STUDY PERFORMANCE REPORT

State: Michigan **Project No.:** F-80-R-4

Study No.: 654 **Title:** Evaluation of brown trout and steelhead competitive interactions in Hunt Creek, Michigan.

Period Covered: October 1, 2002 to September 30, 2003

Study Objective: To determine if the introduction of steelhead into a stream where they presently do not exist will affect the abundance, survival, growth, or disease status of resident trout species.

Summary: Potential effects of competitive interactions between steelhead and resident brown trout in Hunt Creek were evaluated by comparing population dynamics of resident trout in a 3.4 km treatment zone (TZ) before (1995-97) and after (1998-2003) adult steelhead were stocked into the TZ. Resident trout populations were also estimated in reference zones (RZs) without steelhead. We have made nine consecutive annual fall estimates of brook and brown trout populations in the TZ of Hunt Creek, and in RZs located on Hunt and Gilchrist creeks. Adult steelhead were stocked in the TZ each spring 1998-2003. Brook and brown trout abundance, growth, and survival in the TZ were compared between the pre- and post-steelhead stocking periods. Ratios of abundance, survival, and growth of resident trout populations in treatment and reference zones were compared between pre- and post-steelhead stocking periods to help distinguish between possible effects of interspecies interactions and environmental factors.

Introductions of steelhead were associated with significantly lower mean annual survival of age-0 brown trout in the TZ, as compared to the Gilchrist Creek RZ. Reduced survival of year classes of YOY brown trout that interacted with steelhead has resulted in significantly lower abundance of age-1 through age-3 brown trout in the TZ, as compared to the same year classes in the Gilchrist Creek RZ. All age groups of brook trout in the TZ were less abundant after steelhead introductions than during the pretreatment period but brook trout abundance also declined in Gilchrist Creek where there were no steelhead. Mean abundance of YOY brown trout in the TZ has not changed significantly, relative to the Gilchrist Creek RZ, since steelhead were stocked. No significant changes in growth rates of brown trout were detected following steelhead introductions.

Findings: Jobs 2, 3, 5, 6, 7, 8, 9, 10, and 11 were active this year, and progress is reported below.

Job 2. Title: Monitor water temperature in treatment and reference zones.–I recorded water temperatures hourly using electronic thermometers at five sites. One thermometer was located near the upstream boundary of the Hunt Creek RZ, and the other four thermometers were located near the upstream and downstream boundaries of the Hunt Creek TZ and the Gilchrist Creek RZ.

I used water temperature data collected during the primary incubation period, 15-October through April, to estimate whether brown trout fry were likely to emerge before steelhead spawned the following spring. The number of days between brown trout egg deposition and hatch predicted from incubation time models (Crisp 1981, 1988) ranged from 69 d for the 2001- year-class up to 122 d for the 2003 year class (Figure 1). Predicted hatch and swim-up dates were standardized with the assumption that all brown trout spawn on 15-October to allow for comparisons between years. Many brown trout spawn after this date so if model predictions are accurate, numerous brown trout probably hatch and emerge later than the dates shown in Figure 1. Predicted dates for median swim-up were as early as 25-March for the 2001 year class and as late as 30-April for the 1996 year class. The 2003 year class of brown trout was predicted to emerge nearly as late as the 1996 year class. My analysis suggests that substantial numbers of brown trout alevins were still in their redds when steelhead spawning took place during each spring from 1998-2003. Thus, steelhead redds that are superimposed upon brown trout redds dug the previous fall probably cause mortality of brown trout fry. However, in most years less than ten percent of brown trout redds were affected by superimposition of steelhead redds.

Job 3. Title: Monitor water stage and discharge.–Stream discharge is monitored primarily because high stream discharge around the time that fry emerge from redds is known to have strong negative effects on the reproductive success of brown trout (Nuhfer et al. 1994). Because the timing of stochastic events such as floods can differentially affect recruitment of species with different life histories (Strange et al. 1992), stream discharge in Hunt Creek is monitored throughout the year at a site located 2 km upstream of the TZ.

An exceptionally high peak discharge of 100 cfs occurred on 31-March 1998. Mean daily discharge on that date was 87 cfs. This flood did not appear to impair brown trout reproductive success in Hunt Creek but fall YOY abundance in the Gilchrist Creek RZ was substantially lower than normal in 1998. Gilchrist Creek is flashier than Hunt Creek so peak flows in the Gilchrist Creek TZ on 31-March 1998 were higher than in Hunt Creek. I was unable to wade the creek to make an estimate of discharge on that date.

Maximum daily mean discharge during March and April, from 1999 to 2003 ranged from 30 to 55 cfs. These levels of discharge during the hatching and emergence period for brown trout did not appear to impair reproductive success. The 2001-year class of brown trout was relatively strong in all zones in spite of a brief flood peak of 79 cfs on 12-April 2001. Mean daily discharge in upper Hunt Creek on that date was 55 cfs. Mean daily discharge during the primary steelhead incubation period (approximately 15-April to 15-June) was generally quite low and stable. The paucity of significant high-flow events during steelhead incubation periods and consistently high numbers of steelhead YOY from 1998 through 2003 indicate that high flows did not adversely affect steelhead reproductive success during this study.

Job 5. Title: Locate and mark locations of trout redds and measure redd characteristics.– Brown trout redds were counted twice in the 3,400-m Hunt Creek TZ during the latter portion of the spawning period in fall 2002. During past years, redds were usually counted weekly beginning with the first full week of October. The highest number of new redds were usually present during the last week of October. Spawning activity has been consistently highest during the last half of October and actively spawning fish were frequently observed during late October redd counts. On 4-November 2002, 124 "recently" excavated (active) brown trout redds were counted in the TZ. This was the highest weekly count of active redds observed during this study. Redds were not counted during Michigan's firearm deer season (November 15-30) to reduce conflicts with landowners along the creek. Redds were not counted during December 2002 because the number of active redds observed in the first week of December in previous years was consistently low, ranging from zero to five during 1998-2001.

I marked the location of 30 brown trout redds during November 2002 and recorded their dimensions. These marked redds were reexamined in spring 2003 after steelhead spawning was completed to determine if steelhead had constructed redds at the same locations. I recorded redd microhabitat data such as substrate size and level of sand-embeddedness. In addition, water depth and water velocity (0.6 x depth) were recorded immediately upstream of the redd pit and at the approximate crest of the tailspill using methods similar to those described in Schmetterling

(2000). Superimposition of steelhead redds over previously excavated brown trout redds during this study is discussed below under job 9.

Job 6. Title: Collect population and biological data.–We again made mark-and-recapture estimates of brook and brown trout populations during late summer in 2003 in a 3.4 km treatment zone on Hunt Creek, a 0.7 km reference zone on Hunt Creek, and a 2.3 km reference zone on Gilchrist Creek. Similar population estimates have been made each year since 1995. Populations of juvenile steelhead were also estimated during years they were present (1998-2003). Scales collected in 2003 have not been aged. Hence, data analyses reported for this segment do not include comparisons of abundance, survival, or growth for years since 2002. Spring population estimates were made in May 2002 and 2003 in an upstream and downstream reach of the Hunt Creek TZ (400-m at both ends of the TZ) to provide data to estimate over winter mortality. Spring populations were also estimated in a 400-m reach of the Gilchrist Creek RZ. These data will be presented in later segments after scale samples are aged.

Average abundance of steelhead YOY has been 2.6 times higher than that of brown trout in the TZ in years when steelhead were stocked (1998-2002) (Table 1). Brown trout YOY abundance in the TZ during 1998-2002 was significantly lower than during the pre-steelhead-stocking period of 1995-97 ($P < 0.05$). This temporal change in abundance of brown trout YOY may be unrelated to interactions with steelhead, however, because brown trout in the Gilchrist Creek RZ were also significantly less abundant from 1998-2002 than during the pretreatment period (Table 2). Relative abundance of YOY brown trout in the TZ, compared to the Gilchrist RZ, has not changed significantly (Figure 2). Recent declines in abundance of brook trout YOY and older age classes have also been observed in Hunt Creek but again, similar declines also occurred in the Gilchrist Creek RZ (Tables 1 and 2).

Abundance of older age classes of brown trout in the Hunt Creek TZ, ages 1 through 3, that interacted with steelhead as YOY are only half as abundant as during the pre-steelhead period (Table 1). Similar declines in abundance of older age classes of brown trout did not occur in the Gilchrist Creek RZ. Hence, abundance of older age classes of brown trout in the TZ has declined significantly compared to the Gilchrist Creek RZ, as graphically illustrated in Figure 2. Abundance of the sparse populations of brook trout in both Hunt and Gilchrist Creeks has decreased during the same time period. Thus, these declines may be unrelated to interactions with steelhead.

Steelhead introductions into Hunt Creek have significantly reduced survival of YOY brown trout. Before steelhead YOY were present in Hunt Creek, annual survival of YOY brown trout averaged 36 percent whereas it now averages only 21 percent (Table 3). Survival of one- and two-year-old brown trout in the Hunt Creek TZ has not changed, but survival of three-year-old brown trout has increased from 20 to 31 percent (Table 3). By contrast, mean annual survival of YOY, age-one, and age-two brown trout in the Gilchrist Creek RZ increased significantly (Table 3). Mean annual survival of age-0 brown trout was twice as high in the TZ, relative to the Gilchrist Creek RZ, before steelhead were stocked (Figure 3). Mean annual survival of age-1 and age-2 brown trout in the TZ did not change significantly relative to the Gilchrist Creek RZ (Figure 3). However, survival of three-year-old brown trout in the TZ was 2.6 times higher, relative to the Gilchrist Creek RZ, after steelhead were stocked.

Growth rates of brown trout have not changed significantly during the past eight years in either the Hunt Creek TZ or the Gilchrist Creek RZ. There were no statistically significant differences in mean length at age for any age group of brown trout in either the TZ or Gilchrist Creek RZ between test periods (Table 4). In fact, mean length at age was remarkably similar between years in spite of substantial variation in year class abundance.

Job 7. Title: Test fish for BKD and other diseases.–Brown trout were collected for disease screening from Hunt Creek each summer during 1996-2003 and from Gilchrist Creek during 1990, 1994, and 1999. In 1999 and 2001-03, we also collected juvenile steelhead downstream from the Hunt Creek TZ. Brown trout were screened for the presence of *Renibacterium salmoninarum*, *Yersinia ruckeri*, and *Aeromonas salmonica.* Five-fish pools of trout heads were examined for the presence of spores of the parasite *Myxosoma cerebralis.* Virological tests were performed to detect the presence of the hemorrhagic septicemia virus, the infectious pancreatic necrosis virus, and the *Oncorhynchus masou* virus. None of these diseases or parasites were detected in any of the brown trout collected from Gilchrist Creek. No viral diseases or pathogenic bacterial diseases have been detected in brown trout from Hunt Creek. *M. cerebralis* spores were detected in brown trout collected in 1998 and in each year from 2000 to 2002. Relative spore density was determined by making five passes over a 22 by 22 mm cover slip at 200X magnification. Spore densities determined for brown trout by this method have been low. In most years, 60 fish heads were combined into approximately twelve pools before they were examined for spores. In 2002, spores were found in half of the pooled brown trout samples and spore density in positive pools ranged from one to four.

M. cerebralis spores were not found in steelhead screened in 1999 but they were found in eight of twelve pools of steelhead examined in 2001, and in five of thirteen pools examined in 2002. Spore density in steelhead was low, 11 or fewer per screening slide in 2001. In 2002, four of five screening slides had three or fewer spores, but thirty spores were found in one pool of three steelhead heads. With one exception, no clinical signs of whirling disease have been observed in either brown trout or steelhead. One rainbow trout examined in 2002 exhibited a depression in the skull. The consistently high abundance of juvenile steelhead, over 2000 YOY per ha, suggests that whirling disease has not caused any significant mortality.

Disease testing has not been completed, to date, for the fish collected in July 2003.

Job 8. Title: Monitor stocking of adult steelhead.–Adult steelhead were stocked at the downstream end of the Hunt Creek TZ each spring from 1998-2003. Eighty steelhead of each sex were stocked each year. Size at planting, percent ripeness, and estimated egg production is summarized in Table 5. Estimates of egg deposition were higher in 2000-03 than in 1998-99 because female steelhead were larger.

Steelhead redds in the TZ were counted twice weekly beginning 2 d after stocking in 1998-99 and once a week in 2000-03. Redds were counted in a 4.6 km reach of Hunt Creek that includes all stream sections where populations of brown trout and steelhead are estimated each year. Steelhead began spawning within a day after being stocked in all years. The majority of spawning usually occurred within a week after stocking during all years. Few steelhead were observed on redds later than two weeks after stocking. Females apparently dig more than one redd, on average, because the maximum number of redds counted each year usually exceeded the number of females stocked.

Job 9. Title: Characterize steelhead redds.–Steelhead generally spawned in slightly deeper and faster water than brown trout and dug much larger redds (Table 6). However, there was broad overlap in the ranges of water depths and velocities upstream of the redd pit and over the tailspill of redds dug by both species. The higher mean water depth upstream of steelhead redd pits probably occurred because the upstream edge of redd pits were often located where pools "tailed" out into riffles. Hence, water depth upstream of the pit was often deeper than water depth where most eggs were deposited. Steelhead selected larger gravel substrates for redd sites than brown trout. Over 90% of steelhead used gravel larger than 25mm compared to 54% of brown trout. Steelhead also were more likely to completely clean sand from gravel interstices of redds. All steelhead redds were less than 25% embedded with sand compared to 59% for brown trout redds (Table 6).

Steelhead superimposed their redds upon brown trout redds dug the previous fall less than 10% of the time in three out of four years when superimposition was estimated (Table 7). From 18 to 40 brown trout redd locations were marked with permanent markers during four different spawning years. After steelhead spawning was completed the following spring, we determined if steelhead redds had been dug on top of brown trout redds excavated the previous fall. Steelhead superimposed redds over 14.4% of the 118 brown trout redds marked during this study. In 2001, steelhead superimposed redds over 55% of brown trout redds marked in fall 2000. This may have occurred, in part, because we marked more brown trout redds within a 700-m reach of creek close to the planting site where many steelhead had spawned in previous years. In addition, a beaver dam constructed after brown trout redds were marked blocked steelhead access to a 500-m upstream reach where up to ten steelhead redds were dug in previous years. In 2003 only two steelhead redds were superimposed over thirty marked brown trout redds within an upstream reach where steelhead dug at least eleven redds.

I conclude that redd superimposition by steelhead is unlikely to seriously impair brown trout reproduction in a stream like Hunt Creek that has abundant spawning gravel for both species. However, where spawning habitat is more limited, and when steelhead gain access to a stream earlier in the winter, redd superimposition could be a more serious problem. In our study, steelhead were transferred to Hunt Creek in either late March or early April and most spawned within two weeks. Moreover, high numbers of steelhead redds were consistently dug in the first kilometer of stream upstream of the planting site. Transportation of the steelhead by truck appears to prompt many fish to spawn close to the stocking site within a few days of stocking. Upstream redds are generally dug a week or more later. Portions of natural steelhead runs that ascend streams from the lower Great Lakes commence spawning earlier than those stocked for this study. Early run steelhead would probably distribute themselves more evenly over available habitat, and if they spawn earlier and superimpose redds over brown trout redds the alevins are less likely to have emerged.

Job 10: Title: Analyze data and write progress report.–This progress report was prepared.

Job 11: Title: Estimate populations of resident trout and steelhead in additional streams.– During July and August 2000-02 we made mark-and-recapture estimates of resident trout species, steelhead, and other potamodromous species in five additional streams. Streams sampled were the Baldwin River, Houghton Creek, the Little South Branch of the Pere Marquette River, the mainstem Pere Marquette River, and the Platte River. Resident trout species populations were likewise estimated in rivers inaccessible to Great Lakes fish. These streams were the North and South Branch Boardman rivers, Hersey River, mainstem Manistee River, and the North, South, and mainstem Au Sable rivers. Fewer streams were sampled in 2003 due to staffing reductions. I will test hypotheses relating vital statistics of resident trout populations to the presence and abundance of potamodromous salmonids after scale samples are read in 2004.

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Prepared by: Andrew J. Nuhfer
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Table 1.–August-September numbers of brown, brook, and rainbow trout per hectare, by age, in a 3.4-km treatment zone of Hunt Creek, MI where adult steelhead were stocked each spring from 1998 through 2003.

Year	Age 0	1	2	3	4
Brown trout					
1995	1,616	509	199	130	20
1996	970	428	161	74	15
1997	1,283	414	145	64	15
1998	1,048	490	120	92	18
1999	947	297	163	70	26
2000	933	165	98	68	24
2001	1,019	176	64	49	18
2002	902	209	92	35	18
Before Steelhead 1995-97	1,289 [2]	450 [2]	169 [2]	89 [2]	17
After[1] Steelhead	970 [2]	212 [2]	85 [2]	42 [2]	18
Rainbow trout					
1998	2,541	0	0	0	0
1999	2,241	340	0	0	0
2000	2,097	245	0	0	0
2001	2,341	357	2	0	0
2002	3,610	480	6	0	0
Brook trout					
1995	22	8	0.7	0.5	0
1996	80	49	5	0	0
1997	102	51	6	0.4	0
1998	67	35	8	0	0
1999	41	10	2	1	0
2000	41	14	1	0	0
2001	20	7	2	0	0
2002	18	6	1	0	0
Before Steelhead 1995-97	68 [2]	36 [2]	4 [2]	0.3 [2]	0
After[1] Steelhead	38 [2]	9 [2]	1 [2]	0 [2]	0

[1]Different periods were used for different age groups so that only year classes of brown and brook trout that interacted with steelhead as YOY were compared to the pretreatment period means.

[2]Differences between abundance during before and after period are significantly different ($P \leq 0.05$).

Table 2.–August-September numbers of brown and brook trout per hectare, by age, in a 2.3 km section of Gilchrist Creek, MI used as a reference zone, 1995-2002.

Year	Age 0	1	2	3	4
Brown trout					
1995	2,173	731	278	113	12
1996	1,867	403	173	57	16
1997	1,887	537	129	43	15
1998	1,032	694	133	62	23
1999	1,689	435	199	80	7
2000	1,741	461	140	70	15
2001	2,272	612	184	84	15
2002	2,101	597	242	70	17
Before 1995-97	1,976 [1]	557	193	71	15
After 1998-2002	1,767 [1]	560	180	73	15
Brook trout					
1995	14	27	6	0	0
1996	21	30	5	0.5	0
1997	30	22	6	0	0
1998	23	12	8	0	0
1999	17	33	0	0	0
2000	2	9	1	0.5	0
2001	7	10	1	0	0
2002	9	4	2	0	0
Before 1995-97	21	26 [1]	5 [1]	0.2 [1]	0
After 1998-2002	12	14 [1]	2 [1]	0.1 [1]	0

[1]Differences between abundance during before and after period are significantly different ($P \leq 0.05$)

Table 3.–Annual percent survival of brown trout in Hunt and Gilchrist creeks, by age, from the year listed to the following year.

Year	Age 0	Age 1	Age 2	Age 3
Hunt Creek Treatment Zone				
1995	27	32	37	12
1996	43	34	40	20
1997	38	29	63	28
1998	28	33	59	28
1999	17	33	42	34
2000	19	39	50	27
2001	21	52	54	36
Before 1995-97	36 [1]	32	47	20 [1]
After 1998-2001	21 [1]	39	51	31 [1]
Hunt Creek Reference Zone				
1995	18	34	75	31
1996	49	127	62	23
1997	40	77	104	60
1998	17	40	74	18
1999	27	34	32	15
2000	13	16	37	29
2001	25	96	79	48
Before 1995-97	36 [1]	80	80	38
After 1998-2001	20 [1]	47	56	28
Gilchrist Creek Reference Zone				
1995	19	24	21	14
1996	29	32	25	27
1997	37	25	48	53
1998	42	29	60	11
1999	27	32	35	19
2000	35	40	60	22
2001	26	40	38	20
Before 1995-97	28 [1]	27 [1]	31 [1]	31
After 1998-2001	33 [1]	35 [1]	48 [1]	17

[1]Differences between survival during before and after period are significantly different ($P \leq 0.05$)

Table 4.–Mean total length at age (mm) of brown trout in Hunt and Gilchrist creeks during August or September 1995-2002. Fish were sampled during September from 1995 to 2001, and during August in 2002.

	Age				
Year	0	1	2	3	4
Hunt Creek					
1995	90	163	210	265	361
1996	90	164	212	270	334
1997	88	171	229	270	372
1998	92	173	224	271	323
1999	85	174	230	279	336
2000	91	168	230	274	338
2001	85	173	237	289	338
2002	83	170	234	298	345
Before 1995-97	89	166	217	269	355
After 1998-2002	87	171	231	282	336
Gilchrist Creek					
1995	81	153	198	263	338
1996	78	148	197	266	329
1997	80	150	214	272	334
1998	85	148	213	264	323
1999	86	166	217	276	355
2000	85	159	224	269	337
2001	80	152	218	266	336
2002	78	152	221	287	313
Before 1995-97	80	150	203	267	334
After 1998-2002	83	155	219	272	333

Table 5.–Mean total length (mm), weight (kg), and ripeness of adult steelhead stocked in Hunt Creek during 1998-2003. Egg production was estimated from female size and fecundity data collected from steelhead at the Little Manistee River Weir in 1998.

	Year					
Parameter	1998	1999	2000	2001	2002	2003
Mean total length of males	701	686	788	745	781	733
Mean total length of females	694	688	732	727	740	733
Mean weight of males	3.2	3.2	4.7	4.0	4.5	3.7
Mean weight of females	3.2	3.3	3.9	3.9	4.0	3.9
Percent ripe males	38	34	60	61	64	36
Percent ripe females	34	25	36	44	14	22
Estimated egg production	288,267	294,594	346,951	351,850	359,708	347,410

Table 6.–Mesohabitat features of brown trout and steelhead redds in Hunt Creek, MI, 1995-2003. Names of redd morphology features are described in Schmetterling (2000). Data summaries are based on measurements made at approximately 200 brown trout redds and 180 steelhead redds.

Species	Redd morphology feature	Mean	Minimum	Maximum	S.E. of mean
Brown trout	Water depth upstream of pit (m)	0.27 [1]	0.13	0.49	0.007
Steelhead		0.34 [1]	0.19	0.62	0.009
Brown trout	Water depth over tailspill (m)	0.26 [1]	0.06	0.70	0.007
Steelhead		0.24 [1]	0.11	0.55	0.005
Brown trout	Water velocity upstream of pit (m/s)	0.64 [1]	0.20	1.01	0.01
Steelhead		0.68 [1]	0.30	1.20	0.01
Brown trout	Water velocity over tailspill (m/s)	0.81	0.57	1.08	0.03
Steelhead		0.80	0.60	0.99	0.02
Brown trout	Redd size m^2	1.37 [1]	0.08	7.84 [2]	0.10
Steelhead		6.97 [1]	0.66	27.78 [2]	0.44
		Substrate size			
		0-10 mm	11-25 mm	> 25mm	
Brown trout	Percent of redds with substrate sizes indicated	0.6	45.2	54.2	
Steelhead		0.0	8.5	91.5	
		Sand embeddedness rating			
		0-25%	26-50%	52-75%	
Brown trout	Percent of redds by embeddedness rating	59%	33%	8%	
Steelhead		100%	0	0	

[1] Differences between means for brown trout and steelhead are significantly different (ANOVA $P \leq 0.05$).

[2] Some large redds were clearly contiguous redds dug by more than one female but were classified as one redd when no clear boundary between redds was evident

Table 7.–Frequency and percentage of marked brown trout redds that were dug up by steelhead that spawned the following spring.

Year	Number of brown trout redds marked	Number of steelhead redds superimposed on brown trout redds	Percent of brown trout redds affected
1997	30	2	6.7
1998	0	-	-
1999	40	3	7.5
2000	18 [1]	10	55.5
2001	0	-	-
2002	30	2	6.7
All years	118	17	14.4

[1] I marked thirty brown trout redds but a beaver dam built after brown trout spawned blocked steelhead access to an upstream stream segment where twelve marked redds were located.

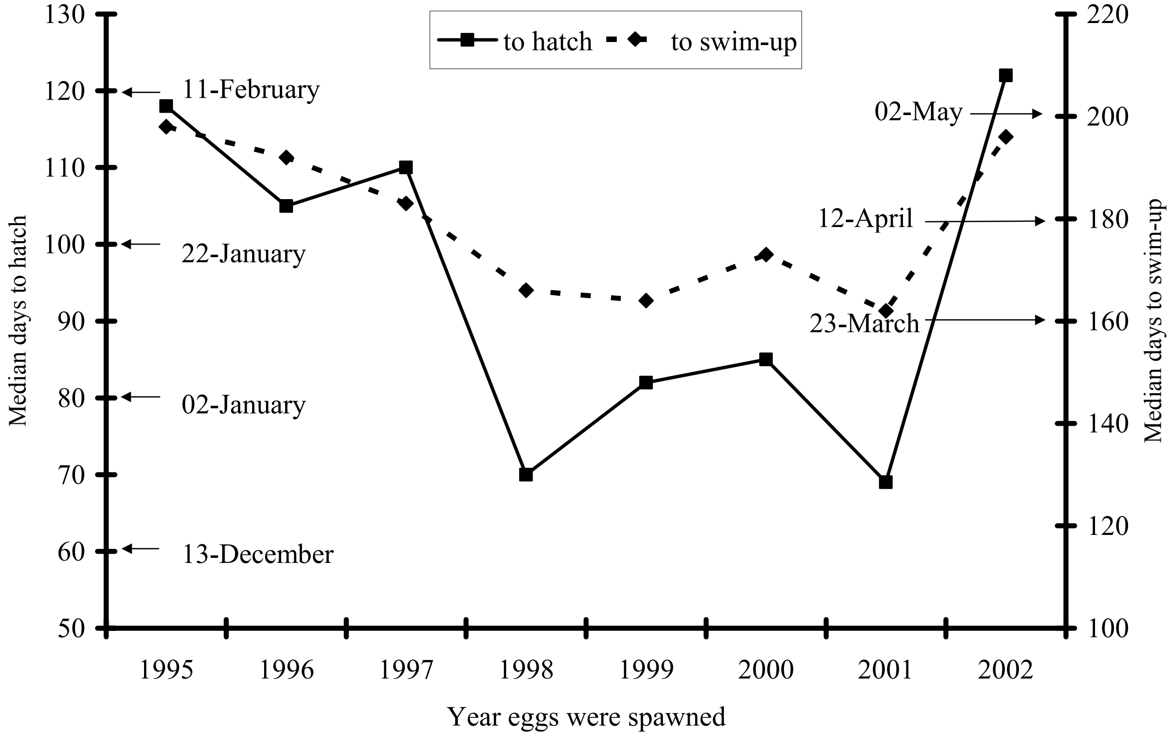

Figure 1.–Median numbers of days to brown trout hatch and swim up for brown trout spawning in the Hunt Creek TZ on 15-October. Projections are based on mean daily water temperatures during the incubation period and predictive models developed by Crisp (1988).

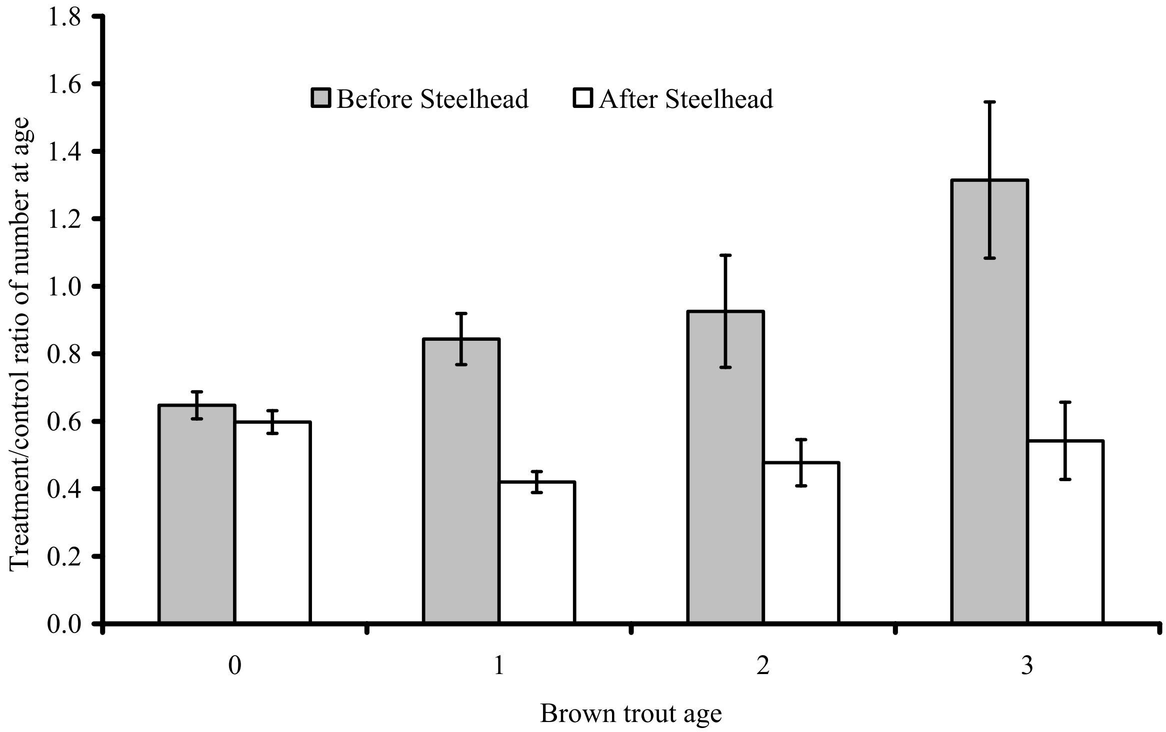

Figure 2.–Ratios of the number/ha of brown trout in the treatment zone of Hunt Creek to number/ha in the Gilchrist Creek reference zone. No steelhead were present in the reference zone during either the before or after periods. The before steelhead period is 1995-97. After steelhead periods vary by age group so that only the abundance ratios of age classes of brown trout that interacted with steelhead as YOY are compared to the ratios for the before steelhead period. Error bars are ±2 SE.

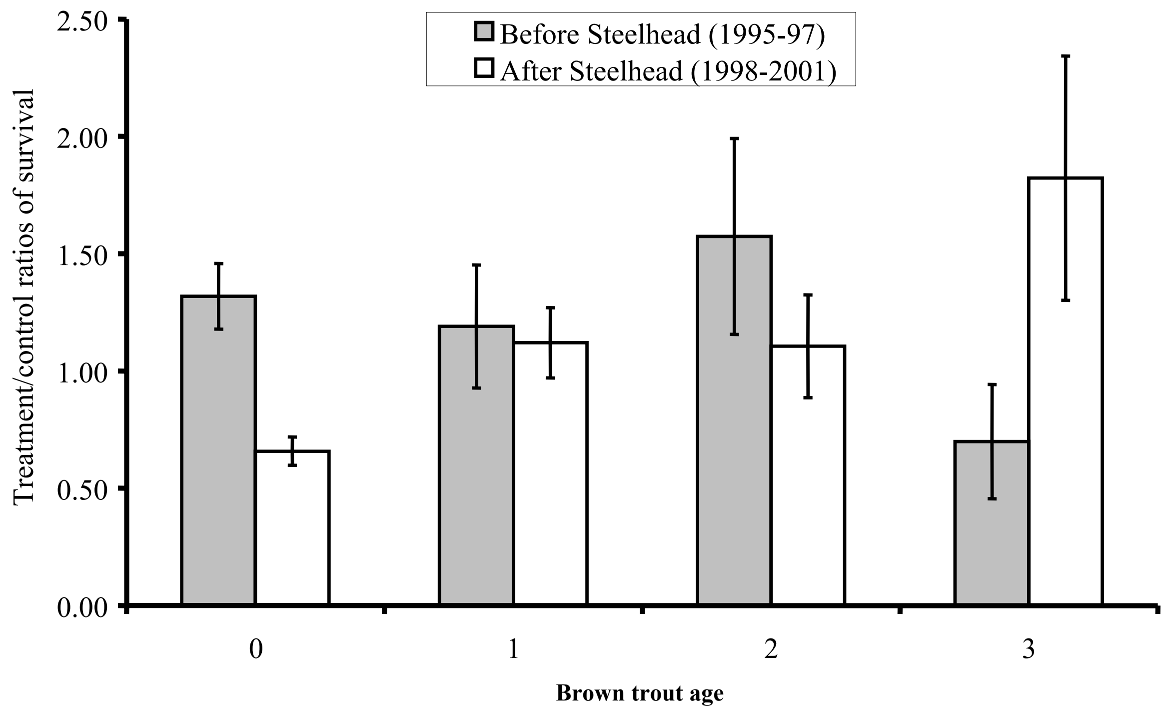

Figure 3.–Ratios of annual brown trout survival in the treatment zone of Hunt Creek to survival in the Gilchrist Creek reference zone. No steelhead were present the reference zone during either the before or after period. Error bars are ±2 SE.