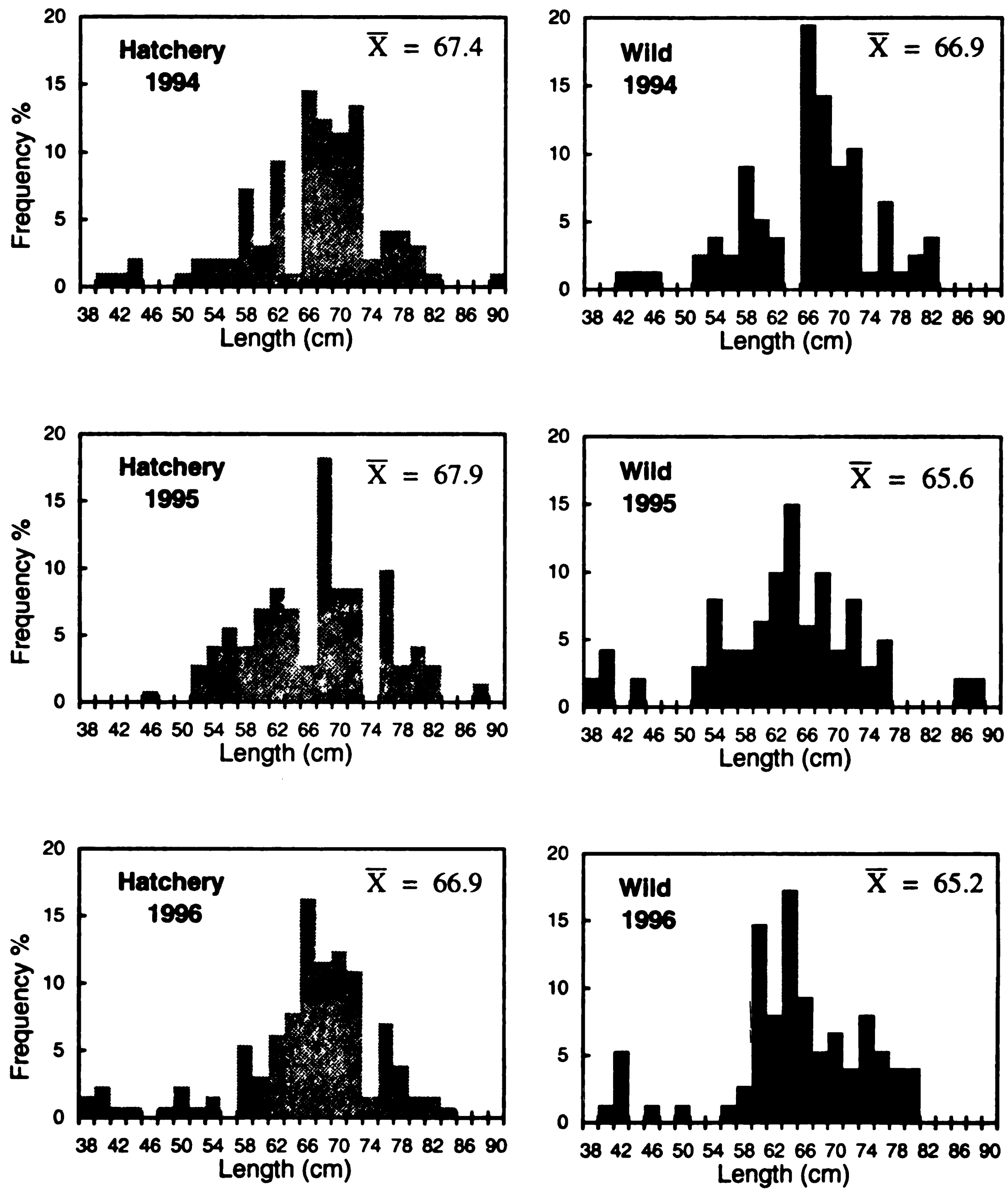


Figure 11. Length frequency distributions of wild and hatchery steelhead by return year. Lengths are grouped in two centimeter intervals.

Length and Growth - Yearly length frequency distributions, as depicted in Figure 11, illustrate the size structure of the spawning populations. Lengths ranged from 39cm to 89cm for wild steelhead and 38cm to 99 cm for hatchery steelhead. Annual overall mean lengths remained consistent throughout 1994-1996. Analysis of variance indicated no length differences among years or origin (Table 10). Lengths at lake age also remained consistent during the three years of study (Figure 12). Wild lengths at lake age did not differ statistically between years, nor did hatchery lengths (Table 10).

Adult steelhead lengths did vary according to age, sex, and spawning history (Table 11). Lengths at maturity of male hatchery spawners increased with each year of lake residence. Wild lengths at maturity of male spawners reached an apparent asymptotic level at lake age-4 whereas hatchery males did not. Comparative length trajectories depicted in Figure 13 portray these growth patterns. The mean lengths of hatchery males at lake age were not significantly different than the respective lengths of wild males (*t*-tests, $P > 0.05$).

Maiden wild and hatchery females were not recruited to the river fishery until lake age-2. Their growth trajectories, however, project a similar pattern to that of the corresponding male steelhead (Figure 13). Mean lengths of hatchery females were not significantly different from their wild counterparts except at lake age-3 (t=2.058, df=46, $P = 0.045$).

The stream age of wild steelhead appeared to significantly affect adult length only at lake age-1. Two year old smolts were longer than one year old smolts only at lake age-1(t=2.614, df=8, $P = 0.031$). After the first year in Lake Michigan, wild adult lengths

Table 10. Two way analysis of variance tests for year and origin effects on steelhead length, 1994-1996.

Lake Age	Effects	*n*	Degrees of Freedom	F	*P* Value
Overall	year	*495*	2, 493	0.76	$P = 0.4690$
	origin		1, 493	3.42	$P = 0.0649$
Lake age1	year	*27*	2, 25	1.60	$P = 0.2262$
	origin		1, 25	0.65	$P = 0.4297$
Lake age2	year	*118*	2, 116	1.29	$P = 0.2799$
	origin		1, 116	0.01	$P = 0.9248$
Lake age 3	year	*240*	2, 238	1.64	$P = 0.1953$
	origin		1, 238	3.53	$P = 0.0616$
Lake age 4	year	*71*	2, 69	2.05	$P = 0.1366$
	origin		1, 69	0.57	$P = 0.4538$

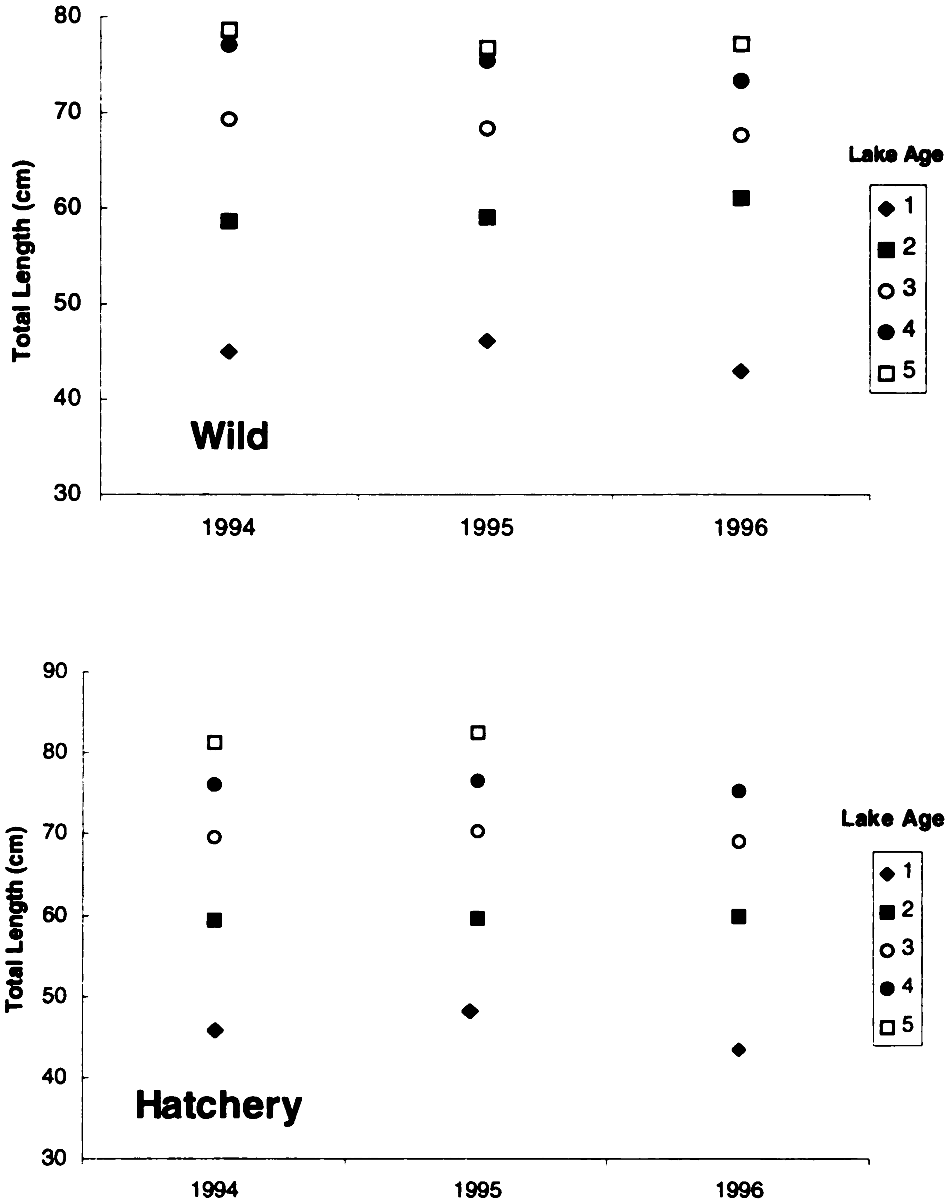


Figure 12. Mean total length at lake age for wild and hatchery steelhead by return year, 1994 - 1996.

Table 11. Mean total length (cm) by age class and sex for wild and hatchery adult steelhead from the Betsie River, 1994 - 1996.

	WILD						HATCHERY					
	Male			Female			Male			Female		
Age Class	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*
Maiden Spawners												
1.1	**42**	0.6	*6*				**47**	1.8	*13*			
1.2	**59**	0.9	*8*	**60**	1.2	*9*	**58**	0.9	*37*	**61**	0.8	*33*
1.3	**72**	1.2	*15*	**68**	1.0	*22*	**70**	0.6	*60*	**69**	0.4	*81*
1.4	**81**	6.3	*2*	**74**	2.5	*2*	**77**	1.1	*15*	**75**	0.9	*20*
1.5	**79**	0	*2*				**85**	2.2	*3*	**81**	-	*1*
2.1	**44**	1.1	*7*									
2.2	**61**	1.7	*15*	**60**	0.7	*21*	**62**	-	*1*	**63**	-	*1*
2.3	**70**	1.0	*21*	**67**	0.9	*24*						
2.4	**77**	3.3	*3*	**71**	2.2	*3*						
2.5	**77**	-	*1*	**72**	-	*1*						
3.3	**69**	-	*1*									
Repeat Spawners												
1.1s1s1							**60**	1.3	*2*			
1.2s1	**61**	-	*1*				**69**	1.0	*7*	**68**	1.0	*6*
1.2s1s1										**73**	2.2	*4*
1.2s1s1s1										**76**	-	*1*
1.3s1	**77**	-	*1*	**74**	3.8	*3*	**75**	2.5	*2*	**75**	2.0	*8*
2.1s1	**53**	2.5	*3*									
2.2s1	**58**	0.2	*3*	**66**	0.8	*13*						
2.2s1s1				**78**	3.8	*5*						
2.2s1s1s1				**77**	3.8	*2*						
2.3s1	**76**	3.6	*2*	**74**	3.9	*3*						

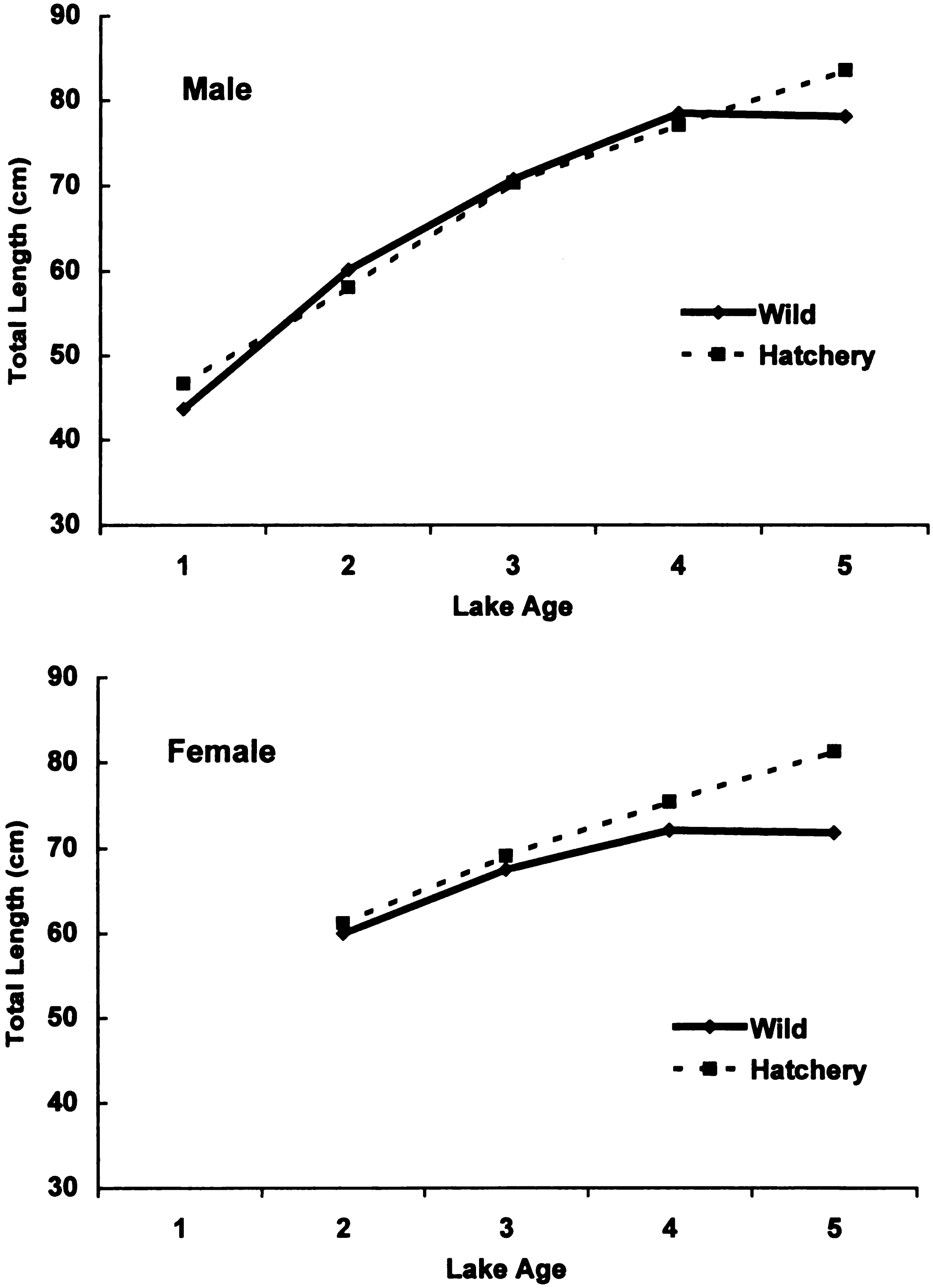


Figure 13. Mean length at maturity (cm) of maiden wild and hatchery steelhead according to sex returning to the river during 1994 - 1996. Stream ages pooled for wild steelhead at each lake age.

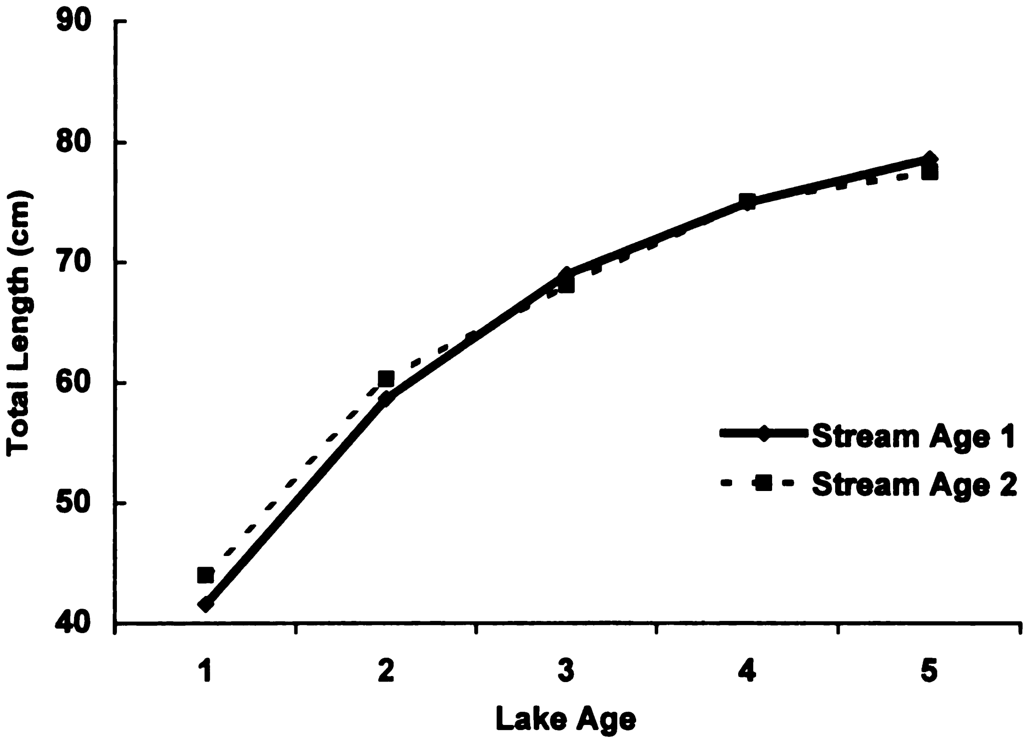


Figure 14. Mean length at maturity (cm) according to stream age of wild adult steelhead returning to the Betsie River during 1994 -1996.

were virtually the same, regardless of stream age history (*t*-tests, $P > 0.05$). Wild steelhead that smolted at age-1 had achieved the same length as age-2 smolts of equal lake residence (Figure 14).

Sex influenced adult length for wild and hatchery fish (Table 12). Wild males were longer than wild females in the lake age-3 category (t=3.559, df=37, $P = 0.001$) and at lake age-4 (t=2.576, df=5, $P = 0.049$). Lake age-2 males were not significantly longer than the corresponding females (t=0.215, df=21, P= 0.832). Hatchery males were also longer than hatchery females at lake age-3 (t=2.015, df=58, $P = 0.048$). Hatchery females were longer than males at lake age-2 (t=2.652, df=29, $P = 0.01$).

Spawning history also influenced adult length. Mean lengths of maiden spawners were generally greater than lengths of repeat spawners of equal lake age (Table 13). Among wild steelhead significant length differences occurred between lake age-2 and -3 maiden and repeat spawners (*t*-tests, $P < 0.01$). A similar difference occurred between hatchery lake age-3 maiden and repeat spawning steelhead (t=4.728, df=14, $P = 0.0003$).

Annual increments of length diminished with each year of lake residence with the exception of lake age-5 hatchery fish . There was no difference in growth rates between wild and hatchery steelhead as measured by walford plots. Comparative walford plots indicated similar growth (Figure 15). Growth coefficients (K) were essentially the same for wild and hatchery fish.

Migration Timing - Wild and hatchery migrants were caught in the Betsie River during the fall and winter months. The majority of these fish, however, were captured in the lower river. Respective spring run timing, as measured by weekly catch at the

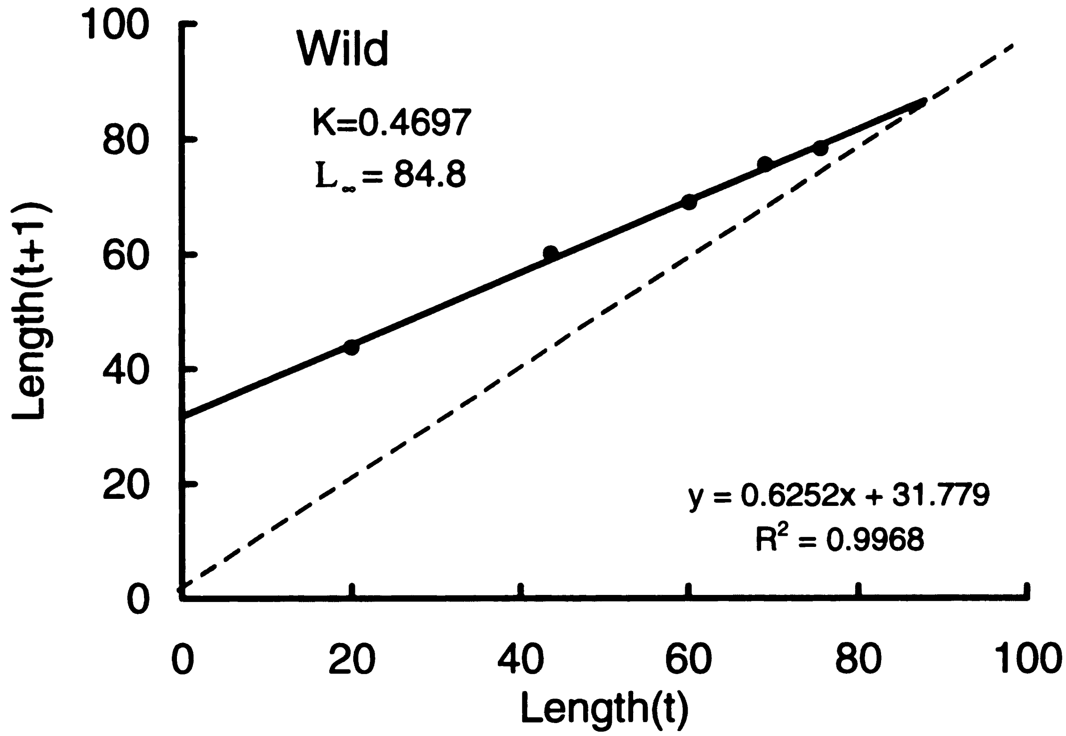
Table 12. Comparison of mean total length (cm) by sex for maiden wild and hatchery steelhead. Significant length differences denoted by asterisk (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = no significant difference).

		LENGTH				
		Male		Female		
Origin	Lake Age	*n*	mean	*n*	mean	*P* Value
Wild	2	*23*	60.2	*30*	60.0	NS
	3	*37*	70.8	*47*	67.5	***
	4	*5*	78.6	*5*	72.1	*
	5	*3*	78.3	*1*	71.8	NS
Hatchery	2	*38*	58.1	*33*	61.2	*
	3	*60*	70.5	*81*	69.1	*
	4	*15*	77.2	*20*	75.4	NS
	5	*3*	85.1	*1*	81.3	NS

Table 13. Comparison of mean total length (cm) by spawning history for wild and hatchery steelhead. Significant length differences denoted by asterisk (* $P< 0.05$; ** $P< 0.01$; *** $P< 0.001$; NS = no significant difference).

		LENGTH				
		Maiden spawners		Repeat spawners		
Origin	Lake Age	n	mean	n	mean	*P* Value
Wild	2	53	60.2	3	53.3	**
	3	84	69.0	17	65.1	**
	4	10	75.5	14	74.6	NS
	5	4	78.3	2	77.5	NS
Hatchery	2	72	59.6	0	-[1]	-
	3	141	69.7	15	67.9	***
	4	35	76.2	14	75.3	NS
	5	4	83.8	1	76.2	NS

[1] no hatchery lake age 2 repeat spawners in sample



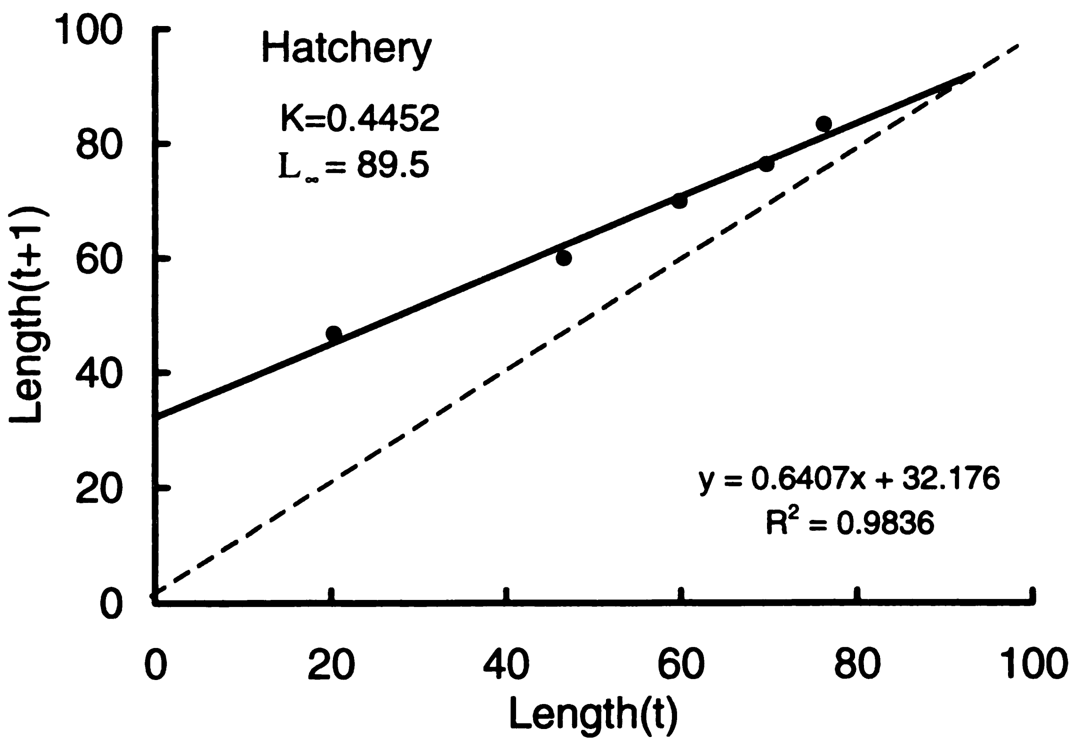


Figure 15. Walfort Plots for wild and hatchery steelhead and their calculated growth coefficients (K) and asymptotic lengths (L_∞)

Homestead weir, was congruous between wild and hatchery steelhead (Figure 16). The distribution of wild and hatchery migration timing was not significantly different in any year (Chi-square tests, $P > 0.05$) Peak immigration of wild fish coincided with the peak immigration of hatchery fish in all three years. Median date of capture for both wild and hatchery immigrants occurred in the first week of April in 1994 and 1995 and the second week of April in 1996.

Migration timing appeared to differ between sexes. Based on weekly catch, males (wild and hatchery) returned earlier than females (Figure 17). The distribution of male migration dates was significantly earlier than that of females for wild and hatchery steelhead (Chi-square tests, $P < 0.001$). Male steelhead made up 78% of the fall and winter catch.

Smolt Size Influence

Influence on Return - I first measured size-dependent selection for return directly from scale data without the potential biasing effects of back-calculation procedures. The form and relative magnitude of selection was determined with two independent samples of the 1993 and 1994 cohorts taken before and after lake residence.

Because scale radius is proportional to fish length, it can therefore be used as an index of size. Smolt scale radius when compared with adult smolt check radius suggested that the probability of return is size dependent for steelhead smolts.

Mean smolt scale radii of surviving hatchery adults from the 1993 and 1994 cohorts were significantly greater than the corresponding scale radii from the same cohort prior to lake residence (Table 14). The greatest difference in mean scale radius

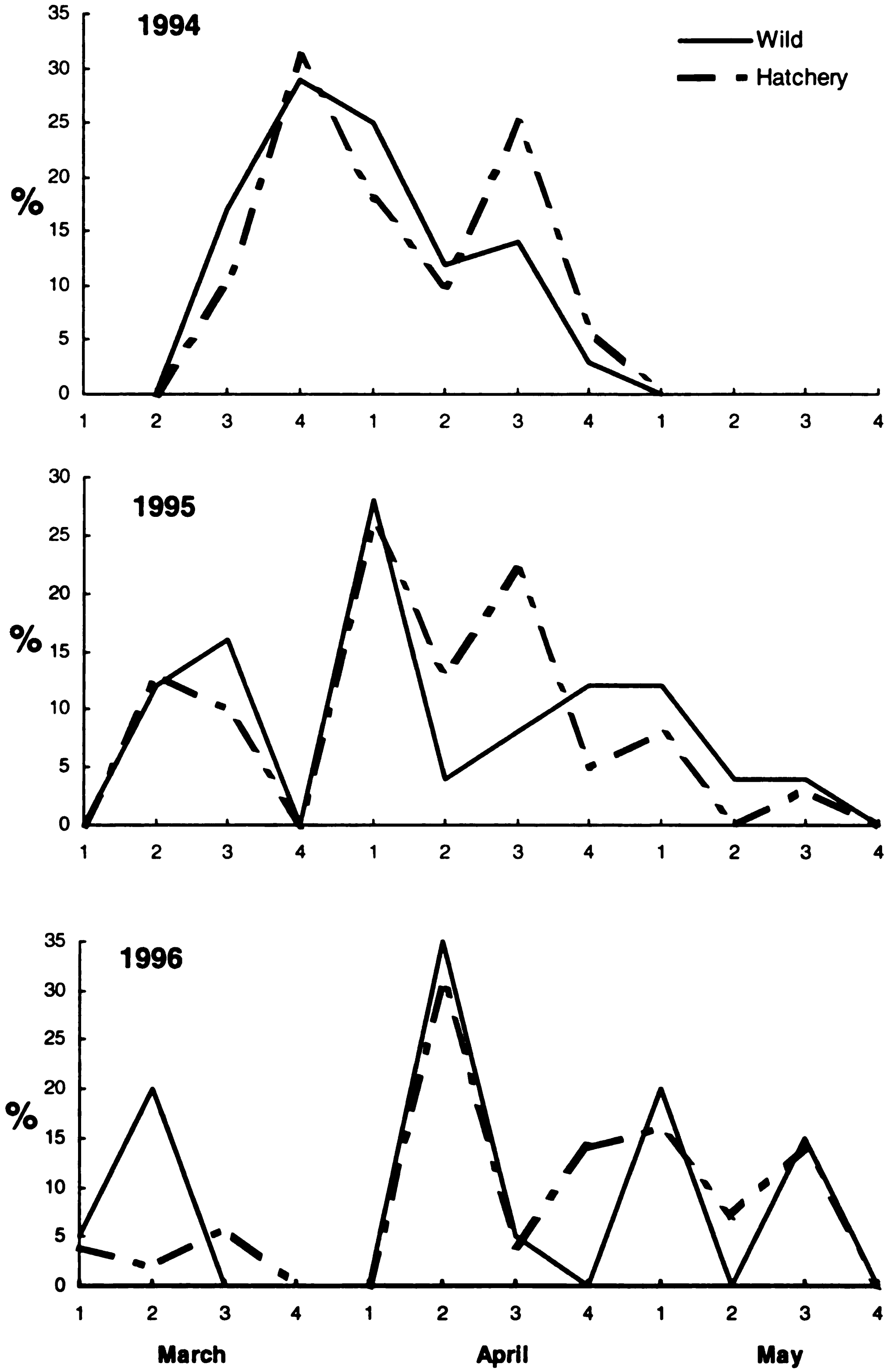
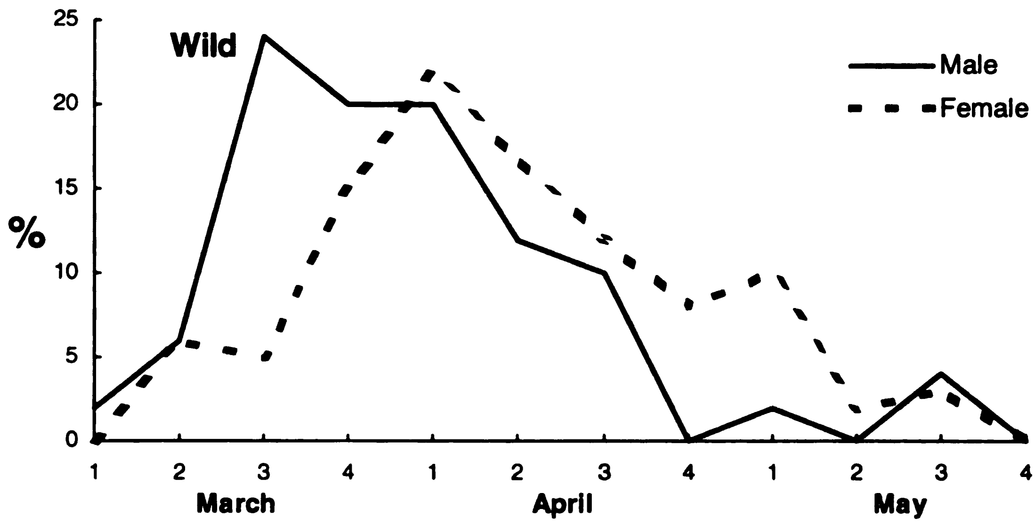


Figure 16. Migration timing based on the weekly catch at Homestead weir from March through May.



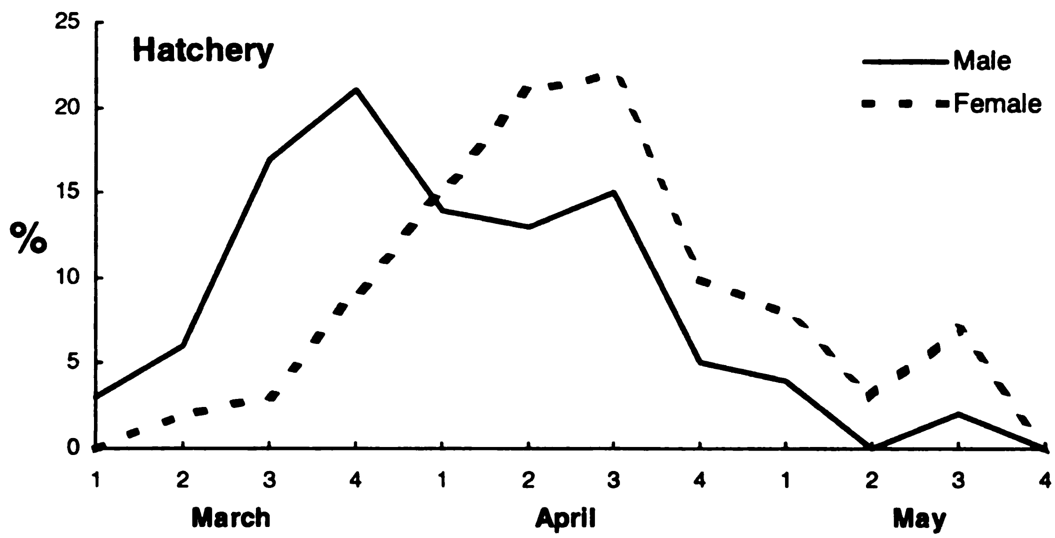


Figure 17. Migration timing by sex of wild and hatchery steelhead based on average weekly catch at the Homestead weir from March through May, 1994-1996

between hatchery adults and smolts occurred in 1993. Adult frequency distributions of scale radii in both years were highly skewed and shifted toward the larger scale sizes.

Wild steelhead comparisons showed a similar size dependent relationship where larger smolts have a greater probability of returning as adults. Adults from the 1994 cohort had significantly larger smolt scale radii than did the 1994 smolts measured prior to lake residence. Mean adult smolt scale radii from the 1993 cohort were larger than the scale radii of the corresponding 1993 smolts. However, the difference was not significant (Table 14). The greatest difference in mean scale radii between wild adults and smolts occurred in 1994. As with hatchery adults, wild adult distributions of scale radii were shifted toward large scale intervals.

Graphical comparison of smolt lengths derived from back-calculation of adult scales and observed measured smolt lengths also suggests that survival is higher for fish that are large size at smolting. Differences in length distributions were apparent mainly in the smaller length intervals (Figures 18 & 19).

Surviving adult hatchery fish had significantly different smolt length distributions than did migrant smolts measured at Homestead in both cohort years (Chi-square tests, $P < 0.0001$; Figure 18). Smolt length distributions of wild adults from the 1994 cohort were significantly ($\chi^2 = 31.01$, $df = 12$, $P = 0.002$) shifted towards larger sizes when compared to wild smolts measured in 1994 (Figure 19). Adult smolt lengths from the 1993 cohort were shifted toward the larger sizes as well. The distribution, however, was not

Table 14. Comparison between adult smolt check radius (mm) and smolt scale radius (mm) of wild and hatchery steelhead according to smolt year. Significant scale radius differences denoted by an asterisk (* $P< 0.05$; **$P< 0.01$; ***$P< 0.001$; NS = no significant difference).

		SMOLT SCALE RADIUS (mm)				
		Adult		Smolt		
Origin	Smolt Year	*n*	mean	*n*	mean	*P* Value
Wild	1993	*45*	.994	*10*	.890	NS
	1994	*32*	1.04	*101*	.905	***
Hatchery	1993	*122*	.950	*10*	.854	*
	1994	*39*	.956	*272*	.905	*

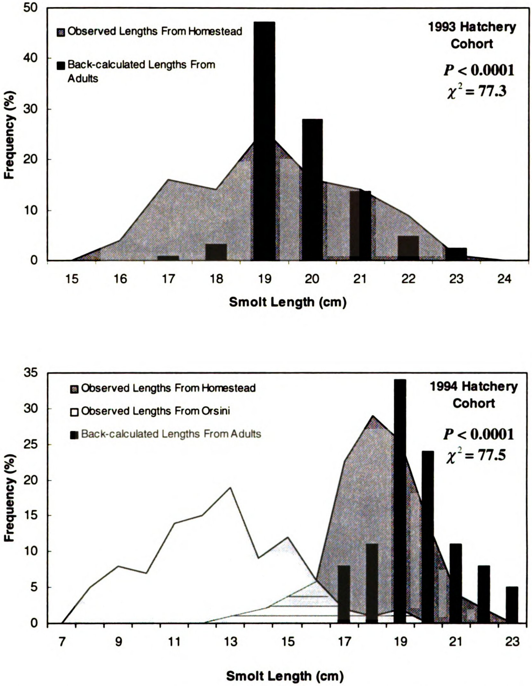
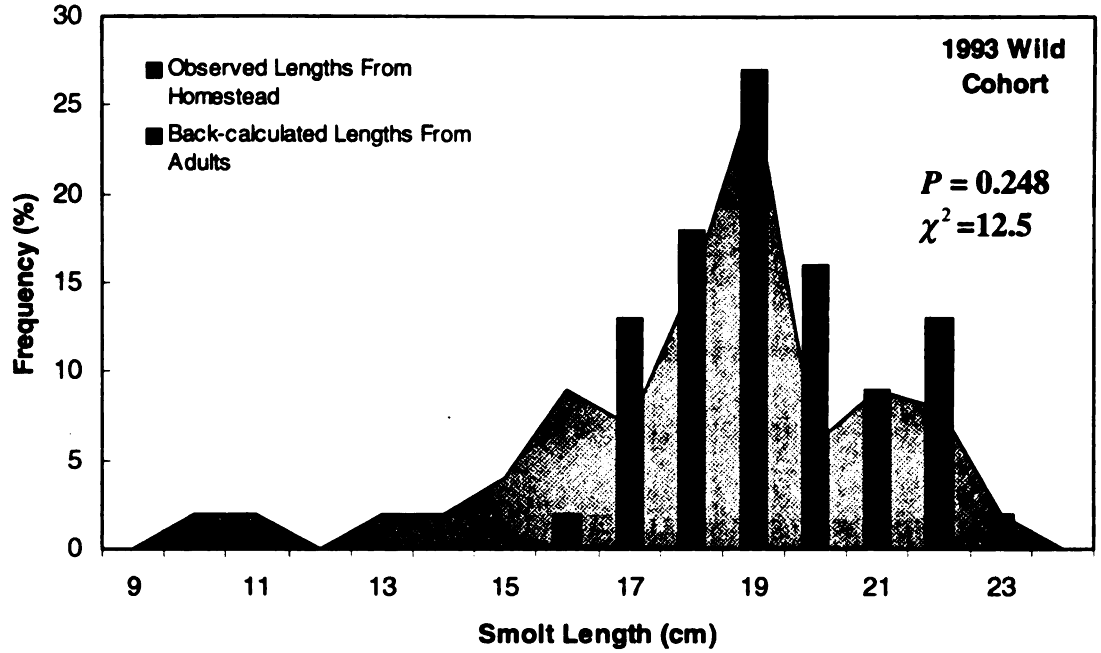


Figure 18. Frequency distributions of observed lengths from migrating hatchery smolts measured at the Homestead weir and back-calculated smolt lengths of surviving adult steelhead from the same cohort. Smolts were also measured at the hatchery prior to release in 1994.



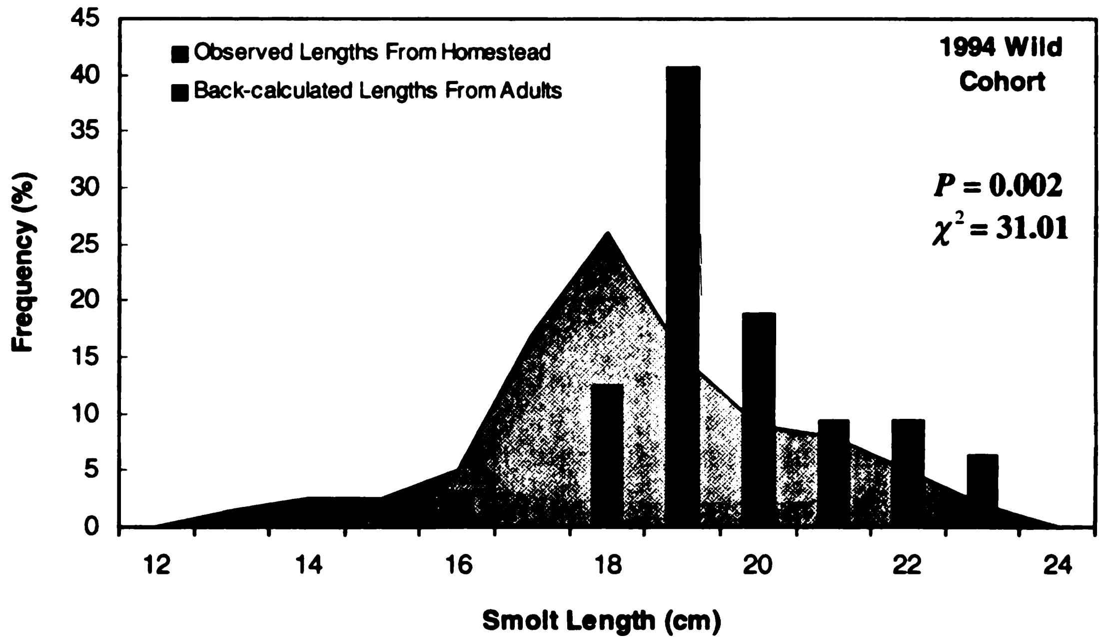


Figure 19. Frequency distributions of observed lengths from migrating wild smolts measured at the Homestead weir and back-calculated smolt lengths of surviving wild adult steelhead from the same cohort.

significantly different than the distribution from the measured smolt lengths of the same cohort ($\chi^2 = 12.5$, $df = 13$, $P = 0.248$).

In both smolt years, wild and hatchery mean back-calculated lengths were greater than observed, measured lengths (Table 15). Mean differences between back-calculated and observed lengths ranged from 0.5cm to 1.3cm. Length differences between male and female smolts determined from scales were not significant for either wild or hatchery steelhead (*t*-tests, P > 0.05).

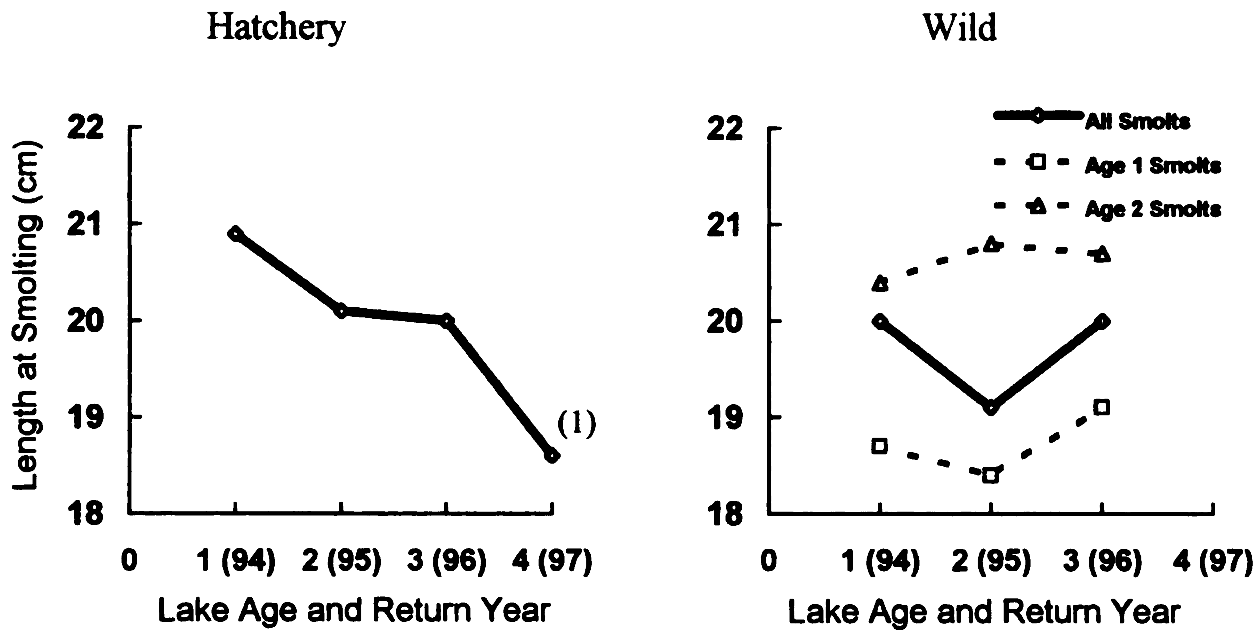
As expected, smolt size increased with stream age according to observed and back-calculated lengths of wild smolts (Table 15). Differences between back-calculated and observed lengths decreased with stream age. Differences were significant at stream age-1 but not significant at stream age-2. This result implies that size selection is more pervasive among the smaller stream age-1 smolts than among stream age-2 smolts.

Influence on Age at Maturity - The length of smolts had some apparent influence on the number of years spent in Lake Michigan prior to spawning. Generally, as years of lake residence increased, smolt length decreased, meaning that large smolts returned earlier than small smolts (Table 15). Smolt length differences between lake age-2 and -3 fish were not significant in either wild or hatchery steelhead (*t*-tests, $P > 0.05$). But the difference between lake age-1 hatchery fish and older lake age hatchery fish was significant (t=2.584, df=17, $P = 0.02$). Wild lake age-1 smolt lengths, although larger on average, were not significantly different than smolt lengths of other lake age fish ((t=1.422, df=13, $P = 0.178$).

Table 15. Observed smolt lengths (OL) and back-calculated smolt lengths (BL) from adults in relation to the smolt cohort year, the stream and lake age, the sex, and the year of return with all cohorts pooled.

Category	WILD Mean OL (cm)	WILD OL *n*	WILD Mean BL (cm)	WILD BL *n*	WILD BL SE	HATCHERY Mean OL (cm)	HATCHERY OL *n*	HATCHERY Mean BL (cm)	HATCHERY BL *n*	HATCHERY BL SE
Smolt Year										
1993	**19.3**	*48*	**19.8**	*45*	1.6	**19.8**	*65*	**20.3**	*116*	1.1
1994	**19.2**	*225*	**20.3**	*37*	1.5	**18.8**	*740*	**20.1**	*38*	1.4
Stream Age										
1	**17.4**	*164*	**19.0**	*37*	1.0					
2	**20.5**	*93*	**20.6**	*46*	1.3					
Lake Age										
1			**20.3**	*14*	1.6			**21.5**	*18*	3.3
2			**19.7**	*36*	1.7			**20.2**	*60*	1.5
3			**19.9**	*33*	1.5			**20.0**	*75*	2.0
4								**18.6**	*1*	-
Sex										
Female			**19.8**	*44*	1.6			**20.2**	*89*	1.3
Male			**19.7**	*39*	1.6			**20.3**	*65*	1.9
Return Year										
1994			**20.2**	*77*	1.7			**20.3**	*97*	1.5
1995			**19.8**	*47*	1.7			**20.5**	*71*	1.5
1996			**20.2**	*75*	1.7			**20.5**	*130*	2.0

1993 Smolt Cohort



1994 Smolt Cohort

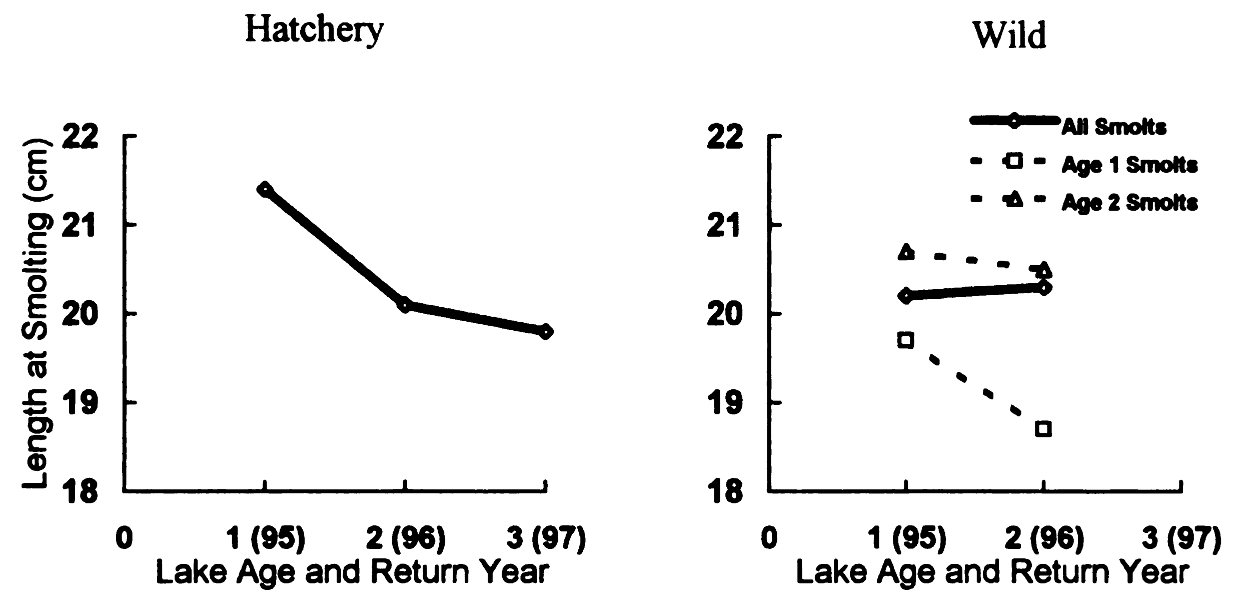


Figure 20. Relationship between mean back-calculated length at smolting and lake age of adult steelhead from the Betsie River, 1994-1997.

Very large hatchery male smolts appeared to return earlier than the rest of the hatchery population as lake age-1 jacks (Figure 20). The same relationship between smolt length and lake age was not as apparent in the wild cohorts.

Lake Distribution and River Straying

Lake Distribution - After leaving the harbor at Frankfort as smolts, the geographic dispersal of hatchery steelhead was determined from the open lake fishery. Lake Michigan ports sampled in creel surveys covered the length and breadth of the lake from Burns Harbor, Indiana up to Big Bay de Noc in Michigan and along the east and west shoreline. Data from these surveys provided information about the distribution of uniquely marked Betsie River steelhead (Figure 21).

Based on returns, RV clipped fish were just beginning to recruit to the fishery in 1994 and were limited to Michigan waters from Onekama to Ludington. By 1995, these fish were well distributed throughout the southern two thirds of the lake. In 1996, this dispersal pattern repeated itself with fish being caught in the waters of all four states bordering Lake Michigan. During the three years, 47% of the Betsie River hatchery returns were caught in Michigan waters, 28% in Wisconsin, 16% in Indiana, and 9% in Illinois. No RV clipped fish were recorded north of Frankfort. Recoveries of Betsie River steelhead in southern Lake Michigan waters represent a minimum movement of 370 km.

Ages of the RV clipped fish (determined by management agency scale readers) ranged from 1.1 to 1.3 and thus represented the 1993-1995 hatchery cohorts. Total lengths ranged from 46-75cm. These fish were harvested during the lake fishery from April through September.

According to agency records, RV clipped steelhead were frequently caught along with other uniquely marked steelhead, suggesting intermingling of stocks in the open lake.

River Straying - Fin clipping of pre-smolts at the Orsini Hatchery began in 1993. Based on weir records, ladder reports, and stream creel surveys, homing imprecision of Betsie River hatchery steelhead was documented in 1995 and 1996 (Figure 22). Straying was observed in five non-natal streams of Lake Michigan as far south as the St. Joseph River on the east shore and the Root River on the west.

Characteristics of the stray fish were similar to fish that had homed accurately back to the Betsie River. Total lengths ranged from 49 - 81cm. Ages of stray steelhead were not documented in most cases. However, length distributions suggest that the majority of strays were lake age-2 and -3 fish. Straying tendency appeared to be independent of sex. The sex ratio was 1:1. This characteristic was similar to the ratios found in the fish sampled in the Betsie River. Most of the stray steelhead (92%) were spring migrants.

Eighty eight percent of the recovered strays were observed in weirs, 8% from stream creel surveys, and 4% from ladder reports. Michigan's four northern Lake Michigan weirs recorded only one Betsie River stray (Little Manistee River Weir). Medusa Creek, Platte River, and Boardman River weir facilities are operated in the fall months only and sample approximately 400 fish. The Little Manistee River weir is operated in the fall and spring. Approximately 400 steelhead are sampled for biological data during each run.

The other strays were found in streams far from the vicinity of the Betsie River. Two Wisconsin rivers shared the largest proportions of recorded strays. Located on the Kewaunee River, the Besadny Facility recorded Betsie River strays in 1995 and 1996. The Root River Steelhead Facility also counted Betsie River strays in both years. These two weir facilities are operated during spring and fall salmonid runs. Over 2000 steelhead are examined at both weirs each year.

Wisconsin creel clerks on the Sheboygan River sampled one Betsie River steelhead in 1995 and one in 1996. The St. Joseph River attracted two known Betsie River fish. One stray was captured in the Berrien Springs Dam ladder during sampling operations in 1995. Indiana creel clerks sampled the other stray steelhead upstream of the French Paper Company Dam in 1996

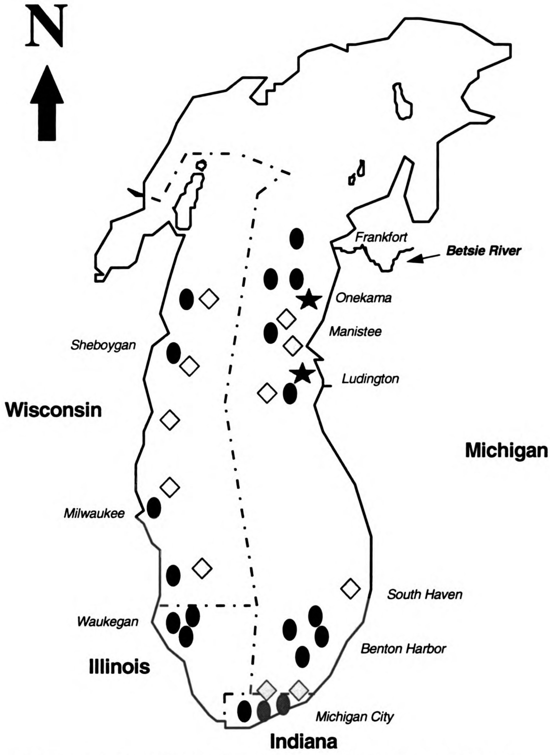


Figure 22. Distribution in Lake Michigan of steelhead stocked as smolts in the Betsie River during 1993 -1995. RV clipped steelhead recovered in 1994 - ★; 1995 - ◇; 1996 - ⬮.

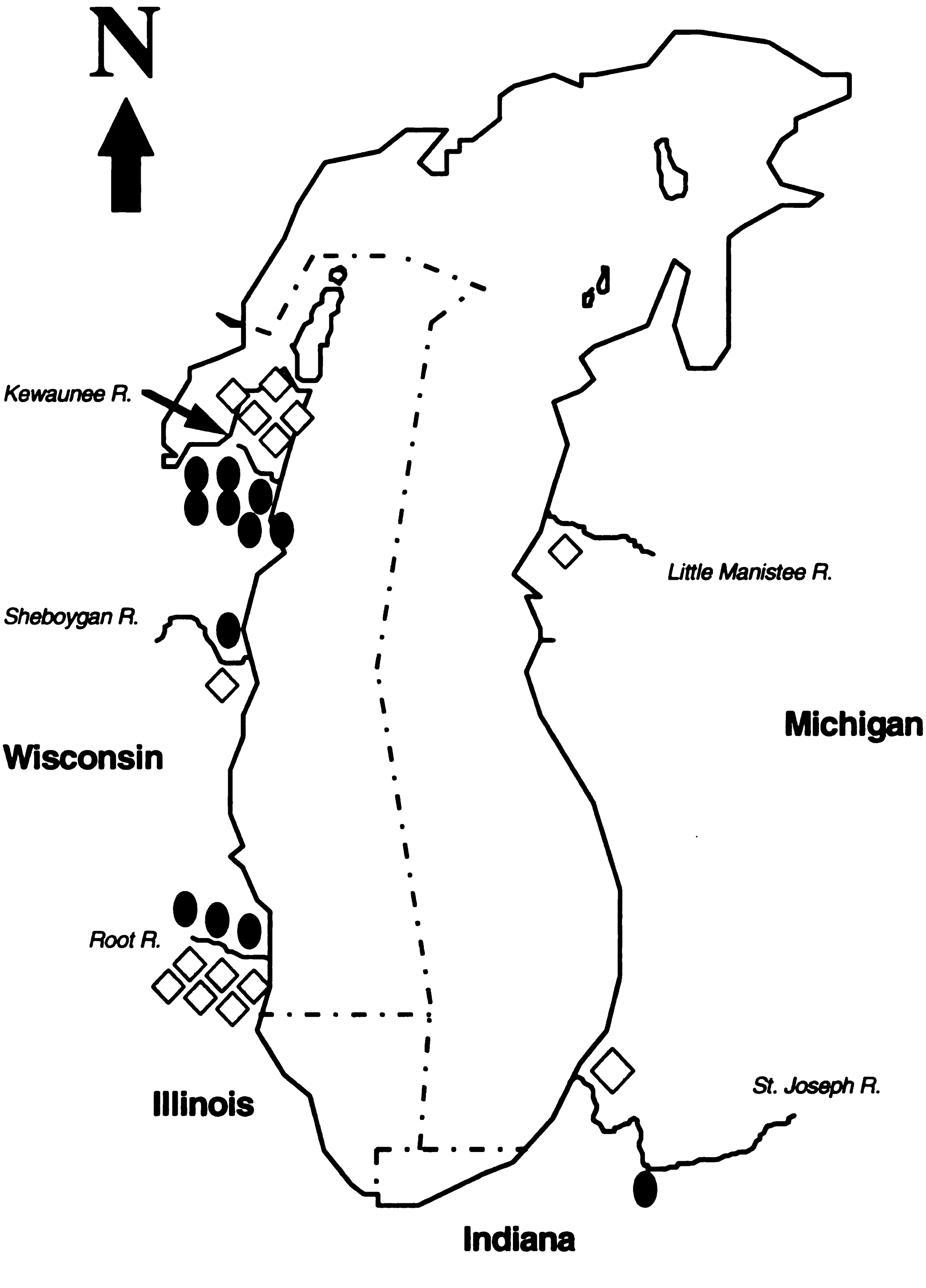


Figure 23. River straying by steelhead stocked as smolts in the Betsie River during 1993 - 1995. RV clipped adults recovered in 1995 - ◇; 1996 - ⬬ .

DISCUSSION

Origins

Accuracy - Classification accuracy and error rates, as assessed from the subsample of Seelbach and Whelan's (1988) archived scale collection, compare favorably with similar studies. Based on the one parameter of ratio 23, I determined assignment frequencies of .898 and .940 for wild and hatchery steelhead respectively for an overall accuracy of 92%. Unwin and Lucas (1993) separated wild and hatchery chinook salmon with accuracy rates of 82-90% using a single scale parameter. Using circuli spacing, Barlow and Gregg (1991) achieved an accuracy rate of 83% in discriminating between wild and hatchery barramundi, *Lates calcarifer*. Bernard and Myers (1997) used a six parameter technique to separate wild and hatchery steelhead from North Pacific populations and obtained a 94% accuracy rate in their test samples.

Quantifiable differences in the scales of Betsie River wild and hatchery steelhead presumably allowed for the same level of accuracy in my samples as in the archived sample. Although not all hatchery steelhead were marked, 96% of the RV clipped fish were correctly identified as having a hatchery origin. Moreover, ratio 23 may be a better discriminator of Betsie River fish than for fish from a more benign system. Scale characteristics such as circuli spacing are strongly influenced by environmental factors like temperature and food availability (Bhatia 1931; Willett 1994). In response to cold temperatures and reduced feeding, circuli spacing narrows. Conversely, spacing widens with increased temperatures and feeding. Such patterns are accentuated with temperature extremes and are less so with more uniform temperatures. The Betsie River is a thermally diverse watershed with relatively wide ranging temperatures (Newcomb 1998). Scales from fish that grew in the Betsie environment would be expected to exhibit patterns reflecting this type of temperature regime. Indeed, stream annuli on wild Betsie River steelhead were generally distinct and easily defined. Also the difference between the mean ratio 23 values of Betsie River wild and hatchery steelhead was greater than the difference between the archived wild and hatchery sample. As the difference between ratio 23 values increases, separation of wild and hatchery fish becomes increasingly accurate.

Composition of Spawning Runs - Assuming equal catchability of hatchery and wild fish, wild steelhead made up 30-46% of the returning adult population in the three study years. This relative contribution is much lower than that measured just 10 years previously. The downward trend in relative abundance of wild fish can be interpreted in two ways. First, the decrease may be only relative to the increase in hatchery numbers. Stocking levels of Betsie River hatchery steelhead have increased four-fold since the early 1980's. Fish are also released at a larger size and higher up in the watershed, both of which should increase returns. Therefore, the same number of wild fish would contribute a smaller proportion due to an increase of hatchery fish returning to the Betsie River.

The other possible explanation for the lower contribution is that fewer wild fish are being produced in the Betsie River. When the Thompsonville Dam failed, sediments held behind the dam were released downstream. Much of the watershed's best spawning gravels were compromised. If wild production is less than what it was in the early 1980's, then the lower proportions reflect an actual decline in wild steelhead numbers. Regardless of the possible explanations for the reduction in relative abundance, wild steelhead are still making important contributions to the fishery.

Proportions of wild steelhead in other marginal tributaries of Lake Michigan that receive hatchery fish have ranged from 55% in the Muskegon River (Seelbach and Whelan 1988) to 3-11% in the St. Joseph and Grand Rivers (Seelbach et al. 1994). The contribution of wild steelhead is much greater in the high quality streams of northwestern lower Michigan where little stocking is required to maintain the fisheries (Seelbach 1987).

Stray hatchery steelhead from rivers other than the Betsie comprised an unknown percentage of the spawning runs. Guides and anglers recorded the clip type of marked steelhead from their catch. Anglers, however, were not aware of the maxillary clips used by the state of Wisconsin during the 1994 and 1995 seasons. In addition, not all hatchery steelhead stocked into Lake Michigan are marked (Anonymous 1975-1995). Therefore, the relative abundance of strays could not be estimated. The origins of the uniquely marked fish appear to be widespread throughout Lake Michigan (Appendix B). Although fish did stray from as far as the St. Joseph River, Indiana, the majority of recorded strays had a Wisconsin origin. These fish, which potentially made significant contributions to the spawning effort, were not only from allopatric sources, but also of differing strains. The Ganaraska, Skamania, and Chambers Creek strains were all represented by the stray steelhead as well as the Little Manistee strain used by Michigan.

An interesting and statistically significant difference existed between the 1996 estimate of wild and hatchery contributions based on the fishery (30% wild) and the 1996 kelt estimate sampled with block nets and electrofishing gear (51% wild). Kelts, by definition, are survivors of spawning. Because the majority of steelhead caught in the fishery upstream from Homestead were hatchery fish (Appendix C), it does not seem likely that the difference is related to greater numbers of wild fish utilizing that section of the watershed. The Orsini Hatchery, from which they were reared and released, would naturally exert a strong influence on the area of return chosen by hatchery fish (Slaney et al. 1993). The hatchery is located upstream of Homestead. Furthermore, based on data from scale analysis, wild steelhead survived maiden spawning episodes and returned to spawn again more frequently than hatchery steelhead. The lower relative abundance of hatchery kelts is probably associated with poorer spawning survival and not fewer hatchery fish returning to the upper watershed. Numerous other studies concur with this finding. Leider et al. (1986) reported a lower incidence of repeat spawning among hatchery steelhead in Washington. Scale data from 16 Vancouver Island streams confirmed a higher repeat spawning frequency among wild steelhead than among hatchery steelhead (Hooton et al. 1987).

Life History Characteristics

Life history characteristics of fish represent a combination of genetic constraints and adaptive responses to environmental pressures (Ricker 1972; Schaffer and Elson 1975). The variability of these characteristics are what enabled the steelhead to colonize

Table 16. Summary of similarities and distinctions in life history traits of Betsie River wild and hatchery steelhead.

SIMILARITIES

Origin	Migration Timing	Length	Growth Rate Coefficient	Sex Ratio
Wild	April median date	66cm	K = 0.47	1:1
Hatchery	April median date	67cm	K = 0.45	1:1

DISTINCTIONS

Origin	Age at Maturity	Age Structure	Repeat Spawning Freq.
Wild	2.6 lake years	18 age categories	18%
Hatchery	2.8 lake years	11 age categories	10%

and adapt to the localized conditions of Great Lakes tributaries. In the Betsie River I found both life history distinctions and similarities between wild and hatchery steelhead which are summarized in Table 16. Four of the seven parameters examined were similar (sex ratios, lengths, growth, and migration timing) and three were distinct (age structure, age at maturity, and repeat spawning frequency).

Age Structure and Composition - The majority of returning wild steelhead were lake age-2 and -3 fish as were returning hatchery fish. Lake age-3 steelhead are the norm for Little Manistee fish which serve as broodstock for the Orsini Hatchery (Seelbach 1993). However, a greater breadth in the age structure of wild steelhead was evident in the number of age categories. A varied age structure may be an adaptive response to a marginal stream such as the Betsie. According to Schaffer and Elson (1975), when environmental conditions are harsh and unpredictable, selection favors individuals that are capable of spawning at different ages. Saunders and Schom (1985) suggested that the variability in age structures of Atlantic salmon is a safeguard against reproductive failure of any one year class. Individuals from one year class return over multiple years, thereby ensuring some contribution from that cohort. Therefore, a population confronted with the Betsie River, might be expected to send its spawners at a variety of different ages.

Males of wild and hatchery origin had an earlier maturation schedule than females. This maturation pattern is typical of Pacific and Great Lakes steelhead populations (Tipping 1991; Biette et al. 1981). The difference in age at maturity between male and female fish is thought to be related to the difference in gonadal investment between the sexes (Moyle and Cech 1988). Males require less growth before reaching sexual maturity than females.

Wild steelhead as a whole matured earlier than hatchery steelhead. I also found a higher proportion of lake age-1 males (jacks) in the wild Betsie River sample than in the Betsie River hatchery sample. Age at maturity is influenced by genetic as well as environmental factors (Gall et al. 1988). Therefore, steelhead maturity can be manipulated by selective breeding practices as demonstrated by Tipping (1984, 1991). Age at maturity was delayed in the progeny of hatchery stock at the Cowliz Trout Hatchery when only older adults were used as spawners. In Michigan, lake age-1 males are not used as spawners at the Little Manistee River weir facility (Peter Makoweski, MDNR, Personal Communication).

In many Great Lakes tributaries, greater than 70% of the returning adults spent 2 years growing in the stream before smolting (Biette et al. 1981; Seelbach 1993). On average, 61% of returning Betsie River wild adults were stream age-2 smolts. Newcomb (1998), however, found the majority of Betsie River wild juveniles to be stream age-1 smolts. The apparent discrepancy is presumably related to higher mortality of the stream age-1 smolts. This hypothesis is supported by comparing smolt length frequencies of adults and smolts from the same cohort and will be discussed further in the section concerning smolt size influence. Similar observations in Great Lake populations, where the majority of emigrating smolts were stream age-1, but the majority of returning adults were stream age-2 smolts, were made by Kwain (1981), Stauffer (1972) and Karges (1987).

The percentage of returning stream age-1 and -2 adults was not constant between years. Stream age classes of emigrating smolts in tributaries to the Finger Lakes were also found to vary. The annual variation was attributed to stream flow and temperature. Low flow and high temperatures caused the early descent of stream age-1 fish (Northcote 1969). A similar environmental mechanism may be operating in the Betsie River watershed.

Repeat Spawning Frequency - Much of the difference between wild and hatchery age structures can be explained by their frequency of repeat spawning. As discussed above, repeat spawning was more prevalent among wild steelhead than in hatchery steelhead.

Life history theory predicts how fish vary reproductive effort in response to their environment (Schaffer 1974; Mitton and Lewis 1989). Species in unpredictable habitats place a premium on multiple spawnings. Hutchings (1993) anticipated a high degree of iteroparity in brook trout populations when associated with unstable, harsh streams. Conversely, Seelbach (1993) suggested that the stable flows of the Little Manistee River would select for fewer spawnings by larger steelhead. The optimal reproductive strategy for a Betsie River steelhead, if the watershed is viewed as harsh and unpredictable, would be to retain an iteroparous life history.

Sex Ratios - Proportions of males to females were close to a 50:50 ratio in both wild and hatchery samples. An even male:female ratio is normally optimal in vertebrate populations with open, polygamous mating systems (Karlin and Lessard 1986). Although both wild and hatchery fish were evenly divided between male and female, deviation from a 50:50 ratio occurred in the kelt sample, where females were favored. Differential mortality between the sexes is attributed to the longer duration on the spawning grounds by the males and their territorial defense of the redd (Shapovalov and Taft 1954). *Saprolegnia* infections were also more prevalent in males than in females. As a result, the majority of repeat spawners are female. Relatively equal sex ratios in the spawning populations are then maintained in part by the yearly contributions of precocious males.

Withler (1966), Kwain (1971), and Seelbach et al. (1994) all reported equal proportions of male and female spawners in steelhead populations. In other systems, salmonid sex ratios have been inadvertently altered by hatchery practices. The Kalninka River chum salmon, *Oncorhynchus keta,* population changed from a 50:50 ratio to a ratio favoring males as a result of selecting only early returning fish for breeding purposes (Altukhov and Salmenkova 1990).

Length and Growth - Lengths of wild and hatchery fish did not differ between calendar years. Similarly, lengths at age also did not change significantly over the three study years. Annual differences, as indexed by the dominant lake age-3 group, were 1.5cm or less in the wild sample and 1.4cm or less in the hatchery sample. Because adult length is primarily a function of lake age (Seelbach and Beyerle 1984), conditions for growth were apparently stable and equal for hatchery and wild steelhead in Lake Michigan during the years of study. Seelbach (1989; 1994) also found little variation in steelhead lengths between years. Considering the stable size structure in Lake Michigan, Seelbach (1994) suggested that population levels are at a point of equilibrium out in the lake.

Examination of length frequencies revealed distinct modes only at the smaller sizes. Therefore, length frequency analysis of Betsie River steelhead may not be appropriate for accurate assignment of age groups. Size distributions better describe the status or balance of a population (Ney 1993). For example, the 1995 length frequency histogram reflects the near absence of age-1 hatchery fish recruited to the fishery in that year.

I found no difference in male lengths between wild and hatchery fish of the same lake age. Nor did I find differences in female length except at lake age-3, for which hatchery females were significantly longer than wild females. Other comparative studies involving lengths of wild and hatchery steelhead offer mixed results. Hooten et al. (1987) and Peterson (1979) found Pacific populations of wild and hatchery steelhead to be of equal length at equal age. Seelbach and Miller (1993) also found similar lengths in a Great Lakes population of wild and hatchery fish. However, wild Kalama River steelhead were longer than their hatchery counterparts (Leider et al. 1986). Finally, hatchery steelhead from the Cowlitz River were smaller than wild steelhead until the source of hatchery broodstock changed from a domesticated strain to a stream-specific broodstock (Tipping 1984).

Lengths of wild male and female steelhead appeared to reach an asymptotic level whereas hatchery lengths did not. Fish growth normally decreases gradually with size and age. The normal approach to an asymptotic length may have been masked by the small sample size at the older age groups (age-5) and the possible presence of Skamania strain steelhead in the hatchery sample. Skamania steelhead were stocked into the Betsie River in the late 1980s and early 1990s and may have recruited to the fishery during the study. Skamania steelhead frequently reach greater length and mature at a later age than the Little Manistee strain (Fielder 1987).

I did find length differences related to sex and spawning history in both wild and hatchery steelhead. The overall mean length of females was greater than the overall length of males in each year. Because of a deferred maturity schedule, females sampled each year were older and thus longer than males. Males, however, were generally longer than females at specific lake age. Males grew significantly longer than females during the third and fourth year of lake residence. Females, as opposed to males, channel more energy into sexual maturity and less energy into somatic growth. Hence, males were both the smallest (precocious jacks) and largest fish in the adult population.

Maiden spawners observed during the study were longer than repeat spawners of lake age-2 and -3. In preparation for spawning, steelhead divert energy into gonadal growth and then deplete reserves during migration and spawning activity. If spawners survive, additional reserves are used to recover from the loss of condition. Maiden steelhead from the same cohorts remain in a lake environment devoting energy to somatic growth.

Interestingly, significant differences between maiden and repeat spawners were not observed in the older age categories of either wild or hatchery fish. If maturity is, in part, related to length (Griffith, 1993), then the similarity between maiden and repeat spawner lengths at older lake ages can be attributed to slower growing individuals that have yet to mature. This older group of maiden spawners would then obscure any length differences associated with repeat spawning.

Smolt age of wild steelhead influenced adult size only at lake age-1 where 2 year old smolts were longer as adults. After the first season in Lake Michigan, Betsie River adults exhibited equivalent lengths at lake age regardless of time spent in the watershed prior to smolting. Hooten et al. (1987), Kwain (1981), and Karges (1987) all published similar results where smolts of different age and size ultimately achieved the same adult length.

Incremental growth rates of wild and hatchery steelhead were not distinguishable. Both wild and hatchery fish obtained considerable length during their first 2 years of lake residence gaining 40.2cm and 39.3cm respectively. Growth coefficients were also nearly identical indicating similar growth. Growth (and growth estimates) can be influenced by food availability, competitive interactions, weather conditions, size selective sampling and mortality (Van Den Avyle 1993). It can thus be inferred that wild and hatchery steelhead are experiencing the same environmental pressures while in Lake Michigan.

Length and growth data from the river sport fishery are not necessarily representative of the entire Betsie River steelhead population. By sampling only the spawning population, may have introduced bias because non-maturing members of the same cohorts remain in the lake and are not sampled. Consequently, lengths determined from the river fishery are actually a function of growth <u>and</u> maturity. However, for the purposes of comparing relative length and growth, these data are beneficial descriptors of wild and hatchery fish at a critical point in their life history.

The data may also be useful in comparing Betsie River fish with steelhead from other systems. Lengths of Betsie River steelhead are within the range reported in other

Lake Michigan populations (Biette et al. 1981; Hansen and Stauffer 1971; Seelbach et al. 1994).

Migration Timing - Timing is an important trait for the long term survival of an anadromous population. Streams may not be in suitable condition if returning adults are not adapted to the watershed. Spawning too early or too late adversely affects embryo development and fry survival (Gharrett and Smoker 1993). Spawning out of synchrony with optimal conditions can have a negative effect on spawner survival (Leider et al. 1984).

Although timing is mediated somewhat by temperature and flow, it is primarily under genetic control (Gharrett and Smoker 1993). Numerous examples of altered run timing have been documented when wild populations were supplemented with hatchery fish (Tipping 1984; Leider et al. 1986; Steward and Bjornn 1990).

Given the long history of steelhead runs reported in the Betsie River (Wicklund and Dean 1958) migration timing does not appear to be maladapted to the watershed. During the study, spring migration of wild and hatchery fish closely paralleled each other. Median migration dates coincided and occurred in the first or second week in April. The duration of the spring runs also matched, ranging from 6-11 weeks.

Wild and hatchery males consistently entered the fishery earlier than females indicating earlier onset of migration. Shapovalov and Taft (1954) and Withler (1966) documented similar behavior in Pacific steelhead populations. The migration profile of Betsie River steelhead also resembles the migrations of most Great Lakes populations summarized by Biette et al. (1981).

Aging Precision - Scale aging based on the comparative results of three readers exhibited considerably consistency (Tables 3 - 5). The APE and CV values were uniformly low across stream, lake and total age determinations indicating a high level of precision. The index of precision (D) value assigned the percent error contributed by each observation (Chang 1982).

Steelhead life histories are quite varied which can potentially lead to erroneous aging. Although low, stream age APE had a higher value relative to the lake age APE value. Betsie River scale readers, therefore, where consistently more in agreement when assigning lake ages than stream ages. Total age was determined with an intermediate level of precision.

These indices (APE, CV, and D) can all be compared to the precision levels obtained in other scale aging evaluations. For example, the APE values determined in this study for stream, lake, and total age were 3.60%, 1.26%, and 2.33% respectively. Karges (1987) calculated an APE for stream, lake, and total age of 4.56%, 4.65%, and 4.03% respectively during an Ontario steelhead study. In Lake Michigan, the APE for total age averaged 2.17% for chinook salmon otolith aging (Hesse 1994) and 3.63% total age APE for chinook salmon scale aging (Wesley 1996).

Smolt Size Influence

Influence on Return - One of the most important factors influencing the adult return of anadromous salmonids is smolt size. A long history of research has shown a positive relationship between steelhead smolt length and rate of adult return (Larson and

Ward 1954; Wagner 1967; Parkinson and Slaney 1975; Ward and Slaney 1988; Seelbach et al. 1994). Likewise, my research suggests that the probability of return is size dependent for Betsie River smolts.

Mean smolt lengths of returning adults were larger than mean lengths of smolts from the same cohort measured during emigration. This observed inverse of Lee's phenomenon could have other explanations beside the apparent size based mortality of the smaller fish. Back-calculation error could potentially bias results. Therefore, I used data directly measured from scales as a surrogate for smolt size as well as data based on back-calculation techniques. Both approaches showed that larger smolts were more likely to return as adults than their smaller cohort members.

Several plausible mechanisms may be associated with smolt size. Size selective mortality has been demonstrated for sockeye salmon (West and Larkin 1987), chinook salmon (Neilson and Geen 1986) and steelhead (Hume and Parkinson 1987). In each of these studies, the smallest members of the cohort suffered the greatest risk of predation. Predation on emigrating Betsie River smolts would presumably also select against the smallest fish. Predator avoidance would be enhanced by larger size (Ward and Slaney 1990). Hence, the surviving adults would exhibit a greater mean smolt length than the entire cohort would at smolting.

Predation by piscivores reduced the numbers of hatchery smolts reaching the Baltic Sea by 26% in a Norwegian stream (Larsson 1985). Smolt loss from avian predators can also be substantial. Wood (1987) found common mergansers, *Mergus merganser,* to be a major source of mortality for salmon and steelhead smolts in British Columbia. Predators found in the Betsie River system include walleye, northern pike, and bowfin, *Amia calva*, all of which potentially prey on small steelhead smolts. Even the merganser may prey on Betsie smolts given the French name for the river, "Bec Scies", meaning saw-toothed duck.

Size based failure to completely migrate may be another mechanism that explains smolt length differences. Residualized smolts which do not leave the river revert to parr. Because they do not mature in a lake or ocean, neither do they recruit to the fishery as large adult steelhead. In addition, their in-stream survival is thought to be low (Seelbach 1987).

It is the smaller sized smolts that consistently show a high rate of residualism (Ewing et al. 1984; Ward and Slaney 1990). In the Betsie River, for example, the mean smolt length of returning adults from the 1994 hatchery cohort was 20.1cm. The smolts from the same cohort measured at the Homestead weir averaged 18.8cm, while smolts measured at the hatchery prior to release averaged only 13.7cm. Differences in smolt length between the hatchery and the weir may have resulted from a high percentage of small smolts remaining in the stream as residuals. Clearly the smaller smolts were less likely to return as adults than the larger smolts. They either failed to migrate, succumbed to predation and other forms of mortality, or both.

Generally, wild steelhead data suggests a similar size dependent relationship between smolt length and adult return. However, the magnitude of difference between smolt length and adult smolt length was greater in the hatchery sample than in the wild sample. Predation mortality may be higher for hatchery steelhead than that experienced by wild fish (Berejikian 1995). Seelbach and Miller (1993) did not detect any size dependent survival in wild steelhead in a Lake Superior tributary. But they did find evidence of higher survival of large hatchery fish stocked in the same stream.

Length frequencies of Betsie River wild fish were significantly different between smolts and surviving adults in the 1994 cohort but not in the 1993 cohort. Lack of significance may be attributed to a real lack of length difference or a small sample size. Nonetheless, as Ricker notes (1969), even a small shift in mean length and size distribution requires a correspondingly large selective mortality exerted on the population.

Size selective pressures operating against wild age-1 smolts were more apparent than in age-2 smolts. Differences between lengths of emigrating smolts and smolt lengths of returning adults decreased with stream age. Intuitively, the smaller age-1 smolts would suffer greater mortality and thus produce greater smolt length differences between emigrating smolts and those that returned as adults. Stauffer (1971) and Kwain (1981) found lower proportions of stream age-1 steelhead in their adult samples than in their smolt samples of the same cohort. Both authors attributed higher mortality of age-1 smolts for the inconsistency.

Influence on Age at Maturity - Although large smolts are advantageous to a population in that greater size results in greater survival and return, large size may also affect age at maturity. Maturity schedules of steelhead are thought to be governed by size as well as genetic factors (Tipping 1991). Wagner (1967) found smolt size inversely related to time spent in the ocean. Ward et al. (1989) also provided evidence that smolt size is related to age at maturity in a Pacific steelhead population.

I followed Betsie River wild and hatchery cohorts according to lake age and year of return to substantiate smolt length influence on maturity. Very large hatchery smolts appeared to mature earlier than other cohort members. Smolt lengths of lake age-1 hatchery fish were significantly longer than the smolt lengths of older lake age steelhead. Smolt lengths of lake age-2 and -3 fish, however, were not different, indicating size had no differential influence on maturity at these ages. Smolt length influences on maturity were not evident in wild cohorts. Length differences were not significant between lake ages.

Partridge (1985) and Tsumura et al. (1987) documented premature sexual development in extraordinarily large hatchery males (>260mm) leading to precocious behavior. In addition, Neilson and Geen (1986) concluded that faster growing males of a chinook salmon cohort matured at an earlier age and often returned as jacks. Similarly, large wild smolts appeared to return more frequently as ocean age-1 steelhead in Vancouver Island populations (Hooten et al. 1987) But no size relationship was evident between ocean age-2 and -3 fish. Back-calculated smolt sizes of the ocean age-2 and -3 fish were approximately the same, as in the Betsie River sample.

Reverse Lee's phenomenon can sometimes be explained by a population's maturity schedule. Smaller size fish may not mature and recruit to a fishery as quickly as larger fish giving the impression of larger size at age if the immature fish are never sampled. Following Betsie River cohorts through time, past the large age-1 fish, indicates that the probability of adult return is smolt size dependent and not an artifact of maturity schedule.

Lake Distribution and River Straying

Lake Distribution - Inferences on the geographical distribution and movements of steelhead in lentic environments are frequently based on marked fish recovered by anglers. In Lake Michigan, port creel surveys suggested wide dispersal of Betsie River hatchery steelhead after leaving the harbor at Frankfort. By 1996, Betsie River fish were recorded in waters of all four states bordering the lake. Widespread dispersal of marked steelhead in Lake Michigan was also noted by Seelbach et al. (1994), substantiating the high mobility of these animals.

Habitats located in the southern two thirds of the lake appeared to be more attractive to the steelhead. Hatchery fish from the study were not reported in surveys north of Frankfort. Fishing effort in northern Lake Michigan may have influenced the likelihood of recovering RV clipped steelhead. However, Hansen and Stauffer (1971) reported a prevailing southerly movement in Lake Michigan according to recoveries from their steelhead study. Miller et al. (1983) found Columbia River juvenile steelhead to also disperse in one direction (north) upon entering the Pacific coast.

Curiously, RV clipped steelhead were absent from the creel along Michigan's coast from south of Ludington to Holland. This is surprising in light of the heavy fishing activity out of the ports in this area (Rakoczy and Svoboda 1994).

In Lake Ontario, Haynes et al. (1986) explained steelhead distribution by temperature and thermal fronts. Generally, steelhead location was associated with water temperatures averaging 9°C and the edge of thermal fronts. These thermal fronts, known on the surface as "scum lines" concentrate terrestrial insects, a preferred food item of steelhead trout (Jude et al. 1987).

Lake Michigan chinook and coho salmon are restricted to the southern basin of the lake by temperature constraints during the winter and early spring (Sommers et al. 1981). Non-maturing steelhead may likewise be influenced by temperature which may, in turn, explain the catch of Betsie River fish in southern Lake Michigan.

River Straying - Steelhead are renowned for their abilities to "home" back to the natal stream. Early this century, Taft and Shapovalov (1938) first documented the high degree of precision by which steelhead return to their stream of origin. Numerous other studies have verified this fidelity (Lister et al. 1981). Yet straying into non-natal streams has also been documented in steelhead populations.

Straying is not entirely detrimental nor benevolent. It can be the mechanism whereby underseeded streams are colonized and can protect populations from localized environmental catastrophes (Moring 1993). Conversely, extensive straying could potentially impact the genetic integrity of discrete stocks and may reduce individual fitness (Lister 1981).

I documented stray Betsie River hatchery steelhead in 5 non-natal streams scattered around Lake Michigan. The life history characteristics of the stray fish appeared to be similar to those fish which homed accurately. Because streams are monitored differently and some not at all, only the occurrence and not the magnitude of straying could be identified. The extent of straying by Betsie River wild steelhead could not be documented and is unknown. One stray hatchery fish was observed in a stream of the same region as the Betsie River. The others strayed to distant streams. Biette et al. (1981) found straying in Great Lakes populations primarily in adjacent or nearby streams to the natal stream. Seelbach and Miller (1993), however, reported extensive straying of hatchery steelhead to distant streams.

Evidence indicates that homing salmonids return to the same spawning area from which they emerged as fry. This finding led to the "sequential imprint hypothesis" (Lister et al. 1981). Olfactory cues stored during smolt emigration and later recalled in reverse order allow migrating adults to return to the site where they were spawned. Imprecise homing is thought to be related to inaccurate olfactory senses or a disruption of olfactory cues (Leider 1989). After the eruption of Mount St. Helens, Leider (1989) found substantial straying of steelhead from impacted streams. He attributed the straying to increased turbidity and wide ranging temperatures which disrupted sensory acuity.

In the case of hatchery supplementation, off site releases away from the rearing station and low in the watershed frequently increase straying (Lister et al. 1981; Chapman et al. 1997). Hatchery steelhead stocked in the Betsie River from the Orsini Hatchery are reared within the watershed and released on site relatively high in the system - a practice shown to minimize straying of cultured fish. Indeed, steelhead from the Orsini Hatchery have been known to home all the way back into the hatchery building itself.

CONCLUSIONS AND RECOMMENDATIONS

The results of this study indicate that the Betsie River steelhead fishery is supported by both hatchery and wild fish. Although still a substantial contributor (30-46%), wild steelhead do not match the relative proportion (93%) reported by Seelbach and Whelan (1988).

Management should give careful consideration regarding the purpose of the hatchery program on the Betsie River. If the only goal for the fishery and hatchery is to provide an adequate local harvest to meet angler demand, then wild contribution is not a concern. Large hatchery releases will likely fill any void in catch rates. If the abundance and sustainability of wild populations in Lake Michigan is a management goal, as put forth by the MDNR Fisheries Division (MDNR 1997) and the Great Lakes Fishery Commission (GLFC 1992), then the Betsie River population warrants further scrutiny.

Estimating harvest or actual numbers of wild adult spawners would be an appropriate management objective. Quantifying wild steelhead numbers answers the question of whether a real decline of wild fish exists or merely a decline relative to hatchery stocking levels.

The three year study gives only a brief overview into the Betsie River steelhead population. Long term data sets are much more valuable in deciphering trends than data sets limited to a few years. Other than continuing the study, one method for extending the Betsie River data would be to examine past scale collections. An annual creel survey was conducted on the Betsie River during the mid to late 1980's. Fishing effort and harvest estimates were calculated along with the collection of scale samples. Origins have never been determined from these scales. Currently, the scales are being archived at the MDNR research station at Charlevoix (Jory Jonas, MDNR, Personal Communications). An analysis of these scales would help in establishing long term trends in the Betsie River without any further scale collection efforts.

Ratio 23 was an accurate discriminator of Betsie River steelhead origins. Until all hatchery steelhead stocked in Lake Michigan are marked, ratio 23 should remain a valuable tool for estimating wild and hatchery composition in a mixed population. Unfortunately, the origins of 9% of the sampled Betsie River fish could not be determined because of poor scale quality. Many steelhead have scales that are regenerated or that have reabsorbed edges. I found that removing at least 10 scales from each fish in the preferred area was necessary to ensure a usable scale sample.

I found life history characteristics of wild and hatchery steelhead to be both similar and distinct. Length and growth, migration timing, and sex ratios were nearly identical. Conversely, age at maturity, repeat spawning frequency, and age structure, were not alike. The Betsie River is a marginal trout stream at best (Newcomb 1998) and will likely always need supplementation to satisfy current angling pressure. Ideally, the life history patterns of the stocked hatchery fish should parallel those of the wild fish. Having phenotypes similar to locally adapted steelhead increases the odds of success for hatchery fish and will not compromise the wild population (Kapuscinski and Jacobson 1987).

The characteristics of the Little Manistee River strain may be similar enough to wild steelhead in the Betsie River to justify its continued use as a donor stock. Genetic differences between the two may, in fact, be small. In addition, the apparent differences in traits may be due to energetic or environmental factors related to hatchery rearing. However, after over 100 years and multiple generations, discrete stocks of steelhead have been identified in Lakes Ontario and Superior (Ferguson et al. 1993; Krueger et al. 1994). Phenotypic traits as well as underlying genetics differed between populations in the two lakes. Therefore, it would be prudent to continue the preliminary genetic study of Lake Michigan steelhead begun by Epifanio (1996).

Hatchery production now contributes the majority of fish in the river fishery. Large smolts stocked into the Betsie River provided the greatest return of adult steelhead. Efforts to raise large smolts of 19cm or more should be encouraged in order to ensure consistent returns. Small smolts may not only be lost to the fishery, but may also adversely affect wild parr (Steward and Bjornn 1990). Further research directed at the effects of smolt size on maturity would also be beneficial in defining an appropriate size range for stocked steelhead hatchery smolts.

Straying by Betsie River hatchery fish was evident in several Lake Michigan streams. Because hatchery fish are currently raised and released relatively high in the watershed, additional options to reduce straying are few. In light of the strays from the Betsie River as well as steelhead straying into the Betsie River, managers should not view Lake Michigan tributaries as entirely isolated reproductive units.

Finally, the angling public has long held the Betsie River and its steelhead fishery in high esteem. It remains a valuable economic and ecological resource that merits continuing evaluation and protective vigilance.

APPENDICES

APPENDIX A

ANGLERS

YOUR HELP IS NEEDED!

The Betsie River Steelhead project needs 200 scale samples and lengths from steelhead caught in the fall 1995 and spring 1996 run.

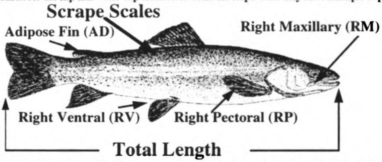
HOW TO SAMPLE

1) Scrape 5 to 10 scales , using a pocket knife, from the side of the fish, below and in front of the dorsal fin.

2) Insert the scales between the paper sheet in the scale envelope. Scale removal does not have to be a fatal procedure and fish that are handled gently with only scales (not skin) removed can be returned to the water if desired.

3) Length should be measured from the tip of the snout to the end of the tail.

4) Check for fin clip and write clip location on scale envelope. Fish may have multiple clips.



Your help is greatly appreciated. We are using the scales to determine the contribution of wild and hatchery fish caught in the Betsie River. We can identify hatchery or wild fish and determine their age and spawning history by magnifying the scales and inspecting their growth ring patterns.

Thank you for your participation!

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If you would like further information about the Betsie River Project, please call us or send a postcard with your name and address.

APPENDIX B

Table 17. Marked hatchery strays and probable origin from the Betsie River fishery 1994-1996 and the 1996 kelt sample.

YEAR	DATE	LENGTH (mm)	FIN CLIP	PROBABLE STRAIN	PROBABLE ORIGIN
1994	4/5	649	LP	Skamania	St. Joseph R., IN
1994	4/17	813	AD	L. Manistee	various rivers, MI
1994	4/19	787	AD	L. Manistee	various rivers, MI
1994	4/20	622	LP	Skamania	St. Joseph R., IN
1995	3/23	584	ADRP	Skamania	St. Joseph R., IN
1995	4/13	578	RP	L. Manistee	various rivers, MI
1995	4/14	572	RP	L. Manistee	various rivers, MI
1995	4/14	578	ADLV	Ganaraska	Kewaunee or Root R, WI
1995	4/26	559	LP	Skamania	St. Joseph R., IN
1995	4/29	610	RP	L. Manistee	various rivers, MI
1996	12/3	419	RP	L. Manistee	various rivers, MI
1996	4/13	775	RM	Skamania	Kewaunee or Root R, WI
1996	4/13	699	RM	Ganaraska	Kewaunee or Root R, WI
1996	4/24	648	LV	Skamania	Kewaunee or Root R, WI
1996	5/2	737	LP	Skamania	St. Joseph R., IN
1996	5/5	711	LP	Skamania	St. Joseph R., IN
1996	5/5	648	RP	L. Manistee	various rivers, MI
1996	5/15	597	RP	L. Manistee	various rivers, MI
1996	5/15	508	RP	L. Manistee	various rivers, MI
96 kelt	5/14	737	LMRV	Chambers Cr	Sheboygan R., WI
96 kelt	5/14	686	LM	Skamania	St. Joseph R., IN
96 kelt	5/14	787	LM	Chambers Cr	Kewaunee or Root R, WI
96 kelt	5/14	706	LM	Chambers Cr	Kewaunee or Root R, WI
96 kelt	5/19	732	LM	Chambers Cr	Kewaunee or Root R, WI
96 kelt	5/19	673	RMRP	Ganaraska	Sheboygan R., WI
96 kelt	5/23	749	RM	Skamania	Kewaunee or Root R, WI

Marked hatchery strays as percentage of sample:
1994 - 2.1% (n=191)
1995 - 4.6% (n=131)
1996 - 5.7% (n=157)
96 Kelt - 11% (n=66)

APPENDIX C

Table 18. Relative composition in 1996 of wild and hatchery steelhead by river section and gear.

Origin	PERCENTAGE				
	Entire River [1]	Lower Section [1]	Middle Section [1]	Upper Section [1,3]	Kelt Sample [2,3]
Wild	30%	40%	32%	14%	51%
Hatchery	70%	60%	68%	86%	49%

[1] Hook and line sample

[2] Temporary block net sample

[3] Sampled from steelhead caught above Homestead weir

APPENDIX D

Table 19a. Preliminary data of Betsie River steelhead collected from the 1994 sampled fish.

Sample ID #	Date	Length (cm)	SEX	Site	Coll	Clip	H/W	AGE
1 94	25-Mar	72	M	HSD	JW		H	1.3
2 94	25-Mar	58	M	HSD	JW		W	2.2
3 94	25-Mar	64	F	HSD	JW		H	1.2
4 94	25-Mar	64	F	HSD	HS		H	1.3
5 94	26-Mar	53	M	HSD	EH		H	1.2
6 94	26-Mar	61	M	HSD	EH		W	1.2S1
7 94	26-Mar	71	F	HSD	EH		?	R.2S1
8 94	26-Mar	83	M	FREDS	DT		W	1.3
9 94	26-Mar	82	M	FREDS	DT		H	1.1S1S1S1
10 94	26-Mar	76	F	RR	HS		H	1.4
11 94	26-Mar	46	M	HSD	HS		H	1.2
12 94	26-Mar	69	F	HSD	HS		W	2.3
13 94	26-Mar	64	M	MDWS	HS		W	2.2
14 94	26-Mar	74	M	HSD	HS		W	2.3
15 94	26-Mar	66	M	HSD	HS		H	1.2
16 94	26-Mar	76	M	HSD	HS		W	2.3
17 94	26-Mar	71	M	HSD	HS		W	2.3
18 94	26-Mar	76	M	HSD	HS		W	2.3
19 94	27-Mar	64	M	HSD	HS		H	1.3
20 94	27-Mar	74	F	HSD	HS		W	2.3
21 94	28-Mar	69	F	HSD	HS		W	1.3
22 94	28-Mar	79	M	HSD	HS		H	1.4
23 94	28-Mar	76	F	HSD	HS		W	1.3
24 94	28-Mar	61	M	HSD	HS		?	R.2
25 94	28-Mar	69	F	HSD	HS		W	2.3S1
26 94	28-Mar	62	F	HSD	EH		H	1.2
27 94	28-Mar	69	M	HSD	EH		W	2.3
28 94	28-Mar	64	M	HSD	HS		W	2.2
29 94	29-Mar	58	M	HSD	HS		W	1.2
30 94	29-Mar	69	F	HSD	HS		?	R.2
31 94	29-Mar	66	F	HSD	HS		W	2.2S1
32 94	29-Mar	66	M	HSD	HS		W	2.3
33 94	29-Mar	71	F	HSD	HS		H	1.3
34 94	29-Mar	61	M	HSD	HS		W	1.2
35 94	29-Mar	66	M	HSD	HS		W	2.2
36 94	29-Mar	69	M	HSD	HS		H	1.2S1

Table 19a (cont'd)

Sample ID #	Date	Length (cm)	SEX	Site	Coll	Clip	H/W	AGE
37 94	29-Mar	74	M	HSD	HS		H	1.3
38 94	29-Mar	74	M	HSD	HS		H	1.3
39 94	29-Mar	69	F	HSD	HS		H	1.3
40 94	30-Mar	71	F	HSD	HS		H	1.3S1
41 94	30-Mar	69	F	HSD	HS		H	1.3
42 94	31-Mar	74	M	HSD	HS		H	1.3
43 94	31-Mar	69	F	HSD	HS		W	2.2S1
44 94	31-Mar	71	M	HSD	HS		W	1.3
45 94	31-Mar	58	F	HSD	HS		H	1.2
46 94	31-Mar	77	M	HSD	HS		H	1.3
47 94	31-Mar	53	F	HSD	HS		W	2.2
48 94	31-Mar	66	F	HSD	HS		H	1.3
49 94	31-Mar	58	M	HSD	HS		H	1.2
50 94	31-Mar	72	M	HSD	HS		W	1.3
51 94	31-Mar	84	M	HSD	HS		W	2.4
52 94	1-Apr	71	F	HSD	EH		W	2.2S1S1
53 94	2-Apr	61	F	HSD	EH		?	R.2
54 94	2-Apr	62	M	HSD	EH		H	1.1
55 94	2-Apr	53	M	HSD	EH		H	1.2
56 94	2-Apr	74	M	HSD	EH		H	1.3
57 94	2-Apr	79	M	HSD	EH		H	1.3
58 94	2-Apr	66	NONE		TN		W	2.3
59 94	2-Apr	41	NONE	RR	TN		H	1.1
60 94	2-Apr	66	F	HSD	HS		W	2.2S1
61 94	2-Apr	84	F	HSD	PS		H	1.3S1
62 94	3-Apr	61	F	HSD	EH		W	1.2
63 94	3-Apr	79	M	HSD	EH		?	R.4
64 94	3-Apr	71	F	HSD	EH		W	1.3
65 94	3-Apr	71	F	HSD	EH		H	1.3
66 94	3-Apr	67	F	HSD	EH		H	1.2
67 94	3-Apr	72	M	HSD	JW		H	1.3
68 94	3-Apr	58	F	HSD	JW		H	1.2
69 94	4-Apr	71	F	RR	PS		H	1.3
70 94	4-Apr	69	M	HSD	PS		W	2.3
71 94	4-Apr	56	F	HSD	PS		?	R.2
72 94	4-Apr	71	M	HSD	PS		W	1.3
73 94	4-Apr	61	M	HSD	PS		H	1.2
74 94	4-Apr	74	F	HSD	PS		H	1.3
75 94	4-Apr	71	F	HSD	PS		W	2.4
76 94	4-Apr	58	M	HSD	PS		W	2.1S1
77 94	4-Apr	64	F	HSD	PS		?	R.2
78 94	4-Apr	50	M	HSD	PS		H	1.1
79 94	4-Apr	62	F	HSD	PS		H	2.2
80 94	4-Apr	72	F	FREDS	DT		H	1.3
81 94	4-Apr	81	F	FREDS	DT		W	1.3S1

Table 19a (cont'd)

Sample ID #	Date	Length (cm)	SEX	Site	Coll	Clip	H/W	AGE
82 94	4-Apr	69	M	FREDS	DT		W	2.3
83 94	4-Apr	70	F	HSD	EH		H	1.3
84 94	4-Apr	77	M	HSD	EH		W	1.3S1
85 94	4-Apr	67	F	HSD	EH		W	1.3
86 94	4-Apr	70	F	HSD	JW		W	1.3
87 94	4-Apr	69	F	HSD	JW		W	2.3
88 94	5-Apr	56	M	HSD	JW		W	2.2
89 94	5-Apr	70	M	HSD	JW		H	1.3
90 94	5-Apr	70	F		JW		H	1.3
91 94	5-Apr	67	F	HSD	JW	LP	H	1.3
92 94	5-Apr	64	F	HSD	JW		?	R.3
93 94	5-Apr	57	F		LT		W	2.2
94 94	5-Apr	67	F		LT		W	2.2S1
95 94	5-Apr	0	M		LT		H	1.3
96 94	5-Apr	70	F	HSD	PS		W	2.3
97 94	6-Apr	74	F	HSD	PS		H	1.4
98 94	6-Apr	64	F	HSD	PS		?	R.2
99 94	7-Apr	61	F	RR	PS		H	1.2
100 94	7-Apr	67	F	RR	DT		H	1.3
101 94	7-Apr	58	M	RR	DT		H	1.2
102 94	8-Apr	69	M	RR	PS		W	2.3
103 94	8-Apr	75	M		PS		H	1.3
104 94	8-Apr	74	M		PS		H	1.2S1
105 94	9-Apr	47	M	RR	DT		W	2.1
106 94	9-Apr	76	M	RR	DT		H	1.3S1
107 94	9-Apr	69	M	LOWER	JW		H	1.3
108 94	9-Apr	74	M	RR	DT		W	1.3
109 94	9-Apr	66	F	HSD	EH		?	R.2
110 94	9-Apr	74	M	HSD	EH		W	2.3
111 94	9-Apr	61	F	HSD	EH		W	2.2
112 94	9-Apr	58	M	LOWER	JW		H	1.2
113 94	9-Apr	69	F	HSD	EH		H	1.3
114 94	10-Apr	75	F	LOWER	LT		H	1.4
115 94	11-Apr	71	F	HSD	EH		H	1.3
116 94	11-Apr	69	F	HSD	EH		H	1.3
117 94	11-Apr	79	F	HSD	EH		W	1.3S1S1
118 94	11-Apr	81	M	HSD	EH		?	R.4
119 94	11-Apr	56	F	HSD	EH		W	1.2
120 94	11-Apr	66	F	HSD	EH		W	2.3
121 94	11-Apr	61	F	HSD	EH		?	R.2
122 94	11-Apr	66	F	HSD	EH		W	2.3
123 94	12-Apr	43	M	HSD	PS		W	2.1
124 94	12-Apr	71	M	PSUTKA	JW		H	1.3
125 94	13-Apr	46	M	PSUTKA	JW		?	R.2
126 94	13-Apr	58	M	HSD	PS		W	1.2

Table 19a (cont'd)

Sample ID #	Date	Length (cm)	SEX	Site	Coll	Clip	H/W	AGE
127 94	14-Apr	66	F	HSD	PS		H	1.3
128 94	14-Apr	55	M	PSUTKA	JW		W	2.2
129 94	15-Apr	57	F	HSD	LT		W	2.2
130 94	15-Apr	76	F	HSD	PS		W	2.3
131 94	16-Apr	76	F	HSD	PS		H	1.4
132 94	16-Apr	64	F	HSD	PS		H	1.3
133 94	16-Apr	56	M	HSD	PS		H	1.2
134 94	16-Apr	72	M	FREDS	DT		H	1.3
135 94	17-Apr	74	M	FREDS	DT		H	1.3
136 94	17-Apr	80	M	HSD	LT		W	2.3S1
137 94	17-Apr	81	M	HSD	PS	AD	H	1.4/1.5
138 94	17-Apr	58	M	HSD	LT		H	1.2
139 94	17-Apr	69	F	HSD	LT		?	R.2S1
140 94	17-Apr	99	F		LT		H	1.5
141 94	17-Apr	66	M	HSD	PS		W	2.3
142 94	17-Apr	66	F	HSD	PS		H	1.3
143 94	17-Apr	59	F	PIER	PS		W	2.2
144 94	17-Apr	56	M	HSD	PS		H	1.2
145 94	18-Apr	67	F	HSD	LT		W	2.3
146 94	18-Apr	66	F	HSD	LT		H	1.3
147 94	18-Apr	66	F	HSD	LT		W	1.3
148 94	18-Apr	66	F	HSD	PS		H	1.3
149 94	19-Apr	66	M	HSD	PS		H	1.3
150 94	19-Apr	67	F	HSD	LT		W	2.3
151 94	19-Apr	79	F	HSD	LT	AD	H	R.2S1S1
152 94	19-Apr	67	M	PSUTKA	JW		H	1.2
153 94	19-Apr	67	F	PSUTKA	JW		W	1.3
154 94	19-Apr	44	M	PSUTKA	JW		W	2.1
155 94	19-Apr	69	F	HSD	EH		H	1.3
156 94	19-Apr	64	F	HSD	EH		H	1.3
157 94	20-Apr	71	F	HSD	EH		H	1.3
158 94	20-Apr	71	M	HSD	EH		H	1.3
159 94	20-Apr	71	F	HSD	EH		H	1.3S1
160 94	20-Apr	79	M	HSD	EH		H	1.4
161 94	20-Apr	62	M	PSUTKA	JW	LP	H	R.2
162 94	20-Apr	84	F	HSD	PS		W	2.2S1S1
163 94	21-Apr	53	M	HSD	PS		W	2.2
164 94	22-Apr	74	M	HSD	PS		W	2.3
165 94	22-Apr	69	F	FREDS	DT		H	1.3
166 94	22-Apr	66	F	HSD	LT		W	2.3
167 94	23-Apr	81	F	HSD	PS		H	1.5
168 94	23-Apr	62	M	FREDS	DT		H	1.2
169 94	23-Apr	74	M		JW		W	2.3
170 94	24-Apr	60	F	FREDS	DT		W	2.2
171 94	24-Apr	60	M	HSD	PS		H	1.2

Table 19a (cont'd)

Sample ID #	Date	Length (cm)	SEX	Site	Coll	Clip	H/W	AGE
172 94	24-Apr	66	F	HSD	PS		H	1.3
173 94	26-Apr	74	F	HSD	PS		H	1.4
174 94	27-Apr	54	F	FREDS	DT		?	R.2
175 94	27-Apr	64	F	HSD	PS		W	2.3
176 94	28-Apr	46	M	HSD	PS		H	1.1
177 94	29-Apr	60	M	HSD	PS		?	R.2
178 94	29-Apr	74	F	PSUTKA	JW		W	1.3
179 94	30-Apr	74	NONE	HSD	PS		H	1.3
180 94	30-Apr	57	M	RR	DT		H	1.2
181 94	5-May	69	NONE		LT		H	1.3
182 94	6-May	71	F	FREDS	DT		H	1.3
183 94	6-May	44	M	FREDS	DT		H	1.1
184 94	6-May	60	F	FREDS	DT		H	1.2
185 94	6-May	67	M	FREDS	DT		H	1.3
186 94	26-Mar	74	M	HSD	HS		W	1.3
187 94	26-Mar	69	M	HSD	HS		W	2.3
188 94	31-Mar	64	M	HSD	HS		H	1.3
189 94	2-Apr	66	M	HSD	HS		H	1.2
190 94	4-Apr	74	M	HSD	HS		?	R.3
191 94	31-Mar	58	M	HSD	HS		W	2.3

Table 19b. Preliminary data of Betsie River steelhead collected from 1995 sampled fish.

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	AGE
F1 94	29-Oct	70	F	GRACE	JW		H	1.3+
F2 94	29-Oct	44	M	RR	JW		W	2.0+
F3 94	25-Nov	77	M	RR	JW		W	2.3+
F4 94	25-Nov	55	M	RR	JW		H	1.1+
F5 94	25-Nov	72	M	RR	JW		W	1.2+
F6 94	27-Nov	69	M	RR	JW		W	2.2+
F7 94	29-Nov	62	M	M20	JW		W	1.1+
F8 94	29-Nov	72	M	M20	JW		H	1.2+
F9 94	1-Dec	74	M	LOWER	JW		H	1.2+
F10 94	9-Dec	64	M	RR	JW		H	1.2+
1 95	4-Jan	71	M	HSD			H	1.4
2 95	4-Jan	64	F	HSD			W	1.3
3 95	22-Mar	69	M	RR	JW		W	3.3
4 95	24-Mar	69	M	HSD			H	1.2S1
5 95	25-Mar	69	M	HSD			H	1.3
6 95	3-Apr	81	F	HSD			H	1.4
7 95	3-Apr	61	M	HSD			H	1.2
8 95	3-Apr	89	F	HSD			W	2.2S1S1
9 95	3-Apr	76	F	HSD			W	1.2S1S1S1
10 95	4-Apr	58	M	HSD	PS		W	1.2
11 95	4-Apr	69	M	HSD			H	1.2S1
12 95	4-Apr	69	F	HSD			W	1.3
13 95	4-Apr	42	M	HSD			W	2.1
14 95	5-Apr	69	M	PTSUKA	JW		W	1.3
15 95	7-Apr	81	M	HSD			H	1.3
16 95	6-Apr	67	F	HSD	JW		W	2.4
17 95	7-Apr	79	M	HSD			H	1.4
18 95	8-Apr	69	F	HSD	TN		H	1.3
19 95	8-Apr	71	F	HSD			H	1.3
20 95	8-Apr	69	F	HSD			H	1.3
21 95	8-Apr	64	M	HSD			H	1.3
22 95	8-Apr	53	F		PETE		H	1.2
23 95	8-Apr	71	F				W	1.3
24 95	9-Apr	48	M		PETE		H	1.1
25 95	10-Apr	89	M		PETE		?	R.5?
26 95	10-Apr	89	M		PETE		H	1.5
27 95	10-Apr	61	F	HSD			W	1.2
28 95	10-Apr	81	F	HSD			H	1.3S1
29 95	10-Apr	69	M	PTSUKA	JW		H	1.3
30 95	12-Apr	84	F	HSD			H	1.4
31 95	13-Apr	61	F	HSD			H	1.2
32 95	13-Apr	71	F	HSD			?	R.3

Table 19b (cont'd)

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	AGE
33 95	13-Apr	58	F	RR		RP	H	R.2
34 95	13-Apr	65	F	RR			W	1.3
35 95	13-Apr	72	M	RR	JW		W	1.3
36 95	13-Apr	56	M	RR			W	1.2
37 95	14-Apr	57	M	RR	ET	RP	H	1.2
38 95	14-Apr	58	M	RR		LV	H	1.2
39 95	14-Apr	57	M	RR			H	1.2
40 95	14-Apr	70	F	RR	JW		H	1.3
41 95	15-Apr	76	F	HSD			H	1.3
42 95	15-Apr	79	F	HSD			H	1.4
43 95	15-Apr	57	F	RR	JW		W	2.2
44 95	16-Apr	72	F	PTSUKA	JW		H	1.3
45 95	17-Apr	61	F	RR	DT		H	1.2
46 95	17-Apr	70	F	RR	DT		W	1.3
47 95	18-Apr	65	F	FREDS	DT		H	1.3
48 95	18-Apr	56	F	FREDS	DT		H	1.2
49 95	19-Apr	71	F	HSD			H	1.3
50 95	19-Apr	69	F	HSD			H	1.3
51 95	19-Apr	74	M	HSD			H	1.3
52 95	19-Apr	58	F	HSD	JW		H	1.2
53 95	20-Apr	64	M	HSD			H	1.3
54 95	20-Apr	53	F	HSD			H	1.2
55 95	20-Apr	64	M	HSD			W	2.2
56 95	20-Apr	69	F	HSD			H	1.2S1
57 95	20-Apr	66	F	HSD			W	1.2
58 95	20-Apr	61	M	HSD			?	R.2
59 95	21-Apr	69	F	PTSUKA	JW		?	R.3
60 95	21-Apr	55	M	PTSUKA	JW		W	1.1
61 95	22-Apr	67	F	KURICK	JW		H	1.3S1
62 95	22-Apr	57	F	KURICK	JW		W	1.3
63 95	22-Apr	77	F	KURICK	JW		H	1.3
64 95	22-Apr	76	F	KURICK	JW		W	1.4
65 95	23-Apr	71	F	FREDS	DT		W	1.4
66 95	26-Apr	56	M	KURICK	JW	LP	H	1.2
67 95	26-Apr	65	F	KURICK	JW		H	1.3
68 95	26-Apr	67	F	KURICK	JW		W	1.3
69 95	28-Apr	55	F	FREDS	DT		W	2.2
70 95	29-Apr	71	M	KURICK	JW		H	1.3
71 95	29-Apr	65	F	FREDS	DT		H	1.2
72 95	29-Apr	64	F	FREDS	DT		W	1.3
73 95	29-Apr	61	M	KURICK	JW		?	R.2
74 95	29-Apr	61	F	KURICK	JW	RP	H	H R.2
75 95	29-Apr	65	M	KURICK	JW		W	2.3
76 95	30-Apr	58	M	KURICK	JW		H	1.2

Table 19b (cont'd)

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	AGE
77 95	30-Apr	64	F	KURICK	JW		H	1.2
78 95	3-May	73	M	HSD	DT		H	1.3
79 95	3-May	40	M	HSD	DT		W	2.1
80 95	3-May	64	F	HSD	DT		W	2.3
81 95	3-May	70	F	HSD	DT		H	1.3
82 95	3-May	63	F	HSD	DT		H	1.2
83 95	5-May	69	F	FREDS	DT		W	2.2S1S1
84 95	9-May	64	F	HSD	JH		W	2.2S1
85 95	10-Mar	65	F	LOWER	JW		W	2.3
86 95	10-Mar	73	NONE	LOWER	JW		W	2.3S1
87 95	10-Mar	64	M	LOWER	JW		H	1.3
88 95	12-Mar	65	M	HSD			H	1.3
89 95	15-Mar	61	M	HSD			W	1.2
90 95	15-Mar	50	M	HSD			?	R.1
91 95	17-Mar	76	M	HSD			H	1.3
92 95	17-Mar	74	M	HSD			W	2.3
93 95	18-Mar	71	F	HSD			H	1.3
94 95	18-Mar	76	M	HSD	JK		?	DET
95 95	18-Mar	61	F		CARL		?	R.2
96 95	18-Mar	66	M	HSD			H	1.2S1
97 95	18-Mar	76	F		PETE		H	1.3
98 95	18-Mar	84	M		PETE		H	1.4
99 95	18-Mar	58	F	HSD	PETE		W	1.2
100 95	18-Mar	62	M	HSD			H	1.2
101 95	19-Mar	56	F				?	R.1S1
102 95	19-Mar	76	F		PETE		?	R.3S1S
103 95	19-Mar	74	M	HSD			W	1.3
104 95	19-Mar	74	M	HSD			H	1.3
105 95	20-Mar	56	F	HSD	PETE		W	1.2
106 95	20-Mar	80	M		MAX		?	DET
107 95	20-Mar	88	M	HSD			W	1.4
108 95	21-Mar	74	F	HSD	LB		W	2.2S1
109 95	21-Mar	74	F		MAX		H	1.3
110 95	23-Mar	58	F	HSD		RPAD	H	1.2
111 95	23-Mar	76	M	HSD			H	1.4
112 95	29-Mar	71	M				?	R.3
113 95	28-Mar	56	F				W	1.2
114 95	29-Mar	61	M				H	1.2
115 95	3-Apr	64	M	HSD			W	1.3
116 95	3-Apr	76	F	HSD	TN		H	1.3
117 95	3-Apr	69	F	HSD	TN		H	1.2
118 95	3-Apr	58	F	HSD	TN		?	R.2
119 95	4-Apr	76	F	HSD	JW		W	3.4S1
120 95	19-May	39	M	HSD	TN		W	1.1
121 95	14-May	70	F	HSD	DW		H	1.4

Table 19c. Preliminary data from Betsie River steelhead collected from 1996 sampled fish.

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	Age
1f 95	29-Oct	41	M	RR	JW		W	1.0+
2f 95	29-Oct	65	M	RR	JW		H	1.2+
3f 95	13-Nov	69	M	M-22	HE		H	1.2+
4f 95	30-Nov	58	M	RR	JW		W	2.1+
5f 95	3-Dec	42	M	RR	JW	RP	H	1.0+
1 96	9-Feb	53	M	HSD	EH	RP	H	1.2
2 96	9-Feb	84	F	HSD	EH		H	1.4
3 96	9-Feb	81	F	HSD	EH		W	2.4S1
4 96	9-Feb	77	M	HSD	EH		W	2.5
5 96	22-Feb	66	F	HSD	EH		W	2.2S1
6 96	22-Feb	64	F	HSD	EH		W	2.2S1
7 96	22-Feb	69	F	HSD	EH		?	R.2S1
8 96	22-Feb	76	M	HSD	EH		H	1.4
9 96	22-Feb	84	M	HSD	EH		H	1.4
10 96	22-Feb	79	M	HSD	EH		W	1.5
11 96	23-Feb	71	M	HSD	EH		H	1.2S1
12 96	23-Feb	69	M	HSD	EH		?	R.3
13 96	23-Feb	74	M	HSD	EH		H	1.3
14 96	23-Feb	0	M	HSD	EH		H	1.3
15 96	23-Feb	0	M	HSD	EH		?	R.2.S1
16 96	25-Feb	71	F		WS		H	1.3
17 96	26-Feb	42	M	RR	JW		W	1.1
18 96	26-Feb	43	M	RR	JW		W	1.1
19 96	27-Feb	42	M	RR			W	1.1
20 96	27-Feb	66	M	RR	JW	RV	H	1.3
21 96	2-Mar	50	M	RR	JW		?	R.2
22 96	2-Mar	69	M	RR	JW		H	1.4
23 96	13-Mar	66	F	HSD	SA		W	2.3
24 96	13-Mar	61	F	HSD	SA		W	2.3
25 96	13-Mar	64	F	HSD	SA		W	1.2S1S1
26 96	16-Mar	79	F	HSD			H	1.3
27 96	16-Mar	69	F	RR	JW		H	1.3
28 96	16-Mar	72	M	RR	JW		H	1.3S1
29 96	17-Mar	71	M	HSD			H	1.3
30 96	17-Mar	64	F	HSD			H	1.3
31 96	17-Mar	43	M	HSD			H	1.2
32 96	22-Mar	61	F	MOUTH			W	2.3
33 96	22-Mar	65	F	MOUTH			H	1.3
34 96	22-Mar	41	M	MOUTH			H	1.1
35 96	22-Mar	67	F	MOUTH			H	1.2
36 96	28-Mar	76	F	RR	JW		?	R.4

Table 19c (cont'd)

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	Age
37 96	28-Mar	51	M	RR	JW		W	1.1S1
38 96	30-Mar	48	M	MOUTH			H	1.1
39 96	1-Apr	67	F	RR	JW		H	1.3
40 96	2-Apr	69	F	RR	JW		W	1.3S1
41 96	2-Apr	71	M	RR	JW		W	1.3
42 96	5-Apr	62	F	RR	JW		W	1.3
43 96	6-Apr	75	F	RR	JW		W	2.4
44 96	6-Apr	64	F	RR	JW		H	1.2
45 96	7-Apr	70	M	RR	JW		W	2.3
46 96	7-Apr	65	F	RR	JW	RV	H	1.3
47 96	7-Apr	72	M	RR	JW	RV	H	1.3
48 96	7-Apr	65	M	RR	JW		H	1.3
49 96	8-Apr	43	M	RR	JH		W	1.1
50 96	8-Apr	64	M	RR	JH		W	2.2
51 96	8-Apr	62	F	MOUTH	TW		H	1.2
52 96	8-Apr	64	F	MOUTH	TW		H	1.3
53 96	9-Apr	73	M	HSD	JH	RV	H	1.3
54 96	9-Apr	74	F	HSD	JH		H	1.3
55 96	9-Apr	75	M	HSD	JH		W	1.4
56 96	9-Apr	66	M	HSD	JH		H	1.3
57 96	9-Apr	69	F	MOUTH	BJ		H	1.2S1
58 96	10-Apr	38	M	RR	JW		H	1.1
59 96	10-Apr	60	F	RR	JW		W	2.3
60 96	10-Apr	64	F	HSD	EH		H	1.2S1S1
61 96	10-Apr	61	F	HSD	EH		W	2.2
62 96	10-Apr	66	M	HSD			W	1.3
63 96	10-Apr	76	F	HSD			H	1.3S1
64 96	11-Apr	67	M	RR	JW		H	1.3
65 96	11-Apr	60	F	RR	JW		H	1.2
66 96	11-Apr	71	M	HSD			H	1.3
67 96	11-Apr	61	M		PETE		?	R.2
68 96	11-Apr	66	F		PETE		H	1.2
69 96	11-Apr	69	F		PETE		H	1.3
70 96	12-Apr	64	F		PETE		H	1.2
71 96	12-Apr	64	F	HSD			H	2.3
72 96	12-Apr	71	M	HSD			H	1.2
73 96	12-Apr	79	M	HSD			H	1.4
74 96	12-Apr	76	M	HSD			H	1.4
75 96	12-Apr	64	F	HSD			W	1.2S1
76 96	12-Apr	67	F	HSD			H	1.3
77 96	12-Apr	58	M	HSD			W	2.2
78 96	12-Apr	69	F	HSD			H	1.3
79 96	12-Apr	79	F				W	1.4S1
80 96	12-Apr	74	F	HSD			H	1.3S1
81 96	12-Apr	76	M	JONES	MEND		?	REG

Table 19c (cont'd)

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	Age
82 96	12-Apr	64	M	HSD			W	2.2
83 96	12-Apr	66	F	JONES	MEND		H	1.2S1
84 96	12-Apr	69	F	HSD	PETE		W	1.3
85 96	12-Apr	74	F		PETE		H	1.4
86 96	12-Apr	76	F		PETE		H	1.4
87 96	12-Apr	61	F		PETE		H	1.3
88 96	12-Apr	64	M	JONES	MERCIER		H	1.3
89 96	13-Apr	70	F	RR	JW	RM	W	2.3
90 96	13-Apr	65	M	RR	JW		H	1.3
91 96	13-Apr	77	M	RR	JW	RM	H	1.3S1
92 96	13-Apr	61	F	MOUTH			W	2.2
93 96	13-Apr	69	F	MOUTH			H	1.3
94 96	13-Apr	79	F	MOUTH	TN	RV	H	1.3
95 96	13-Apr	60	F	MOUTH	TN		W	2.2
96 96	13-Apr	66	M	HSD	TN		?	R.2
97 96	13-Apr	76	F	MOUTH			W	2.3
98 96	13-Apr	51	M	MOUTH			H	1.2
99 96	17-Apr	75	M				?	R.3
100 96	17-Apr	76	F	HSD	JW		W	2.2S1S1
101 96	17-Apr	72	M				H	1.3
102 96	19-Apr	56	F	HSD			H	1.2
103 96	19-Apr	66	F	HSD			H	1.3
104 96	21-Apr	70	F	PSUTKA	JW	RV	H	1.3
105 96	22-Apr	71	F	PSUTKA	JW		H	1.3
106 96	23-Apr	69	F	HSD	EH		?	DET
107 96	23-Apr	69	F	HSD	EH		?	DET
108 96	23-Apr	66	F	HSD	EH		?	DET
109 96	23-Apr	70	F	PSUTKA	JW		H	1.4
110 96	24-Apr	69	M	PSUTKA	JW		H	1.3
111 96	24-Apr	60	M	PSUTKA	JW		H	1.2
112 96	24-Apr	67	M	PSUTKA	JW		H	1.2S1
113 96	24-Apr	67	M	PSUTKA	JW		H	1.3
114 96	24-Apr	65	F	PSUTKA	JW	LV	H	1.2S1
115 96	24-Apr	71	F	HSD			H	1.2S1
116 96	24-Apr	69	F	HSD			H	1.3
117 96	25-Apr	46	M	HSD			H	1.1
118 96	25-Apr	76	F	HSD			H	1.4
119 96	25-Apr	71	F	HSD			H	1.3
120 96	26-Apr	60	F	HSD	JW	RV	H	1.3
121 96	27-Apr	77	M	PSUTKA	JW	RV	H	1.3
122 96	27-Apr	69	M	PSUTKA	JW		W	2.3
123 96	27-Apr	66	F	PSUTKA	JW		H	1.3
124 96	28-Apr	67	F	PSUTKA	JW		H	1.3
125 96	28-Apr	80	M	PSUTKA	JW		H	1.4
126 96	28-Apr	77	M	PSUTKA	JW		H	1.4
127 96	30-Apr	74	M	PSUTKA	JW	RV	H	1.3

Table 19c (cont'd)

	Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	Age
	128 96	30-Apr	66	M	KURICK	JW		W	1.3
	129 96	30-Apr	70	F	PSUTKA	JW	RV	H	1.3
	130 96	1-May	58	M	HSD	JH		H	1.2
	131 96	2-May	61	F	HSD	JH		W	2.2
	132 96	2-May	69	F	HSD	JH		W	2.3
	133 96	2-May	79	F	HSD	JH		H	1.3S1
	134 96	2-May	74	M	HSD	JH	LP	H	1.4
	135 96	2-May	66	F	HSD	JH		W	2.3
	136 96	2-May	74	F	HSD	JH		H	1.3
	137 96	2-May	58	F	HSD	JH		H	1.2
	138 96	2-May	61	F	HSD	JH		W	2.2
	139 96	2-May	74	F	HSD	JH		H	1.4
	140 96	3-May	71	F	HSD	JH	D	H	1.2S1
	141 96	5-May	65	F	HSD	TN	RP	H	1.3
	142 96	5-May	71	F	HSD	TN	LP	H	1.3S1
	143 96	8-May	76	F	HSD	MW		H	1.4
	144 96	13-May	71	F	HSD	MW		H	1.3
	145 96	13-May	66	F	HSD	MW		H	1.3
	146 96	13-May	66	F	HSD	MW		H	1.3
	147 96	14-May	47	M	HSD	TN		W	2.1
	148 96	15-May	51	M	HSD		RP	H	1.1
	149 96	15-May	60	F	HSD		RP	H	R.2
	150 96	15-May	62	F	HSD			W	2.2
	151 96	15-May	69	F	HSD			H	1.2S1S1
	152 96	15-May	81	F	HSD			W	2.3S1
Kelts	*1k 96	14-May	79	M	HSD	JH			
	*2k 96	14-May	79	M	HSD	JH	LM	W	1.5
	*3k 96	14-May	70	M	HSD	JH	LM	H	1.3
	4k 96	14-May	55	M	HSD	JH		H	1.2
	*5k 96	14-May	72	M	HSD	JH			
	6k 96	14-May	67	M	HSD	JH		H	1.2
	7k 96	14-May	74	F	HSD	JH	RV	H	1.3
	8k 96	14-May	74	F	HSD	JH		W	2.2s1s1s1
	9k 96	14-May	66	F	HSD	JH		W	2.2
	10k 96	14-May	64	F	HSD	JH		W	2.2
	11k 96	14-May	74	F	HSD	JH	RVLM	H	1.3
	12k 96	14-May	72	F	HSD	JH		W	1.3S1
	13k 96	14-May	77	M	HSD	JH		W	1.3
	14k 96	14-May	51	M	HSD	JH	RV	H	1.2
	15k 96	14-May	78	F	HSD	JH		H	*2.3
	16k 96	14-May	65	F	HSD	JH		W	2.2
	17k 96	14-May	62	F	HSD	JH		W	2.3
	18k 96	14-May	69	F	HSD	JH		H	1.3
	19k 96	14-May	60	F	HSD	JH		?	REGEN
	20k 96	14-May	81	M	HSD	JH	LM	H	1.3

Table 19c (cont'd)

Sample ID #	Date	Length (cm)	Sex	Site	Coll	Clip	H/W	Age
21k 96	14-May	73	M	HSD	JH		W	2.4
22k 96	14-May	66	M	HSD	JH		H	1.3
23k 96	14-May	80	F	HSD	JH		W	1.3
24k 96	14-May	63	F	HSD	JH		W	2.3
25k 96	14-May	72	F	HSD	JH		W	2.5
26k 96	19-May	69	F	HSD	JH	LM	H	1.4
27k 96	19-May	66	F	HSD	JH		H	1.2
28k 96	19-May	74	F	HSD	JH		H	1.3
29k 96	19-May	64	F	HSD	JH		W	2.3
30k 96	19-May	71	F	HSD	JH		W	1.3
31k 96	19-May	58	F	HSD	JH		H	1.1S1S1
32k 96	19-May	39	M	HSD	JH	RV	H	*2.1
33k 96	19-May	67	F	HSD	JH	RPRM	H	1.3
34k 96	19-May	60	F	HSD	JH		W	2.2
35k 96	19-May	62	M	HSD	JH		W	2.2
36k 96	19-May	62	F	HSD	JH		W	2.2
37k 96	19-May	56	F	HSD	JH		W	2.2
38k 96	19-May	71	M	HSD	JH		H	1.3
39k 96	19-May	64	F	HSD	JH		W	1.2
40k 96	19-May	66	M	HSD	JH		H	1.3
41k 96	19-May	65	F	HSD	JH		H	1.2
42k 96	19-May	74	M	HSD	JH		W	2.3
43k 96	19-May	62	F	HSD	JH		H	1.2
44k 96	19-May	60	M	HSD	JH		W	? 2.2
45k 96	19-May	65	F	HSD	JH		W	1.3
46k 96	19-May	72	F	HSD	JH	RV	H	1.3
47k 96	19-May	75	M	HSD	JH	RV	H	1.3
48k 96	19-May	72	M	HSD	JH		H	1.3
49k 96	19-May	71	F	HSD	JH		W	1.3
50k 96	19-May	67	F	HSD	JH		H	1.3
51k 96	19-May	66	F	HSD	JH		H	1.2S1
52k 96	19-May	39		HSD	JH	RV	H	* R.1
53k 96	23-May	58	M	HSD	JH		H	1.2
54k 96	23-May	71	M	HSD	JH		?	R.3
55k 96	23-May	75	M	HSD	JH		W	2.4
56k 96	23-May	69	M	HSD	JH	RM	H	1.3
57k 96	23-May	65	M	HSD	JH		W	2.2
58k 96	23-May	58	F	HSD	JH		H	1.2
59k 96	23-May	64	F	HSD	JH		H	1.3
60k 96	23-May	60	F	HSD	JH		W	1.2
61k 96	23-May	65	F	HSD	JH		W	2.2
62k 96	23-May	75	F	HSD	JH		H	1.2S1S1
63k 96	23-May	71	F	HSD	JH		?	R.2S1
64k 96	23-May	71	F	HSD	JH		H	1.3
65k 96	23-May	67	F	HSD	JH		W	1.3
66k 96	23-May	75	M	HSD	JH		W	2.3

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