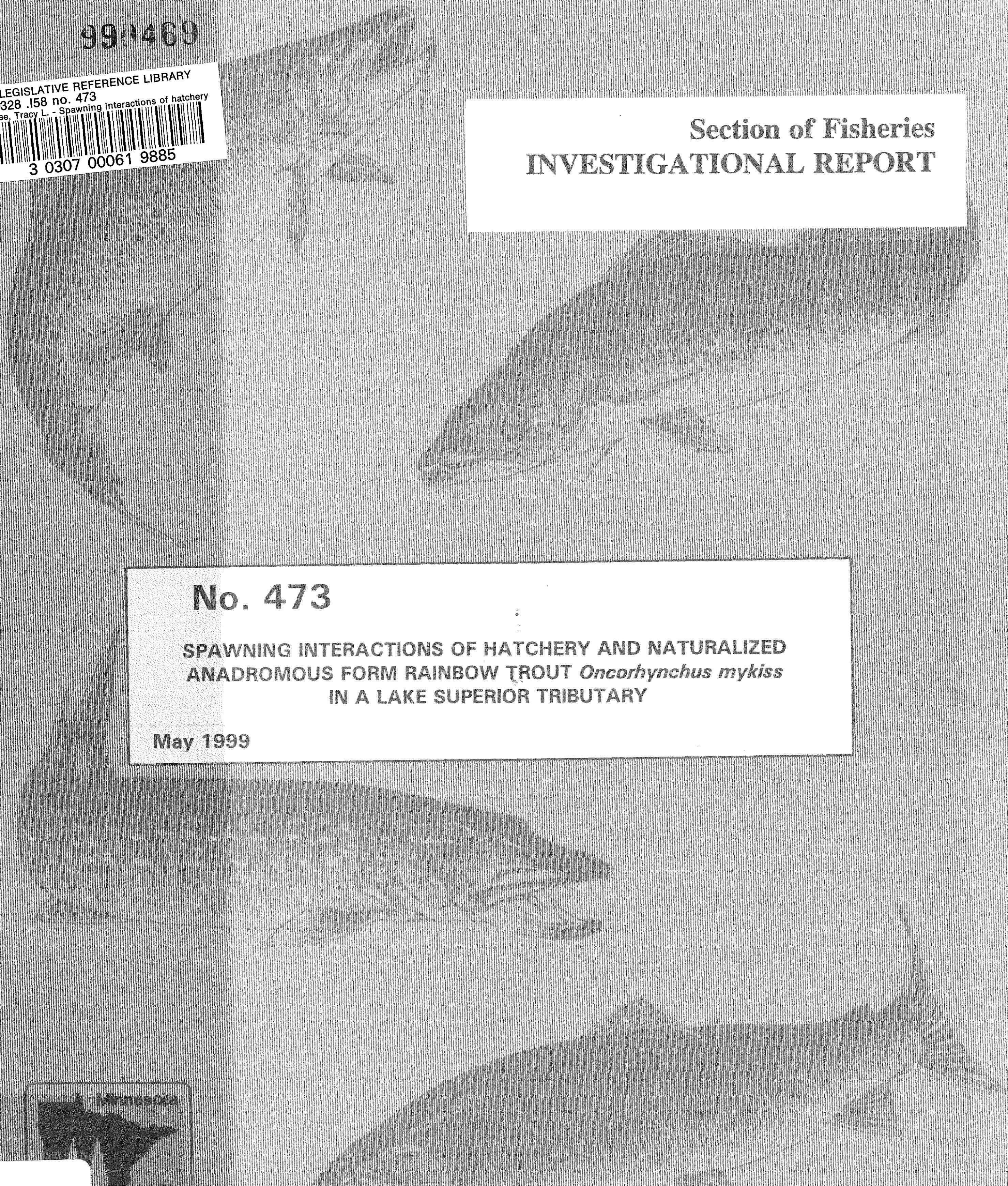

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SPAWNING INTERACTIONS OF HATCHERY AND NATURALIZED ANADROMOUS FORM RAINBOW TROUT *Oncorhynchus mykiss* IN A LAKE SUPERIOR TRIBUTARY

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SPAWNING INTERACTIONS OF HATCHERY AND NATURALIZED ANADROMOUS FORM RAINBOW TROUT *Oncorhynchus mykiss* IN A LAKE SUPERIOR TRIBUTARY[1]

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Abstract.--Two strains of rainbow trout *Oncorhynchus mykiss* are managed in the Minnesota waters of Lake Superior. Abundance of the naturalized and self-sustaining steelhead strain has declined since a hatchery strain called "kamloops" was introduced in the 1970s. There are several possible causes for the decline, but hybridization of the two strains is suspected of contributing to the steelhead decline. Forty-six steelhead and kamloops spawners with strain specific homozygous alleles at the IDH-2 locus were radio tagged and stocked into a 1,200 m study reach to observe movements to spawning areas, observe spawning interactions, and to measure juvenile production and survival. Spawners of both strains distributed in the reach and most spawners remained in the study reach long enough to spawn. Young-of-the-year (YOY) densities were low in the fall when 44 hybrid and 13 pure strain steelhead YOY were captured. Seven hybrids and six steelhead were captured one year later. It was not possible to determine how many spawning pairs produced the captured hybrids, thus the apparent difference in overwinter survival may have been a parental effect and not a strain effect. We now know that viable hybrids can be produced in the wild and that they can survive North Shore stream winters. If appropriate non-lethal genetic markers can be identified, additional work is needed to measure juvenile kamloops and hybrid survival in the wild, the extent of past hybridization, and the practicality of genetically rehabilitating the steelhead stock.

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Introduction

Anglers report that abundance of spawning naturalized steelhead *Oncorhynchus mykiss* has declined in Minnesota's tributaries to Lake Superior since the 1970s. Steelhead (STT) have been present in Lake Superior for about 100 years (MacCrimmon and Gots 1972). Several anadromous forms were introduced in the late 1800s, quickly resulting in a naturalized stock called "steelhead" by local anglers (Hassinger et al. 1974). A popular fishery developed for steelhead in the 1950s and 1960s in Minnesota's North Shore tributary streams during a period of low lake trout abundance. Anglers report that steelhead abundance declined during the 1970s and 1980s and is currently at an all time low. Adult steelhead abundance data are sparse because steelhead comprise a small proportion of the fish biomass in Lake Superior, making netting assessment unreliable. Trap net catches of returning adults in the French River and Wisconsin's Brule River suggest stable long term abundance, and angler catches have remained stable in many North Shore streams (MNDNR file data; WIDNR file data). Fisheries professionals, however, generally accept the assertion that the number of spawners has declined in select streams, most notably, the Knife River, Minnesota's largest steelhead stream. The Section of Fisheries developed a steelhead management plan in 1991 (Minnesota Department of Natural Resources 1991), and identified maintenance of a self-sustaining steelhead stock as the preferred strategy to insure a viable rainbow trout fishery in Lake Superior. Harvest was immediately restricted, with a minimum size limit of 28 inches, and in 1998, all steelhead harvest was banned. The Section of Fisheries resolved to identify the factors limiting steelhead survival, identify barriers to rehabilitation, halt the decline of abundance, and attempt to increase steelhead abundance so that steelhead fishing will improve (Minnesota Department of Natural Resources 1991).

Kamloops, a hatchery strain of rainbow trout, has been stocked in Lake Superior to create a put-grow-and-take fishery. The "kamloops" strain (KAM) was developed from several shipments of eggs from the Ennis National Fish Hatchery (Don Woods, Minnesota Department of Natural Resources, retired, personal communication). KAM broodstock were originally believed to have come from the Kamloops region of British Columbia. Krueger et al. (1994), however, reported that allelic frequencies at two allozyme loci differed from those expected for inland rainbow trout from the Kamloops region. Thus, there is some ambiguity about the original egg source and the strain should not be confused with the Kamloops strain recognized by aquaculturists. Since 1976, kamloops eggs have been collected from feral broodstock, reared to yearling size at French River State Fish Hatchery, and stocked into several North Shore streams. Many kamloops anglers assert that kamloops are less aggressive swimmers than steelhead and segregate from steelhead during spawning by only ascending streams a short distance, making hybridization unlikely. Evidence collected to date suggests that the kamloops population is sustained exclusively by stocking (Krueger et al. 1994). The adipose fin of stocked yearlings is removed so that anglers can distinguish kamloops from steelhead, and kamloops harvest is encouraged, with a daily limit of three.

When hatchery fish hybridize with wild fish, abundance of wild fish can decline from reduced recruitment and loss of genetic diversity. Hatchery fish are almost always poorly adapted to wild environments (Reisenbichler and McIntyre 1977; Bachman 1984; Nickelson et al. 1986; Leider et al. 1990), and hybrids inherit maladaptive genes from their domesticated parent (Hindar et al. 1991; Johnsson and Abrahams 1991; Johnsson et al. 1993). If hybrids are poorly adapted and do not survive, abundance of wild fish can decline in the short term from reduced recruitment. Reduced recruitment results in a smaller effective population size and genetic diversity is lost (outbreeding depression). As genetic diversity is lost, the population becomes more susceptible to inbreeding depression (mating of closely related individuals), and worsening genetic stresses all making catastrophic extinction more likely. Reduced survival and reproductive success of hatchery and hatchery X wild fish has been documented in a wild steelhead population in Washington state (Leider et al. 1990) and a brown trout population in Norway (Skaala et al. 1996).

Geneticists have recommended that North Shore fishery managers reduce the risk of outbreeding depression in the steelhead stock. After finding evidence of hybridization between the local stock and stocked steelhead of Lake Michigan origin, Krueger et al. (1994) recommended that all stocking of non-indigenous rainbow trout be discontinued. Stocking of fry from Lake Michigan was halted immediately. There appeared to be some risk from kamloops stocking, as spawning habitat is often limited to a few hundred meters in North Shore streams, making spawning interactions likely. Spawning times overlap (Negus 1996) and anglers have reported catching kamloops in all North Shore streams. Although Krueger et al. (1994) found no evidence of hybridization, their sample sizes were small, their statistical power to detect back crosses was low, and hybrid survival may have been poor. Public comment on the steelhead management plan, however, strongly favored continuation of the kamloops program despite the biological risks. It was clear that anglers were not willing to sacrifice the popular kamloops fishery because of hypothetical risks. A compromise was crafted to limit kamloops stocking to the extreme southwest portion of Lake Superior where most of the kamloops were harvested. Theoretically, this minimized opportunities for hybridization. More definitive evidence on the viability of hybrid offspring was needed.

Before we can fully evaluate the risks of hybridization between the strains, we need to know more about the spawning behavior of adult kamloops, and the survival potential of kamloops and hybrid parr. Fleming and Gross (1989, 1993) reported that hatchery fish have relaxed breeding competition and as a result, spawning and breeding performance are reduced. If adult kamloops are behaviorally ill equipped to find and use suitable spawning areas or compete for mates, hybrids may be rare and the rate of introgression slow. In laboratory experiments, Negus (in press) observed reduced hatching success and fright response of fry of STT X KAM hybrids compared to STT X STT fish, demonstrating outbreeding depression (Leary et al. 1995). Hybrid and kamloops fry mortality, however, was not 100% and nothing is known about the survival of kamloops and hybrid parr in North Shore streams. If hybrid progeny are produced and survive to maturity, introgression could occur. Our lack of knowledge of kamloops spawning behavior and the survival potential of hybrid parr limits our ability to fully assess the risks of continued kamloops stocking.

The objectives of this work were to determine if spawning steelhead and kamloops segregate in space, to determine if STT and KAM could hybridize in the wild, and to evaluate juvenile survival by comparing the overwinter survival of KAM and KAM X STT parr to that of STT X STT parr.

Study Area

Lester River, a tributary to Lake Superior near the city of Duluth, was selected as our study site. The reach is 1,200 m long, is accessible for stocking, and is bounded upstream and downstream by barrier falls, precluding uncontrolled spawning and upstream escape of fish from the study reach. The Lester River is currently stocked with kamloops below the study reach and is near the French River where our spawners were captured. Ample spawning gravel was available in this reach, and stocked steelhead survived to at least age 1+ there in the past.

Methods

In April and May of 1995, 29 genetically marked steelhead and 17 genetically marked kamloops were released into the Lester River study reach. They were selected as study fish from a pool of 69 kamloops and 39 hatchery reared steelhead that were captured as returning adults in the French River and screened for their IDH-2 genotypes. The steelhead that were stocked were homozygous for the *83 allele (slow), and the kamloops that were stocked were homozygous for the *100 allele (fast). The pool of returning adults was identified to strain by fin-clips applied when the fish were stocked as yearlings. Few wild steelhead were captured in the French River in 1995, and we did not wish to reduce egg collections by stocking wild brood stock in the Lester River. Alternatively, steelhead possessing a fin-clip which indicated they had a Knife River origin and had been reared to smolt size at French River Coldwater Hatchery, were genetically screened and stocked in the Lester River. During the selection process, each candidate spawner was tagged with a numbered Floy[2] tag and held in a tank until its genotype was determined. Krueger et al. (1994, revised by personal communication) showed that about 25% of the kamloops population was homozygous for the *100 allele of the enzyme and about 95% of the steelhead population was homozygous for the *83 allele, suggesting its potential as a genetic marker for discriminating the strains. Genotypes were determined from muscle tissue plugs weighing ~0.25 g removed from the area immediately posterior and lateral to the dorsal fin with a skin biopsy punch. Tissue samples from females were collected only from green females (no free flowing eggs). IDH-2 genotypes were identified with starch gel electrophoresis[3]. Homozygous fast alleles were found in 12 male and 5 female kamloops, and homozygous slow alleles were found in 14 male and 15 female steelhead. These fish were selected for stocking.

Proper data interpretation required that we know how long each spawner remained in the study reach. Neither strain was imprinted to the Lester River and we anticipated that the fish might leave immediately or be caught by anglers before they could spawn, so we inserted gastric implant radio transmitters to monitor fish activity (Adams et al. 1998). Gastric implant transmitters do not affect migrational or spawning behavior (Eiler 1990), and thus were preferred to surgical implants or externally attached transmitters. Fish movement and location were monitored periodically during daylight hours by scanning for radio signals at nine sites on the canyon rim with a receiver using a hand held loop antenna. Spawners were also marked with a highly visible and numbered Floy streamer tag, color coded for strain, and inserted on either the right or left side to differentiate the sexes. Spawners were genetically screened, marked, and stocked in the study reach as soon as possible after capture to minimize stress on the fish and insure that their spawning behavior was as natural as possible. Observations of spawning behavior were attempted at several times of day using binoculars until all the fish had emigrated downstream.

A 500 m section of river above the study reach was electrofished using backpack gear in July 1995 to determine if wild young-of-the-year (YOY) rainbow trout had confounded our study. Lester River has a small self-sustaining population of resident rainbow trout (strain unknown) that escaped from a private fish pond.

The study reach was electrofished in early August 1995 in an attempt to collect a sample of 100 progeny of the transplanted spawners. Electrofishing was done with an electrofisher mounted in a tote barge. Captured YOY were placed on ice after capture and shipped whole to the Illinois Natural History laboratory for IDH-2 genotyping. The fish were flash frozen at the laboratory for later analysis. In July 1996, the reach was intensively electrofished again with backpack gear to remove as many surviving age 1+ parr as possible for a similar analysis. The difference between the hybrid to steelhead ratios found for each age-class was analyzed for statistical significance using the Z-test ($\alpha=0.05$) for proportions with a continuity correction (Freund 1984).

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[2]Use of trade names does not imply endorsement of products.

[3]The tissue plugs were analyzed by the Illinois Natural History Survey Genetics Laboratory in Champaign Illinois.

Results

Spawner Behavior

Timing of spawning and spawning behavior were not barriers to hybridization. The direction of movement after stocking was random for both strains (Table 1, Figure 1). Generally, radio signals from individual fish were detected at more than one site, so the location of the fish could only be approximated from the signal strength to within ± 50 m. Therefore, we cannot be certain how many mixed strain spawning aggregations developed. Both strains occupied the reach at the same time and remained in the reach long enough to spawn (Figure 2). However, 3 kamloops (18%) and 11 steelhead (38%) were detected by radio signal only once, within a day or two after stocking. They may have left the study reach immediately, spawned quickly and left, or their transmitters may have malfunctioned. Three steelhead, all males, immediately migrated back to the French River, were recaptured in the fish trap, were restocked in the study reach, and immediately left again. Attempts to observe spawning interactions failed. Surface turbulence, water turbidity, and our inability to precisely pinpoint fish by signal strength contributed to our lack of success.

Reproductive Success and Survival

No wild rainbow trout were found upstream of the study reach in 1995. Since no rainbow trout were captured in 500 m of the Lester River immediately above the study reach, we assumed that no wild YOY rainbow trout had drifted downstream into the study reach.

Catches of YOY and age 1+ parr in the study reach were lower than expected for both steelhead and kamloops (Figure 3). Exhaustive electrofishing effort yielded only 57 YOY in the study reach in 1995. Forty-four (77%) were heterozygous for the IDH-2 allele, indicating that they were hybrids. Thirteen were homozygous for the slow allele, indicating that they were pure strain steelhead. Neither YOY kamloops nor adult resident rainbow trout were collected. Our experience with similar electrofishing gear under similar stream conditions suggests that we captured at least 30% of the YOY in the reach. In 1996, seven hybrids and six pure strain steelhead were captured, and again, no kamloops or adult or YOY resident rainbow trout were found. Given the limited sample sizes, the ratios of hybrids to pure steelhead were not significantly different between age-classes at the 0.05 level ($Z= 1.656$, $P= 0.09$); nevertheless, the most likely estimate was that hybrid over-winter survival of hybrids was 0.34 times that of the pure steelhead.

Discussion

Any hybridization of steelhead and kamloops in North Shore streams would pose two kinds of risk to the wild steelhead populations; an immediate risk of reduced recruitment, and a long-term risk of genetic introgression and reduced fitness. Hybridization may occur because the strains do not segregate in space or time when spawning. Most North Shore streams have very limited spawning area, often less than that available in our study reach, thus mixed strain spawning aggregations may be common. Our observations, however, do not rule out the possibility of spatial segregation in streams such as the Sucker River, where greater migration distances are possible. Both strains occupied our study reach for similar periods, and Negus (1996) reported that steelhead and kamloops spawning runs were essentially synchronous.

Hatchery fish, in general, stray more than wild fish (Quinn 1993), increasing the likelihood of hybridization. Many fin clipped kamloops, for example, have been observed in rivers north of Dorian, Ontario. From 1991-1994, up to one-half of the spawning fish captured in the Steele River, Ontario, were clipped kamloops (Jon George, Ontario Ministry of Natural Resources, personal communication). The Steele River is 254 km from the nearest stocking site in the Brule River in Minnesota. In contrast, Krueger et al. (1994)

Table 1. Distribution of stocked spawners in the Lester River Study reach (See Figure 1). Location was estimated by signal strength and is ± 50 m upstream or downstream of the indicated site. S = steelhead, K = kamloops

Date	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Stocking Site	Site 7	Site 8	Site 9
4/20							3♂K			
							3♀S,2♂S			
4/22							1♀K,3♂K			
							4♀S,3♂S			
4/24				2♂K		1♀K,2♂K				
	1♀S	1♂S		2♀S,1♂S		2♂S				
4/28			1♀K	1♂K	1♂K	1♂K		2♂K		
		1♂S		2♀S,1♂S				2♂S		
4/29							3♀K			
							3♀S,4♂S			
5/2		1♀K	1♂K	1♂K		2♀K,1♂K	1♀K,3♂K	1♂K		1♂K
	1♀S	1♂S		1♀S		1♀S,3♂S	2♀S,2♂S			1♀S,1♂S
5/5	1♀K			1♀K,1♂K	1♀K		1♂K		1♂K	1♂K
	1♀S	2♂S		2♂S		1♀S,2♂S			1♂S	2♀S
5/10							3♂K			
							3♀S,2♂S			
5/11			1♀K	3♂K		3♂K		1♀K,1♂K		3♂K
	2♀S		1♀S	1♀S,3♂S		3♂S				3♀S
5/15	1♀K,1♂K	1♂K	1♂K			2♂K		1♀K	1♂K	1♂K
	1♂S			2♂S						1♂S
5/19	1♀K,1♂K				1♂K			1♀K		2♂K
	2♂S				1♂S					
6/2	1♀K,2♂K					1♀K				1♂K

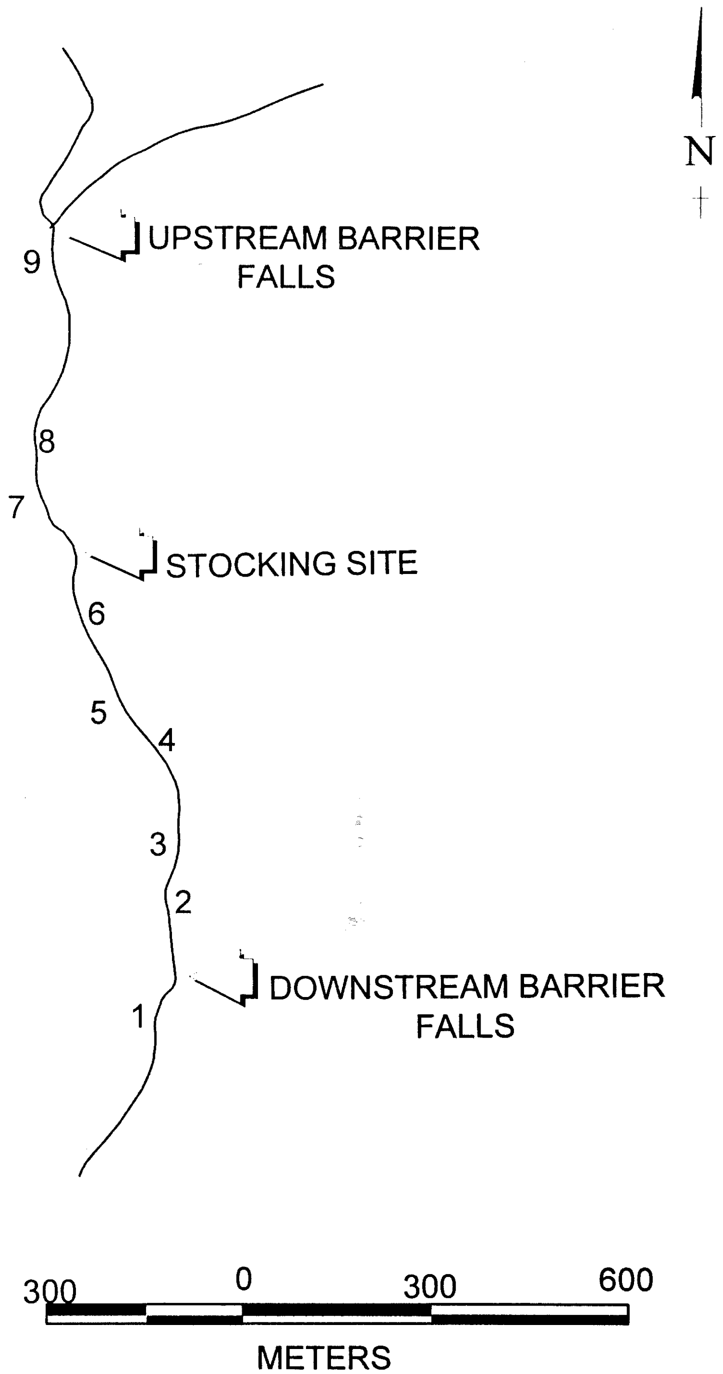

Figure 1. Lester River study reach showing the locations where radio signals were scanned.

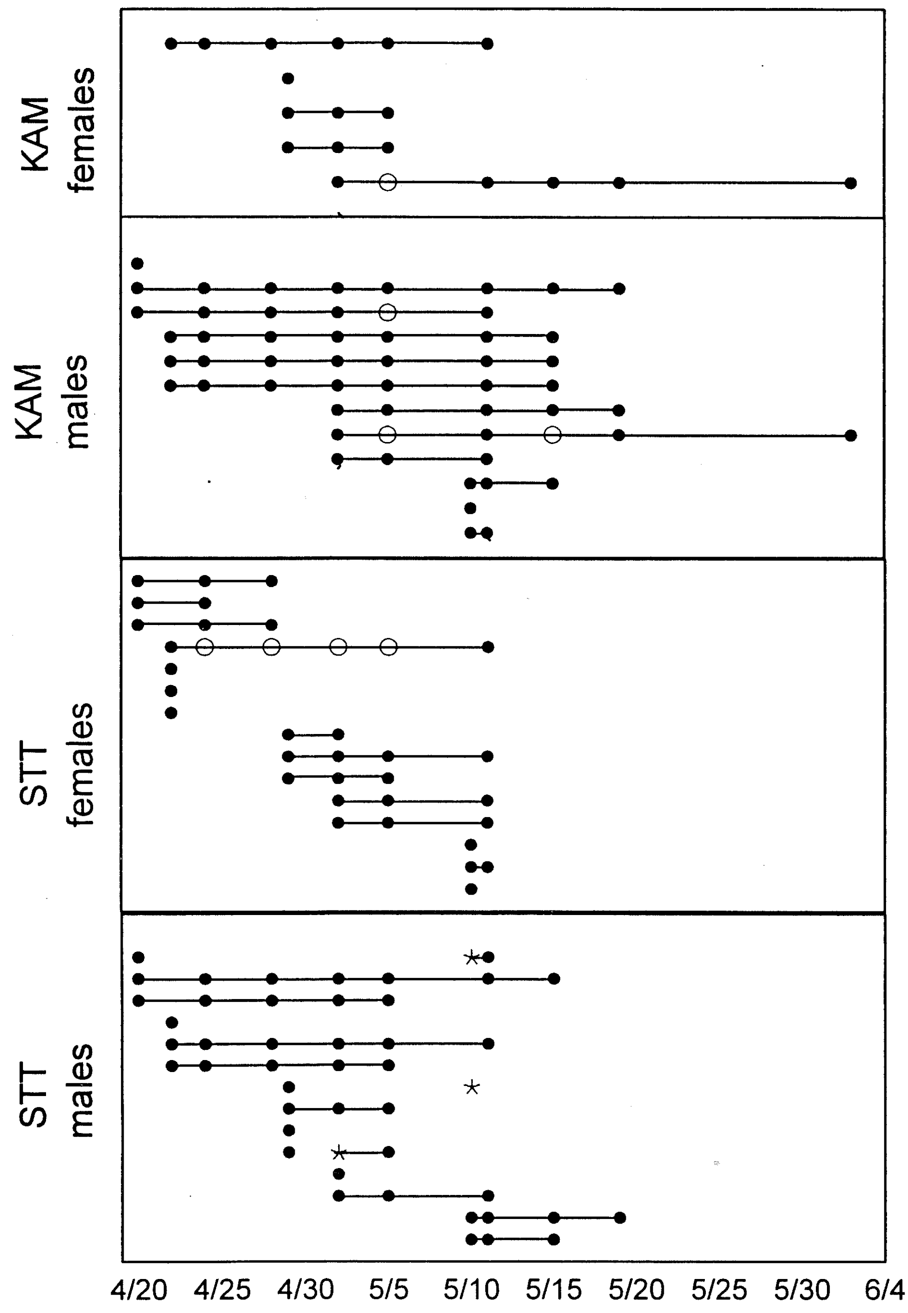

Figure 2. Observations of spawners stocked in the Lester River study reach. Solid circles show a fish that was either stocked that day or was detected by radio signal. Open circles represent fish that were not detected by radio signal on that day, but were detected on a later date. Asterisks represent fish that left the sector, were recaptured and restocked. STT = steelhead, KAM = kamloops.

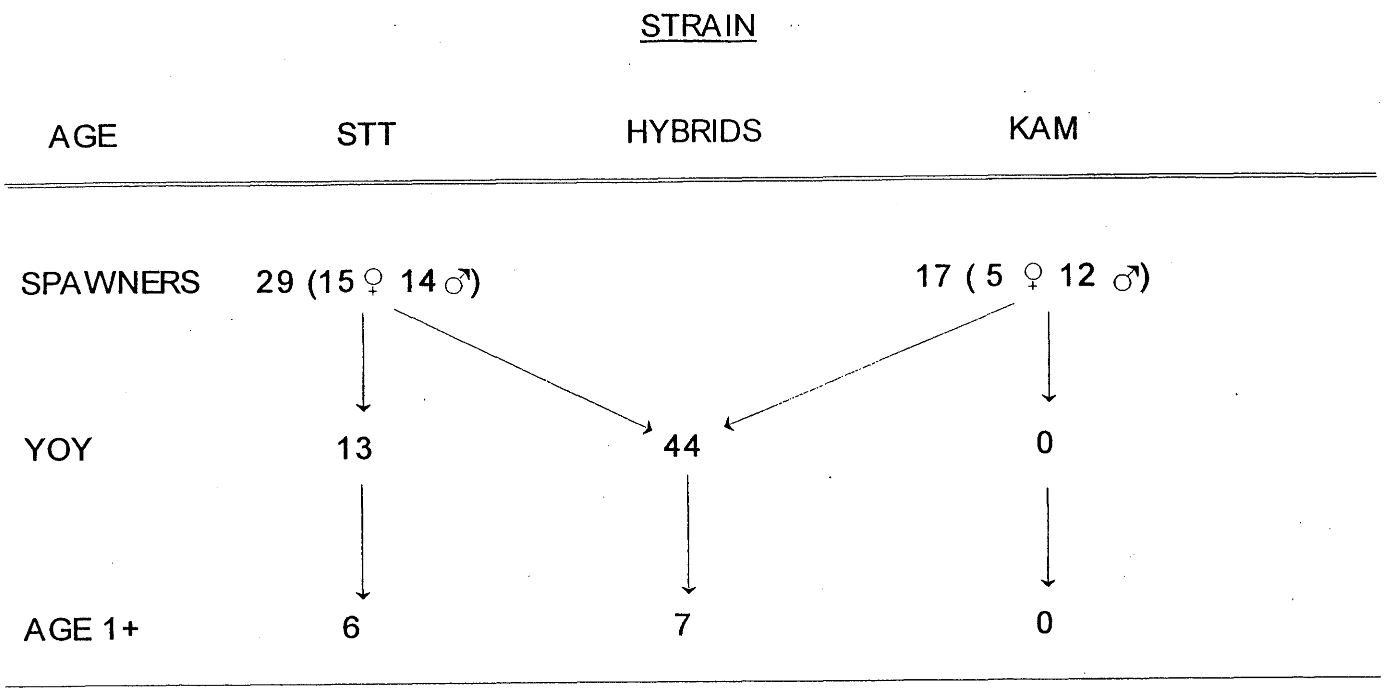

Figure 3. Juvenile rainbow trout survival in the Lester River study reach.

identified local stocks of steelhead in North Shore streams, suggesting rigid homing to natal streams. Restricting stocking of kamloops to a confined area may reduce hybridization but not prevent it.

Viable hybrids can be produced in the wild and can over-winter. Prior to this work, we knew that the strains could hybridize, but it appeared that they did not or that few hybrids survived to age 1+ (Krueger et al. 1994). A closer examination of the frequency of hybridization and the fate of the hybrids is now appropriate, but may depend on development of new genetic probes. Such a study would allow estimation of the degree to which hybridization reduces the recruitment of steelhead and survival to adulthood.

The adult steelhead used in this study had been raised in the hatchery until they were stocked as smolts, thus their fitness may have been lower than that of wild fish and more similar to that of kamloops and hybrids. If all the females spawned in the study reach, about 78,000 eggs would have been produced (Fred Tureson, Minnesota Department of Natural Resources, personal communication). We do not have egg survival data from North Shore streams; however, egg survival rates in a hatchery ranged from 50% to 75% at ambient stream temperatures (Negus 1996). If we assume an egg survival rate of 10% and survival from hatch to age 1 of 12.4% (Close and Anderson 1997), there should have been about 1,000 YOY in the study reach in July 1995. In contrast, the capture of 57 YOY (estimated 190 produced) suggests that survival was low. A majority (77%) of the YOY captured were hybrids. Although not statistically significant, the difference in the steelhead to hybrid ratios between age groups suggests that steelhead survived the winter at a greater rate. It was not possible to determine how many spawning pairs produced the fingerlings and yearlings. It is possible that any survival differences to age 1+ may be a parental effect rather than a strain effect. The sample was insufficient to draw conclusions about the relative fitness of kamloops, steelhead, and hybrids.

Because hybrids survived to age 1+, there should be greater concern that some survive to smolt and to mature. If hybrids survive to maturity and reproduce, they may depress the fitness of the wild stock by infusing maladaptive genes (introgression), and breaking down coadapted gene complexes (Templeton 1986; Waples 1991; Leary et al. 1995).

The Minnesota DNR stocked Michigan strain steelhead fry prior to 1991. It was thought that the genetic risks were much lower than for stocking kamloops. Stocking of the Michigan strain was discontinued in 1991 on the advice of Dr. Krueger and his colleagues (subsequently published in Krueger et al. 1994). Maladaptive genes are unlikely to have been introduced from the Michigan strain, as the eggs were collected from lake run brood stock that were most likely hatched and reared in the wild (Seelbach 1987; Seelbach and Whelan 1988). Secondly, rearing environments of Lakes Superior and Michigan, and their tributaries, are not dramatically different. Lastly, the Michigan strain fish were stocked as unfed fry in Minnesota, subjecting them to the natural selection encountered during stream rearing by Lake Superior's indigenous stock.

If steelhead rehabilitation remains the DNR's management goal, the genome of unclipped adult rainbow trout (presumably steelhead) should be reexamined for kamloops genes to determine if introgression has occurred. If kamloops genes are found, this will confirm that hybrids have survived to reproduce. Diagnostic microsatellite markers (Rassman et al. 1991) must be identified so that we can screen fish scales or fin tissue for the appropriate markers which would allow the use of non-lethal samples to evaluate the extent of introgression.

It may be possible to reverse the introgression of kamloops genes if it has already occurred. The results of Krueger et al. (1994) suggest that if adult hybrids exist, they are probably rare. The lack of pure strain kamloops in their samples and ours suggests that kamloops could be eradicated in five or six years, simply by halting stocking. Furthermore, with diagnostic genetic markers in hand, genetically pure steelhead could be identified and used in a fry stocking program to genetically restore the steelhead stock. Based on Leary et al. (1995), if less than 10% of the unclipped rainbow trout have kamloops genes, it should be practical to genetically restore the stock.

Management Implications

The steelhead of Lake Superior have been self-sustaining for over 100 years. Steelhead abundance will increase and fishing improve only if the factors limiting steelhead survival are identified and mitigated. Continued kamloops stocking appears to have the potential to reduce steelhead recruitment through hybridization. This could potentially result in a hybrid strain with unknown characteristics. If steelhead were selected as the sole strain for management, some efforts may be needed to genetically rehabilitate the stock so that the steelhead could stay as healthy as possible to provide angling opportunities. Anglers and fisheries professionals must work together to identify the important limiting factors where they are related to loss of habitat, lack of suitable forage, or spawning interactions with kamloops. Anglers must clearly understand the potential risks involved in managing both strains at the same time so that they can provide educated input into the management decision on stocking kamloops.

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