

**Steelhead and Resident Rainbow Trout:  
Early Life History and Habitat Use  
in the Deschutes River, Oregon**

*Pelton Round Butte Hydroelectric Project  
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Prepared for Portland General Electric Company by

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# ***Chapter 1: Introduction and Overview***

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## INTRODUCTION

The relationship of migratory and resident forms of rainbow trout (*Oncorhynchus mykiss*) has long confused biologists. Steelhead, the migratory form, and resident rainbow trout represent two life history forms of the same species. The relation between resident and anadromous forms of the same species is poorly understood (see Northcote 1992 for a review) and is particularly unresolved for steelhead and resident rainbow trout in the Deschutes River. Do steelhead and resident rainbow trout represent “ecophenotypes” within a single gene pool or do they each represent reproductively isolated populations? Questions regarding the relationship of anadromous and resident forms of salmonids are becoming increasingly important (Johnson et al. 1994). Understanding how the life-history forms of these species interact and use habitat is crucial to the management of this species.

Steelhead and resident rainbow trout populations support important sport fisheries in the lower Deschutes River (Schroeder and Smith 1989; ODFW 1991). As a result, understanding the relationship of the two forms is critical. To examine the relationship of steelhead and resident rainbow trout in the Deschutes River, I am conducting a series of investigations related to the use of spawning and rearing habitats, behavior by newly emerged fry, and biological differences between the two life history forms. In 1995, I began these studies under the direction of Dr. Gordon Reeves. The purpose of these studies was to examine interactions between and habitat use by steelhead and resident rainbow trout in the Deschutes River (Zimmerman and Reeves 1996, 1997, 1998, 1999). These studies include an examination of the timing and location of spawning, size of fry and timing of emergence, and juvenile microhabitat use.

## ORGANIZATION OF THIS REPORT

This report is presented in five chapters. The first chapter provides an introduction and summary of all work completed. The following chapters are presented as manuscripts that have either been submitted for peer review and publication or will be within the next year. In addition to the work presented in these chapters, the introduction includes discussion of some work that is still in progress and for which a manuscript has not yet been prepared.

Chapter 1. Introduction and overview.

Chapter 2. Population structure of sympatric steelhead and resident rainbow trout (*Oncorhynchus mykiss*): evidence from otolith microchemistry.

Chapter 3. Spawning by anadromous and non-anadromous rainbow trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon: evidence of reproductive isolation.

Chapter 4. Timing of emergence and size of fry at emergence of steelhead and resident rainbow trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon.

Chapter 5. Differential recruitment of steelhead and resident rainbow trout (*Oncorhynchus mykiss*) fry immediately following emergence.

## SUMMARY OF CHAPTERS

### Chapter 1. Introduction and Overview

In this chapter, I provide summaries of all work presented and a summary of microhabitat investigations. During 1996 and 1997, we investigated microhabitat use by juvenile *O. mykiss* at several sites throughout the mainstem and Shitike Creek. Analysis of these studies is still in progress. Differences in day and night habitat use by juveniles are evident by variable among locations.

## **Chapter 2. Population Structure of Sympatric Steelhead and Resident Rainbow Trout (*Oncorhynchus mykiss*): Evidence from Otolith Microchemistry**

I determined the population structure of sympatric anadromous steelhead and resident rainbow trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon, and Babine River, British Columbia, based on the maternal origin of anadromous and resident adults. Maternal origin was identified by comparing Sr/Ca ratios in the primordia and freshwater growth regions of the otolith using a wavelength-dispersive electron microprobe. This method is based on the rationale that Sr/Ca ratios in the primordia of juveniles with a steelhead maternal parent will be greater than that in the freshwater growth region of the same individual. Transects of Sr/Ca ratios were similar to those described for other anadromous and resident salmonids. In the Deschutes River, Oregon, only steelhead of steelhead maternal origin and resident rainbow trout of resident rainbow trout origin were observed. In the Babine River, British Columbia steelhead of resident rainbow trout origin and resident rainbow trout of steelhead maternal origin were also observed. Based on these findings, I conclude that steelhead and resident rainbow trout in the Deschutes River constitute reproductively isolated populations. In contrast, steelhead and resident rainbow trout in the Babine River weir area represent phenotypic polymorphisms within the same population. A single explanation concerning the population structure of sympatric steelhead and rainbow trout cannot be constructed; rather it varies among locations.

## **Chapter 3. Spawning by Anadromous and Non-anadromous Rainbow Trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon: Evidence of Reproductive Isolation**

Timing of spawning and redd site selection by sympatric resident rainbow trout and steelhead trout were examined in the Deschutes River, Oregon, from 1995 through 1997. Steelhead spawning occurred from mid-March through May, and resident rainbow trout spawning occurred from mid-March through August in the three years studied. Although there was an overlap in the timing of spawning, only 9 to 15 % of the total rainbow trout spawning occurred during the period when steelhead spawned. The timing of 50% spawning by steelhead was 9 to 10 weeks earlier than that by resident rainbow trout. Spawning sites selected by steelhead were in deeper water and had larger substrate than those selected by resident rainbow

trout. We concluded that steelhead and resident rainbow trout in the Deschutes River are reproductively isolated based on a combination of spatial and temporal segregating mechanisms.

#### **Chapter 4. Timing of Emergence and Size of Fry at Emergence of Steelhead and Resident Rainbow Trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon**

The timing of emergence and size of fry at emergence was determined for steelhead and resident rainbow trout in the Deschutes River, Oregon. Traps placed over redds of known origin were used to capture fry emerging from the gravel. There was an overlap in the timing of steelhead and resident rainbow trout emergence, which was similar to the overlap in the timing of spawning. There was no apparent size difference between newly emerged steelhead and resident rainbow trout.

#### **Chapter 5. Differential Recruitment of Steelhead and Resident Rainbow Trout (*Oncorhynchus mykiss*) Fry Immediately Following Emergence**

Territoriality and levels of aggression were determined for sympatric steelhead and resident rainbow trout from the Deschutes River, Oregon. Steelhead and resident rainbow trout fry were introduced as emerging fry from redds within artificial stream channels. Three treatments were examined: steelhead alone, steelhead and resident rainbow trout, and resident rainbow trout alone. Treatments containing steelhead were characterized by higher levels of aggression, higher initial rates of emigration, and lower densities of fish at the conclusion of the 20-day experimental trials.

## SUMMARY OF OTHER WORK (IN PROGRESS)

### **Relative Composition of Juvenile Steelhead and Resident Rainbow Trout in Mainstem and Tributary Rearing Habitats, Deschutes River, Oregon**

We collected juvenile *O. mykiss* from mainstem and tributary rearing habitats. Mainstem rearing habitats sampled were primarily side channels between the Pelton Reregulating Dam and the mouth of the Warm Springs River. In addition, we sampled two tributaries that are partially intermittent during summer months. Tenmile Creek, a tributary to Trout Creek, and Nena Creek were sampled. Otolith microchemistry was employed to identify maternal origin of juveniles (steelhead or resident rainbow trout). Samples of both young-of-year and yearling individuals from mainstem sites were dominated by resident rainbow trout. The lower sections of both Nena Creek and Tenmile Creek were exclusively inhabited by steelhead juveniles. Above the falls on Tenmile Creek, only resident rainbow trout juveniles were present. These findings suggest that intermittent tributaries may provide important refugia for steelhead in the lower Deschutes River basin.

### **Diel Variation in Microhabitat Use by Juvenile *Oncorhynchus mykiss***

During 1996 and 1997, we examined microhabitat use by juvenile steelhead and resident rainbow trout. Microhabitat study sites (Table 1-1), which varied in length from 15 m to 42 m, were selected to contain a variety of physical characteristics (i.e., depth, current velocity, and substrate).

Each site was divided into 3-m squares and the corners marked with painted washers. Two divers, with mask and snorkel, began at the downstream end of a site and proceeded slowly upstream. Species, size, and location were recorded on a Plexiglas slate with the grid pattern of the site inscribed on it. Observations were conducted in the morning (starting between 0900 and 1030), in the late afternoon (starting between 1530 and 1700), and at night (starting between 2200 and 2400). At night, divers used underwater lights.

**Table 1-1.** Locations of microhabitat study sites and dates visited.

Name	Location	Dates Visited
Upper Shitike	Tributary	31 May – 4 June 1996 20–22 August 1996 19–21 August 1997
Lower Shitike	Tributary	31 May – 4 June 1996 20–22 August 1996 19–21 August 1997
Dizney	RM 99.0	1–3 July 1996 26–28 August 1996 19–21 August 1997
Upper Trout Creek Campground	RM 87.3	21–25 June 1996 13–15 August 1996
Lower Trout Creek Campground	RM 87.3	21–25 June 1996 13–15 August 1996
South Junction	RM 83.7	16–18 July 1996 3–6 September 1996
RM 92.0 Side channel	RM 92.0	22–24 July 1996
RM 10.4	RM 10.4	25–27 August 1997

Observations of fish were made on two consecutive days, and physical characteristics of the site were measured on the third day. Physical characteristics measured included: substrate composition, water depth, current velocity 5 cm below the surface (referred to as surface velocity), mean current velocity (at 0.6 depth of water column measured from the surface), and cover (instream and overhead). Measures of each factor were made at the corners of each grid section or at more frequent intervals when a factor changed significantly in a short distance. Current velocities were measured with a portable electronic current meter. Substrate was grouped into diameter categories of <2, 2-5, 5-10, 10-20, 20-40, and >40 cm.

Distribution of juvenile *O. mykiss* was analyzed in two ways. First, the distribution of fish was examined relative to each physical factor. Measures for each factor were grouped and the contours of each class drawn on a map of the site. Classes of depth and velocity were at 15-cm and 15 cm/s intervals, respectively. The total area of each class was calculated and the

density of each class of fish was estimated for each factor. Separate estimates were made for each time and day.

Distribution relative to the physical factors was also determined with stepwise discriminant function analysis. The range intervals for each factor were assigned a rank, with 1 the lowest interval, 2 the next interval, and so on. Data from each day were combined for this analysis, and separate discriminant functions were derived for each time of day. All possible pairs of the mean discriminant score for each group were compared by a *t*-test to determine if the means were significantly different.

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Zimmerman, C.E., and G.H. Reeves. 1997. Steelhead and rainbow trout early life history and habitat use in the Deschutes River, Oregon: 1996 Annual Report. U.S. Forest Service, Pacific Northwest Research Station. Corvallis, Oregon.

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Zimmerman, C.E., and G.H. Reeves. 1999. Steelhead and rainbow trout early life history and habitat use in the Deschutes River, Oregon: 1998 Annual Report. U.S. Forest Service, Pacific Northwest Research Station. Corvallis, Oregon.

**Chapter 2: Population Structure of Sympatric Steelhead and Resident Rainbow Trout (*Oncorhynchus mykiss*): Evidence from Otolith Microchemistry**

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## ABSTRACT

I determined the population structure of sympatric anadromous steelhead and resident rainbow trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon, and Babine River, British Columbia, based on the maternal origin of anadromous and resident adults. Maternal origin was identified by comparing Sr/Ca ratios in the primordia and freshwater growth regions of the otolith using a wavelength-dispersive electron microprobe. This method is based on the rationale that Sr/Ca ratios in the primordia of juveniles with a steelhead maternal parent will be greater than that in the freshwater growth region of the same individual. Transects of Sr/Ca ratios were similar to those described for other anadromous and resident salmonids. In the Deschutes River, Oregon, only steelhead of steelhead maternal origin and resident rainbow trout of resident rainbow trout origin were observed. In the Babine River, British Columbia, steelhead of resident rainbow trout origin and resident rainbow trout of steelhead maternal origin were also observed. Based on these findings, I conclude that steelhead and resident rainbow trout in the Deschutes River constitute reproductively isolated populations. In contrast, steelhead and resident rainbow trout in the Babine River weir area represent phenotypic polymorphisms within the same population. A single explanation concerning the population structure of sympatric steelhead and rainbow trout cannot be constructed; rather it varies among locations.

## INTRODUCTION

The genetic and ecological relationship of resident and anadromous rainbow trout (*Oncorhynchus mykiss*) has long confused biologists. The disparity in appearance, behavior, and morphology among different life history forms originally led to the classification of multiple species of rainbow trout (Jordan and Evermann 1905; Behnke 1992). Differences in migratory behavior among and within river systems contributed greatly to this taxonomic confusion. The migratory behavior of salmonids is diverse and well documented (Gross 1987; Gross et al. 1988; Northcote 1992), with migrations ranging from relatively short potomadromous migrations between streams and lakes to long distance anadromous migrations to the open ocean.

There is a range of variation in migratory behavior among salmonids. Pink salmon (*Oncorhynchus gorbuscha*; Heard 1991) and chum salmon (*O. keta*; Salo 1991) exhibit only anadromous life history forms. Chinook salmon (*O. tshawytscha*; Healy 1991) and coho salmon (*O. kisutch*; Sandercock 1991) exhibit obligate anadromy with some individuals (precocial males) exhibiting a resident-like life history. Other species exhibit variations in migratory behavior that is evident in multiple life history forms. Rainbow trout, coastal cutthroat trout (*O. clarki clarki*; Zimmerman et al. 1997), sockeye salmon (*O. nerka*; Burgner 1991), brown trout (*Salmo trutta*; Jonsson 1985), and Arctic charr (*Salvelinus alpinus*; Nordeng 1983) exhibit dual or multiple life history forms that may reside sympatrically within the same stream. Within this group, there is no single explanation for the occurrence of dual life history forms. The relation between sympatric alternate life history forms is poorly understood, yet has significant implications concerning population dynamics and management.

Do resident and migratory forms represent “ecophenotypes” within a single gene pool or do they each represent genetically distinct populations? Foote et al. (1989) identified three possible genetic relationships between life history forms. First, alternative life history forms are genetically isolated and represent separate populations. Second, alternative life history forms are not genetically distinct. Third, alternative life history forms are genetically distinct within a local area but are more similar to one another than they are to their respective forms outside of the local area.

Genetic divergence of populations requires reproductive isolation. Zimmerman and Reeves (in review) found temporal and spatial segregation between steelhead and resident rainbow trout spawning in the Deschutes River, Oregon, and suggested that such segregation could contribute to reproductive isolation. In contrast, Burgner et al. (1992), in a review of steelhead biology, suggested that where steelhead and rainbow trout occur in sympatry it is likely that the progeny of resident rainbow trout may migrate to sea and the progeny of steelhead may remain in streams as resident fish. Neave (1944) considered the relationship of steelhead and resident rainbow trout in the Cowichan River, British Columbia and concluded that steelhead and rainbow trout should be treated as two separate species. Neave (1944) conducted both descriptive studies of meristic characters and rearing experiments. Savvaitova et al. (1997), in a

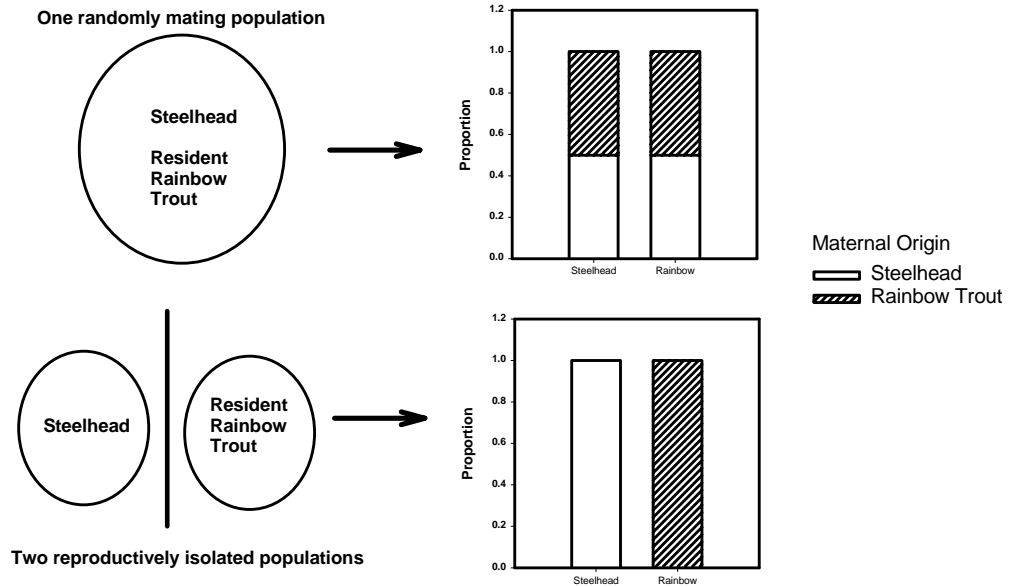
study of three life history forms of rainbow trout (resident, estuary migrating, and anadromous) in Kamchatka, concluded that the three forms represented a single randomly mating population.

Studies concerning the relationship of sympatric steelhead and resident rainbow trout have long been plagued by the inability to discriminate between juveniles. Further, identification of the life history of the maternal parent, the maternal origin (e.g., steelhead or resident rainbow trout), of individual fish can potentially provide important information concerning the population structure of sympatric steelhead and rainbow trout. Rybock et al. (1975) distinguished steelhead and rainbow trout progeny in the Deschutes River, Oregon, based on otolith nuclear dimensions, but a reexamination by Currens et al. (1988) suggested that the method did not reliably distinguish steelhead and resident rainbow trout. The ability to identify maternal origin of steelhead and resident rainbow trout can provide important information concerning the inheritance of life history.

Otolith microchemistry can be used to identify maternal origin based on examination of the ratio of strontium (Sr) and calcium (Ca) (Kalish 1990). Kalish (1990) and Rieman et al. (1994) used wavelength-dispersive electron spectroscopy to map transects of Sr/Ca ratios in the otoliths of salmonids and determine maternal origin of individual fish. Strontium, an element with binding characteristics similar to calcium, is substituted for calcium in the calcium carbonate matrix of the otolith at levels relative to the concentration in the environment (Kalish 1990). The concentration of strontium is greater in seawater compared to freshwater. Therefore, examination of Sr/Ca ratios across the otolith of a fish can describe the migrational history of that fish. Further, comparison of Sr/Ca ratios in the primordia and freshwater growth region can be used to determine maternal origin (resident or anadromous) based on the assumption that primordia composition reflects the environment in which yolk precursors develop (in the ocean for anadromous forms) (Kalish 1990). Using these techniques, Rieman et al. (1994) were able to determine the maternal origin of juvenile sockeye salmon and their resident form, kokanee, in the Snake River, Idaho.

If steelhead and rainbow trout represent ecophenotypes within a single gene pool, steelhead of resident maternal origin and resident rainbow trout of steelhead maternal origin would be commonly encountered (Figure 2-1). If the two life history forms are reproductively isolated, steelhead of rainbow trout maternal origin and rainbow trout of steelhead maternal

origin would not be present (Figure 2-1). In this study I describe the population structure of sympatric steelhead and rainbow trout populations from the Deschutes River, Oregon, and the Babine River weir area, British Columbia.



**Figure 2-1.** Potential population structure of steelhead and resident rainbow trout populations and expected proportions of individuals of resident and steelhead maternal origin in the adult populations of each life history form.

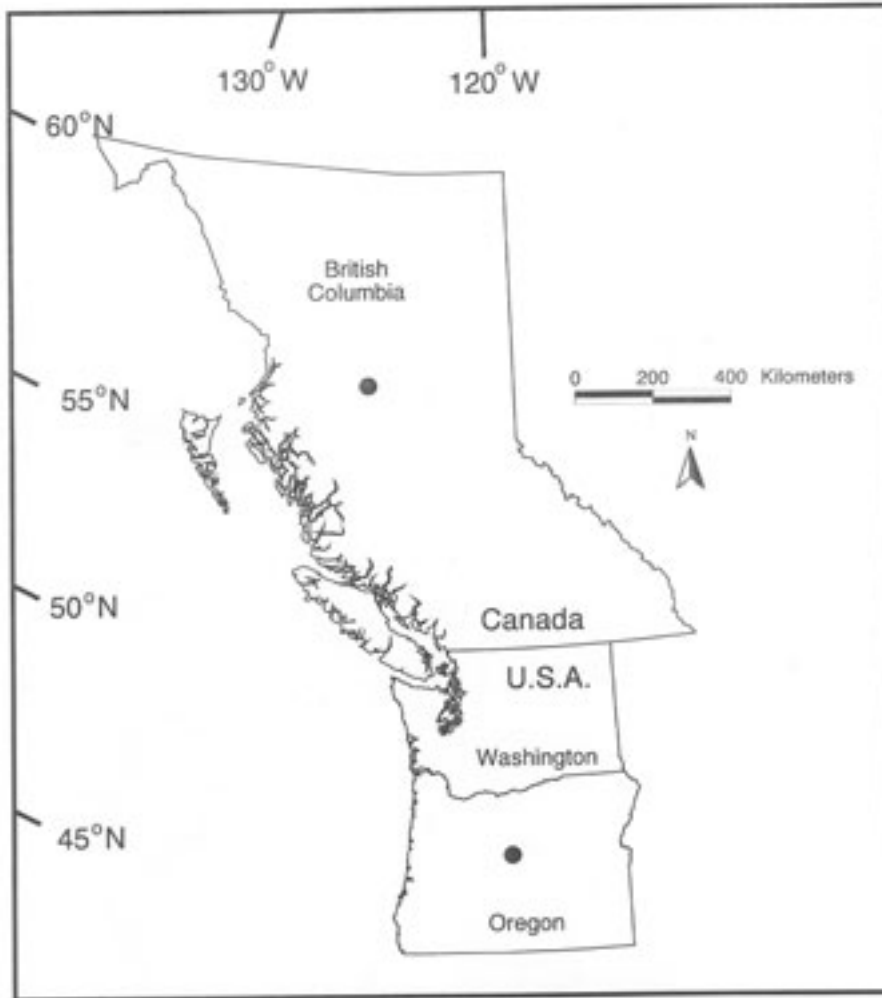
## MATERIALS AND METHODS

### Otolith Collection

Sagittal otoliths were collected from adult rainbow trout and steelhead in the Deschutes River, Oregon, and the Babine River weir area, British Columbia (Figure 2-2). Deschutes River steelhead otoliths were collected from wild adult steelhead returning to the Pelton Fish Trap at river km 160 and from carcasses encountered during spawning surveys. Adult rainbow trout were collected by electrofishing a 3-km segment of the river bank with a drift boat mounted electroshocker and from carcasses encountered during spawning surveys. Only fish older than age 2 were included in these analyses. Rainbow trout in the Deschutes River reach maturity at age 3 and steelhead smolt at age 1 or 2 (Olsen et al. 1994; Schroeder and Smith 1989). By including only mature post-smolt ages, I was able to ensure that I was comparing adult steelhead and resident rainbow trout. Babine River steelhead otoliths were collected from mortalities encountered at the Babine Lake salmon counting weir, and resident rainbow trout were collected from the stream in the vicinity of the weir. All resident rainbow trout from the Babine River were age 4 or 5. Most steelhead in the Babine River smolt at age 3 (Narver 1969).

### Otolith Preparation and Microchemical Analysis

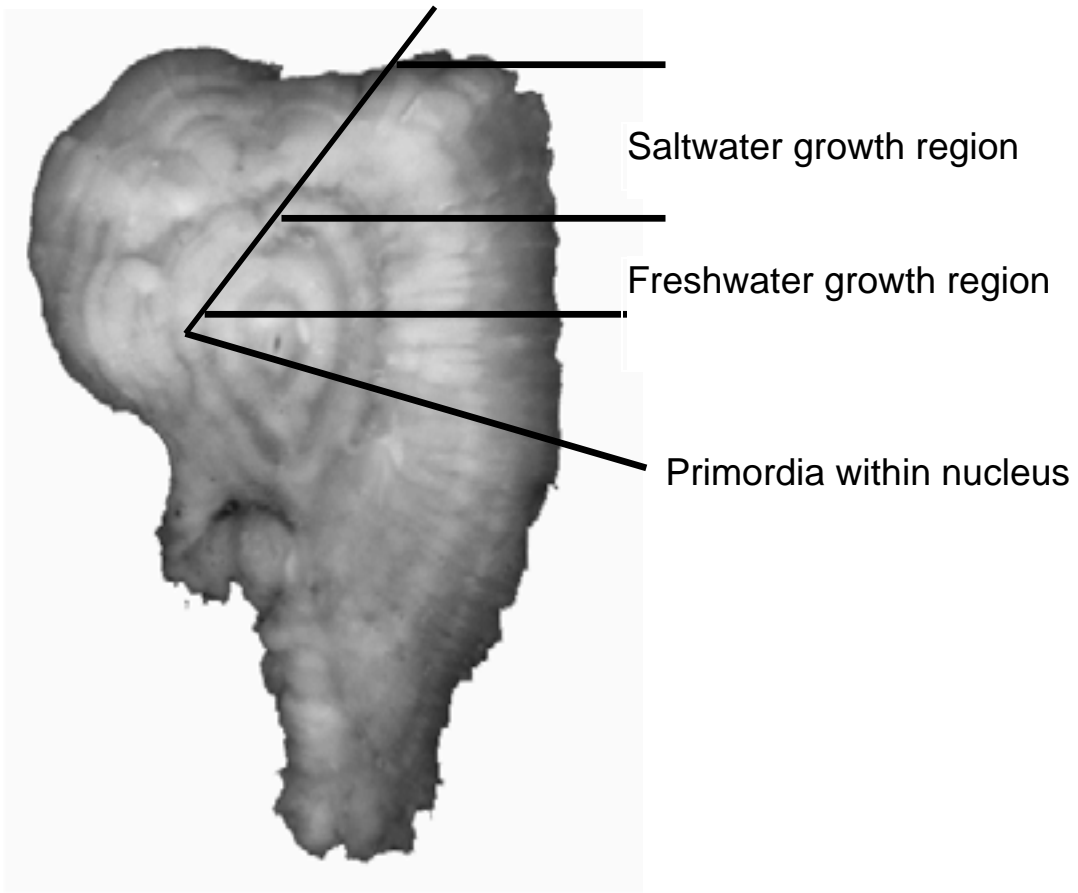
One sagittal otolith from each fish was mounted sulcus side down with crystal bond 509 on a microscope coverslip attached to a standard microscope slide. The otolith was then ground in the sagittal plane to the level of the nucleus with 1200-grit sandpaper. The mounting medium was heated and the otolith turned sulcus side-up. The otolith was then ground in the sagittal plane to the level of the primordia with 1200-grit and 2000-grit sandpaper and polished with a slurry of 0.05  $\mu\text{m}$  alumina paste. The coverslip was then cut with a scribe so that several prepared otoliths could be mounted on a petrographic slide for microprobe analysis. The slide containing several otoliths was rinsed with deionized water, air dried, and coated with a 200 Å carbon layer.



**Figure 2-2.** Otolith sampling locations in the Babine River, British Columbia, and the Deschutes River, Oregon.

Elemental analysis was conducted with a Cameca SX-50 wavelength dispersive microprobe. A 15 kv, 50 nA, 7  $\mu\text{m}$  diameter beam was used for all analyses. Strontiantite ( $\text{SrCO}_3$  - USNM R10065) and calcite ( $\text{CaCO}_3$  - USNM 136321) were used as standards for Sr and Ca, respectively. Each element was analyzed simultaneously, and a counting time of 40 s was used to maximize precision (Toole and Nielsen 1992).

Otolith regions were classified as primordia, freshwater growth region, and saltwater growth region based on growth rates inferred from banding patterns (Figure 2-3). The freshwater growth region included the area between the nucleus and the point of saltwater entry for anadromous fish or the area between the nucleus and the last annulus for resident fish. The saltwater growth region included the area between the freshwater growth region and preceding the last annulus for anadromous fish. Identification of freshwater and saltwater annuli was based on the methods of McKern et al. (1974). On all otoliths, microprobe sample points included all primordia and transects of at least 10 points in both the freshwater growth region and saltwater growth region (in steelhead). In most samples, the freshwater growth region was sampled within the summer growth of the first year. On a subsample of otoliths, a transect of sample points bisecting a primordium and continuing to the edge of the otolith (life history transect) was conducted for comparison with expected transects of Sr/Ca described by Kalish (1990). Maternal origin was determined by comparing Sr/Ca in the primordia with Sr/Ca in the freshwater growth region. A fish was determined to be of anadromous maternal origin if the Sr/Ca ratio in the primordia was significantly higher than in the freshwater growth region based on an unpaired two-tailed t-test with  $\alpha = 0.05$ .



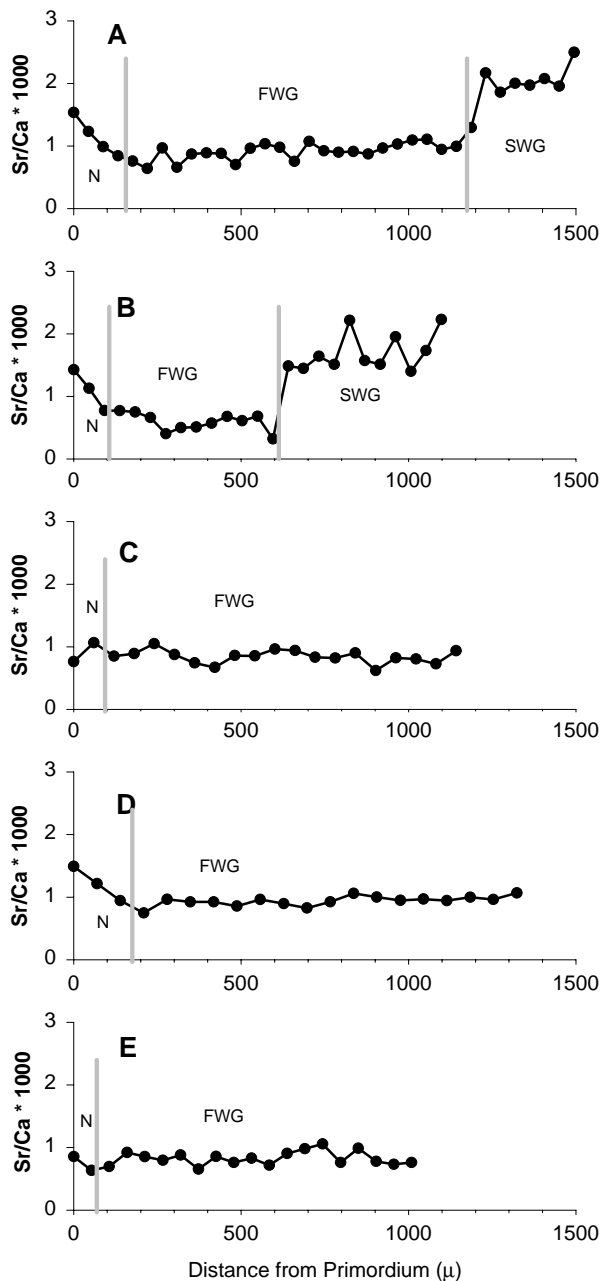
**Figure 2-3.** Sampling areas within the otolith of an adult steelhead.

## RESULTS

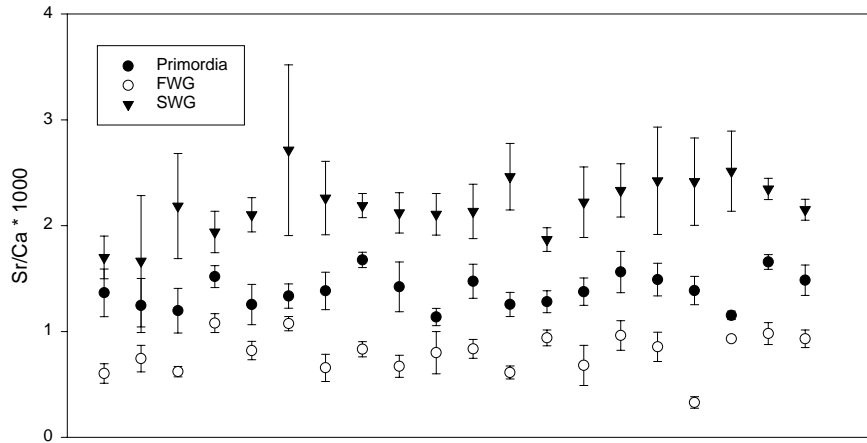
Life history transects of steelhead were similar to those described by Kalish (1990) for anadromous salmonids with lower Sr/Ca in the freshwater growth regions and increased Sr/Ca in saltwater growth regions (Figures 2-4a and 2-4b). Resident rainbow trout life history transects were characterized by constant low Sr/Ca (Figures 2-4c and 2-4e). Adult resident rainbow trout of steelhead maternal origin were characterized by increased Sr/Ca in the primordia and nucleus and constant lower Sr/Ca throughout the rest of the otolith (Figure 2-4d).

The relation between the life history of an individual and the life history of the maternal parent varied between the Deschutes and Babine Rivers. Of the 20 steelhead otoliths examined from the Deschutes River, all had significantly higher Sr/Ca in the primordia compared to the freshwater growth region ( $P < 0.05$ ), indicating that at least the maternal parent was a steelhead (Figure 2-5). None of the 38 resident rainbow trout otoliths from the Deschutes River had significantly higher Sr/Ca in the primordia than in the freshwater growth region ( $P > 0.05$ ), indicating that at least the maternal parent was a resident rainbow trout (Figure 2-6).

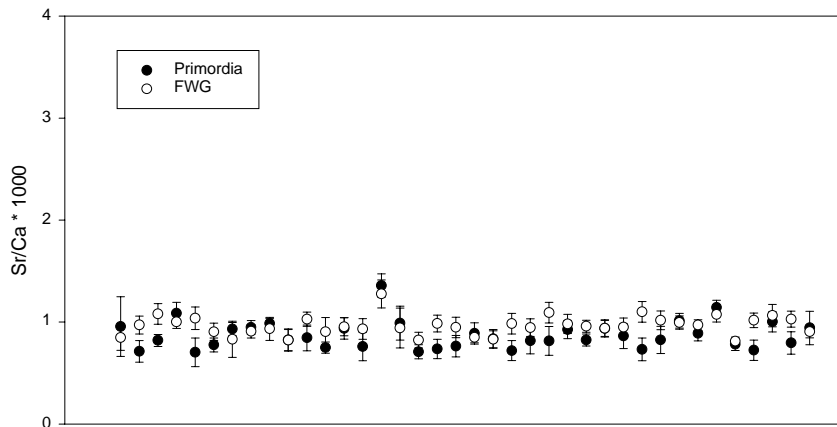
The relation between individual life history and the life history of the maternal parent of fish in the Babine River was less consistent. Of the 24 steelhead otoliths from the Babine River weir area examined, all but one had higher Sr/Ca in the primordia compared to the freshwater growth region ( $P < 0.05$ ), indicating steelhead maternal origin (Figure 2-7). The Sr/Ca in the primordia of one Babine River steelhead was not significantly higher than the freshwater growth region ( $t = 1.46$ ,  $P = 0.09$ ), indicating that the maternal parent was a resident rainbow trout (Figure 2-7). Two of the nine resident rainbow trout otoliths from the Babine River weir area had significantly higher Sr/Ca in the primordia compared to the freshwater growth region ( $P < 0.05$ ; Figure 2-8). This suggests that maternal parents of two fish were steelhead (Figure 2-8). The remaining seven resident rainbow trout did not have significant differences between Sr/Ca in the primordia or freshwater growth regions ( $P > 0.05$ ), indicating that the maternal parents were resident rainbow trout (Figure 2-8).



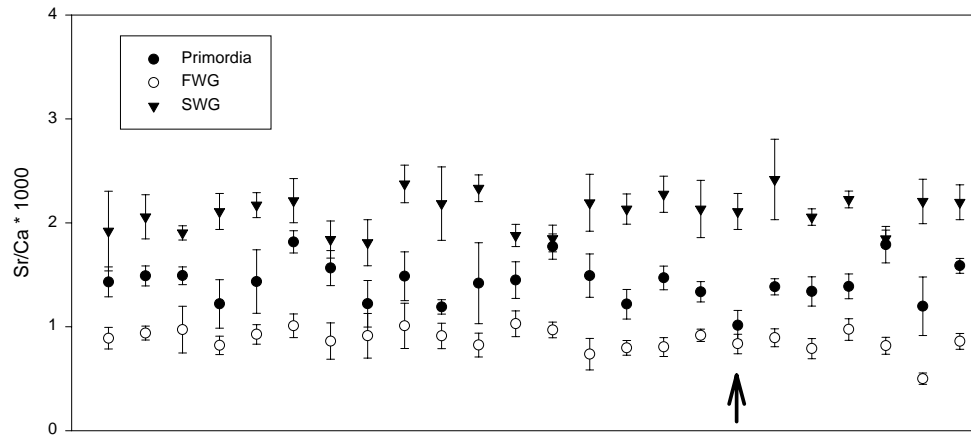
**Figure 2-4.** Transects of otolith Sr/Ca measured from a primordium to the otolith edge. Each point represents a single measurement. (A) Deschutes River adult steelhead; (B) Babine River adult steelhead; (C) Deschutes River adult rainbow trout; (D) Babine River adult rainbow trout whose maternal parent was a steelhead; and (E) Babine River adult rainbow trout whose maternal parent was a resident rainbow trout. N = nucleus, FWG = freshwater growth region, and SWG = saltwater growth region.



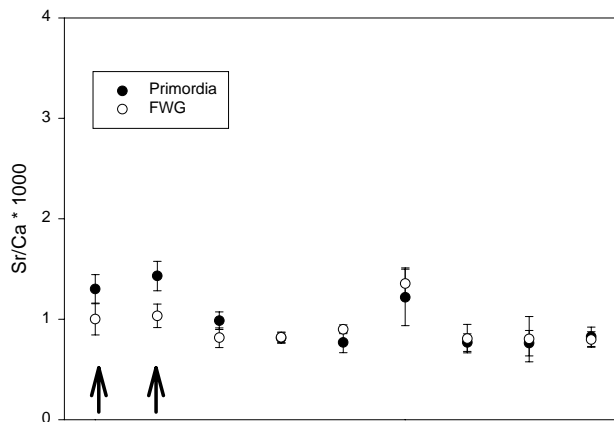
**Figure 2-5.** Mean and 95% confidence intervals of Sr/Ca ratios in primordia, freshwater growth region (FWG), and saltwater growth region (SWG) in otoliths of adult steelhead from the Deschutes River, Oregon.



**Figure 2-6.** Mean and 95% confidence intervals of Sr/Ca ratios in primordia and freshwater growth region (FWG) in otoliths of adult resident rainbow trout from the Deschutes River, Oregon.



**Figure 2-7.** Mean and 95% confidence intervals of Sr/Ca ratios in primordia, freshwater growth region (FWG), and saltwater growth region (SWG) in otoliths of adult steelhead from the Babine River weir area, British Columbia. Arrow indicates a fish whose maternal parent appears to have been a resident rainbow trout.



**Figure 2-8.** Mean and 95% confidence intervals of Sr/Ca ratios in primordia and freshwater growth region (FWG) in otoliths of adult resident rainbow trout from the Babine River weir area, British Columbia. The arrows indicate fish whose maternal parent appears to be a steelhead.

## DISCUSSION

The extent of reproductive isolation between resident rainbow trout and steelhead differed between the Deschutes and Babine Rivers. The life history of individuals from the Deschutes River was similar to the maternal parent. This was not true for all individuals from the Babine River. The majority of individuals from the Babine River had the same life history as the maternal parent. However, 4.2 % of the steelhead appear to have had a resident maternal parent and 22.2 % of the resident rainbow trout in the weir area had a steelhead maternal parent. These patterns suggest that there is a greater degree of reproductive isolation between steelhead and resident rainbow trout in the Deschutes River than in the Babine River.

Describing the degree of reproductive isolation between sympatric life history forms of the same species is critical in the definition of units of conservation and management (Waples 1995). Whether sympatric life history forms are managed as single populations exhibiting polymorphism or as reproductively isolated populations has profound implications in decisions related to protection and recovery of species. For example, in considering the status of coastal cutthroat trout in the North Umpqua River in Oregon, the resident and sea-run forms were treated as one single unit under the assumption that both life history forms could give rise to the other (Waples 1995). This would not be appropriate for Deschutes River steelhead and resident rainbow trout, which, given the segregation of spawning habitat and potential reproductive isolation, should be treated as two species. Steelhead and resident rainbow trout in the Babine River weir area can be treated as polymorphisms within the same population. Within the Babine River basin, it is likely that this population is reproductively isolated from other rainbow trout populations. For example, rainbow trout in streams at the southern end of Babine Lake are likely to be reproductively isolated from those in the weir area (Robert Hooton, British Columbia Ministry of Environment, Land, and Parks, pers. comm.).

Comparison of Sr/Ca in the primordia and freshwater growth regions can only identify maternal origin. Therefore, it is unknown whether male resident rainbow trout contributed to the anadromous population or whether male anadromous trout contributed to the resident population. It is possible that gene flow between life history forms may occur in this manner, although Zimmerman and Reeves (in review) observed only two instances in 4,302 observations in the

Deschutes River where steelhead and rainbow trout spawned together. Assortative mating has been shown to limit spawning between sockeye salmon and kokanee (Foote and Larkin 1988). Like sockeye salmon and kokanee, steelhead and resident rainbow trout are often characterized by differences in size, which can lead to assortative mating. In both the Deschutes and Babine Rivers, adult steelhead are larger than adult resident rainbow trout. Zimmerman and Reeves (in review) described spatial and temporal segregation of spawning by steelhead and resident rainbow trout that could serve to reproductively isolate the two populations in the Deschutes River.

Resident populations can give rise to anadromous juveniles (Northcote 1992). For example, Rieman et al. (1994) found juveniles of both kokanee and sockeye origin in samples of emigrants (presumed smolt emigration) in Redfish Lake, Idaho. However, of the five adult sockeye salmon returning to Redfish Lake in 1991, all had a sockeye maternal parent. Likewise, in presumed steelhead smolts collected from the estuary a small central California coastal stream, juveniles of both steelhead and resident rainbow trout maternal origin were present (Zimmerman, unpublished data). This suggests that resident fish may contribute to the recruitment of smolts, but only examination of adult steelhead can confirm that resident fish contribute to the recruitment of adult steelhead. The selection pressures on resident rainbow trout and steelhead are likely to be very different. Experimental studies with sockeye salmon and kokanee have demonstrated behavioral, ecological, and developmental differences between the two forms (Wood and Foote 1990). This is an important avenue of future research on the dynamics of sympatric steelhead and rainbow trout.

The formation of the present population structure of sympatric salmonid life history forms is likely to be the result of geographic isolation followed by local adaptation and genetic divergence (McPhail 1997). Kurenkov (1978) postulated that two forms of kokanee in Lake Kronotskiy, Kanchatka, resulted from a lava flow that blocked access to the sea for spring and summer races of sockeye salmon. Once contact with sockeye salmon was eliminated by the blockage, divergence between the two kokanee stocks was rapid and resulted in two biological species (Kurenkov 1978; McPhail 1997). A similar scenario was suggested by Zimmerman and Reeves (in review) for steelhead and resident rainbow trout in the Deschutes River, where large landslides blocked passage by steelhead for several hundred years. During such events,

divergence between the landlocked rainbow trout above the impoundment and steelhead below could have led to differences that are maintained in the present population structure.

Understanding the relationship of sympatric life history forms is critical to the development of adequate conservation measures. Successful management of sympatric steelhead and resident rainbow trout populations that are reproductively isolated will essentially require that the two life history forms be managed as separate species. In situations where a single randomly mating population develops into multiple life history forms, the two forms can be managed as a single unit. In such cases, the recovery of one life history form may result from the other form.

## **ACKNOWLEDGMENTS**

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**Chapter 3: Spawning by Anadromous and Non-anadromous  
Rainbow Trout (*Oncorhynchus mykiss*) in the  
Deschutes River, Oregon: Evidence of Reproductive  
Isolation**

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## ABSTRACT

Timing of spawning and redd site selection by sympatric resident rainbow trout and steelhead trout were examined in the Deschutes River, Oregon, from 1995 through 1997. Steelhead spawning occurred from mid-March through May, and resident rainbow trout spawning occurred from mid-March through August in the three years studied. Although there was an overlap in the timing of spawning, only 9 to 15 % of the total rainbow trout spawning occurred during the period when steelhead spawned. The timing of 50% spawning by steelhead was 9 to 10 weeks earlier than that by resident rainbow trout. Spawning sites selected by steelhead were in deeper water and had larger substrate than those selected by resident rainbow trout. We conclude that steelhead and resident rainbow trout in the Deschutes River are reproductively isolated based on a combination of spatial and temporal segregating mechanisms.

## INTRODUCTION

The term “partial migration” describes the phenomenon of populations divided into migratory and non-migratory or resident individuals (Jonsson and Jonsson 1993). A variety of animal taxa from insects to birds and fish exhibit this phenomenon (Snyder and Dingle 1990; Berthold 1991; Wood 1995). Resident and migratory forms of a species may represent “ecophenotypes” within a single gene pool or they may represent reproductively isolated populations.

Several species of salmonids exhibit partial migrations. Within such populations, migratory behavior is diverse and well documented (Gross 1987; Thorpe 1987; Northcote 1992). Migrations range from relatively short migrations between streams and lakes to long distance migrations to the open ocean. Rainbow trout (*Oncorhynchus mykiss*; Neave 1944), coastal cutthroat trout (*O. clarki clarki*; Zimmerman et al. 1997), sockeye salmon (*O. nerka*; Wood 1995), Atlantic salmon (*Salmo salar*; Verspoor and Cole 1989), brown trout (*S. trutta*; Skaala and Nævdal 1989) and arctic charr (*Salvelinus alpinus*; Nordeng 1983) exhibit dual or multiple life-history forms that may reside in the same stream.

Footo et al. (1989) identified three possible genetic relationships between life history forms. First, alternative life history forms are genetically isolated and represent separate populations. Second, alternative life history forms are not genetically distinct. Third, alternative life history forms are genetically distinct within a local area but are more similar to one another than they are to their respective forms outside of the local area. Understanding the relation of sympatric life history forms is critical to the study and management of such species.

Genetic divergence of populations requires reproductive isolation, which can result from barriers that isolate the populations or from the spatial or temporal separation of spawning activity. Leider et al. (1984) found evidence of reproductive isolation between the wild components of sympatric ecotypes (summer and winter runs) of steelhead (*O. mykiss*), the migratory form of rainbow trout. Although some gene flow between the populations occurred, they concluded temporal segregation of spawning led to reproductive isolating mechanisms that were sufficient to maintain the racial identity of the populations. In a study of brown trout, Baglinière et al. (1989) found spatial separation of spawning between resident and migratory populations in a small stream in France. This segregation of spawning habitat did not lead to reproductive isolation because the progeny of resident and migratory spawners could contribute to either life history form.

Rainbow trout are native to western North America from northwest Mexico to the Kuskokwim River, Alaska (Scott and Crossman 1973). Resident and migratory life histories have been described throughout this range. The anadromous form, or steelhead, spawns in streams or rivers with access to the ocean. Juvenile steelhead rear in freshwater habitats for one to three years before migrating to the ocean. After one to three years, the adult steelhead returns to freshwater to spawn. Resident rainbow trout remain in freshwater throughout the life cycle.

The relationship of migratory and resident forms of rainbow trout has long confused biologists. Variation in appearance, behavior (including migratory differences) and morphology led to their original classification as different species (Jordan and Evermann 1905; Behnke 1992).

The purpose of this study was to determine the extent of segregation in timing and use of spawning habitat by sympatric steelhead and resident rainbow trout in the Deschutes River,

Oregon. Understanding the temporal and spatial use of spawning habitat provides an indication of potential reproductive isolation between the two life history forms. Combined with evidence concerning the heritability of migratory behavior, such evidence can be used to determine reproductive isolation between life history forms of rainbow trout.

## METHODS

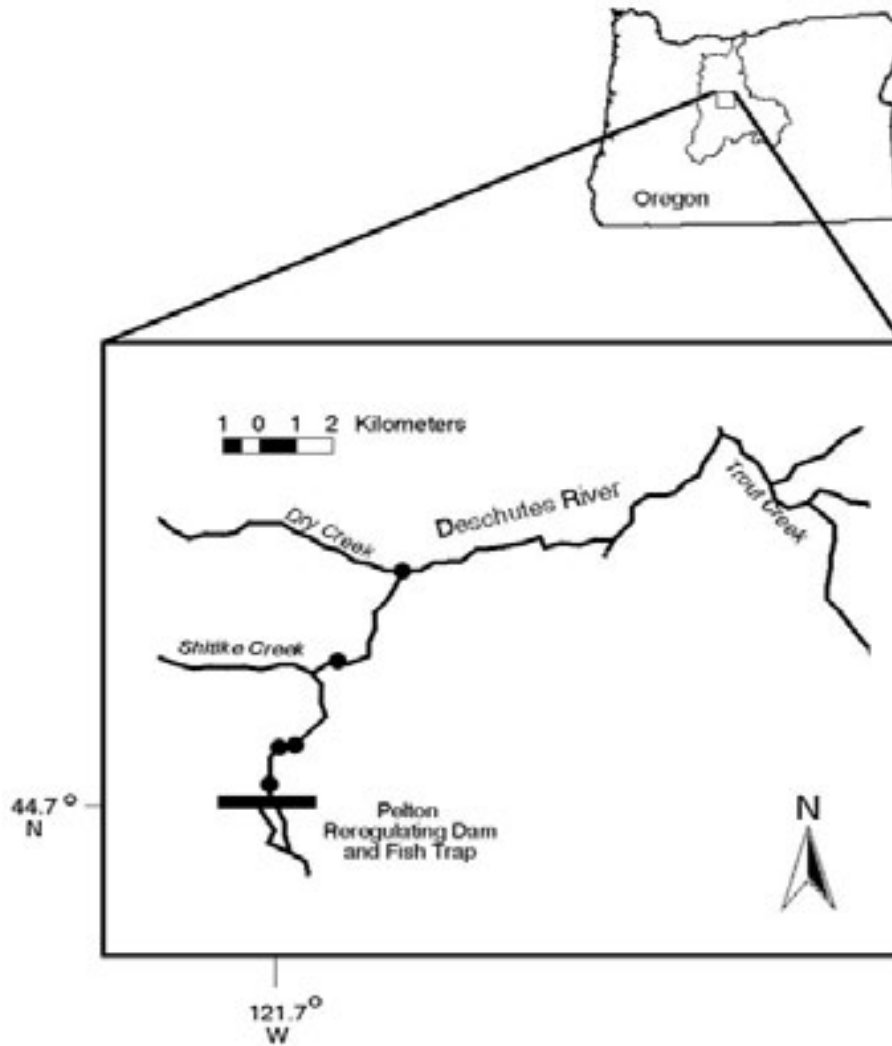
### Study Area

The Deschutes River (44° 40' N 120° 57' W) is a tributary to the Columbia River and drains 26,700 km<sup>2</sup> of north central Oregon (Figure 3-1). The Deschutes River is well known for its stability of flow, which is more uniform than any other river of its size (Henshaw et al. 1914). Flows in the study area are controlled by dams and ranged from 115 m<sup>3</sup>·s<sup>-1</sup> to 179 m<sup>3</sup>·s<sup>-1</sup>. Average gradient is 0.2% (McClure 1997).

Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead once inhabited much of the basin, but since 1968 have been limited by the Pelton-Round Butte Dam complex to the lower 160 km. The lower Deschutes River supports populations of spring and fall chinook salmon, steelhead, rainbow trout, mountain whitefish (*Prosopium williamsoni*), bull trout (*Salvelinus confluentus*), northern pikeminnow (*Ptychocheilus oregonensis*), suckers (*Catostomus* spp.), speckled dace (*Rhinichthys osculus*), and sculpins (*Cottus* spp.).

This study focused on the 21 km of mainstem river between the Pelton Reregulating Dam at river km 160 and the Trout Creek campground at river km 139 (Figure 3-1). Through this reach, the river averages 67 m in width (Huntington 1985). During 1995, the entire 21 km of river was examined. The study area was subsequently limited to five study sites because a large number of rainbow trout redds were encountered. Five island-associated side channels ranging in length from 45m to 225m and in width from 5m to 20m were chosen for direct examination of spawning. The five selected sites contained 68% of all steelhead redds constructed during 1995. We concluded that they adequately represented the spawning habitats of the two life history forms. Helicopter surveys in 1995 and 1996 did not indicate any significant aggregations of

steelhead spawning occurring outside the five study sites. Only one additional steelhead redd was observed during the 1995 helicopter survey that had been missed in stream surveys.



**Figure 3-1.** Location of study area for spawning surveys, Deschutes River, Oregon. Study sites are identified with solid dots.

## Spawning Surveys

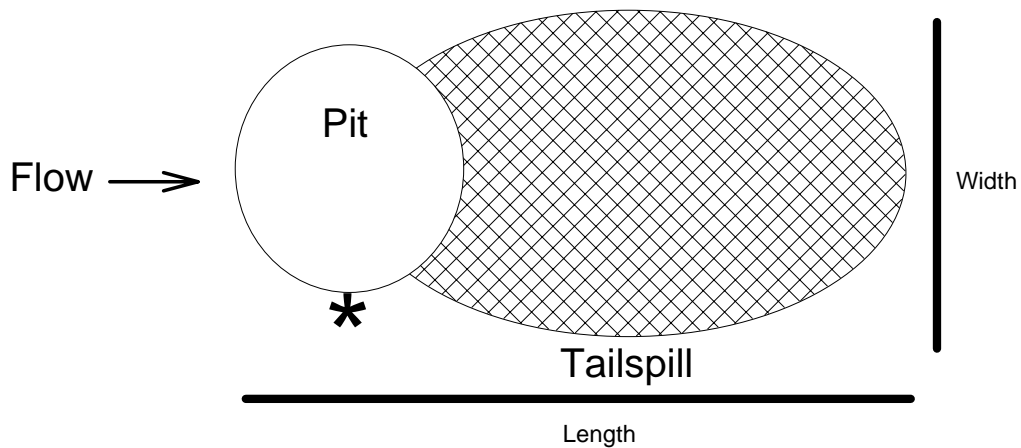
Spawning surveys were made weekly in 1995, 1996, and 1997. Surveys began in the second week in March and continued until the cessation of spawning, which was generally the second week of August. We made periodic examinations of the study reach prior to the start of data collection to determine if spawning began earlier, but none was observed prior to the second week of March.

The observer walked upstream through the study site and mapped the location of all new redds. The origin of redds (steelhead or rainbow trout) was determined based on sightings of fish in the vicinity of the redd or based on the size of the redd. Steelhead and resident rainbow trout observed adjacent to redds or actively spawning were identified based on coloration, body shape, and size. Steelhead were larger, more fusiform, and had less spotting than resident rainbow trout. Average length of adult steelhead in the Deschutes River ranges from 61 to 69 cm (Olsen et al. 1994). Adult rainbow trout range from 16 cm to 50 cm, with over 70% of the population ranging between 20 cm and 35 cm. (Schroeder and Smith 1989). On each spawning survey, new redds and locations of fish were recorded on maps of each site. New redds were identified by the presence of actively spawning fish or by coloration of the substrate and algae growth. Gravel in new redds was cleaner and brighter than that in older redds or where there were no redds. Within one week, growth of periphyton and settlement of fine sediment would change the color of the redd. By observing known redds on a daily and weekly basis, a practiced observer could gauge the age of unknown redds based on these characteristics. To examine temporal distribution of spawning, the percent of total redds constructed by each life history form was plotted against week. A Kolmogorov-Smirnov two-sample test was used to determine the significance of differences in the timing of steelhead and rainbow trout spawning by comparing the cumulative frequency distributions within each year.

## Microhabitat Measurements of Redd Sites

To describe microhabitat features of the location of redds used by spawning steelhead and resident rainbow trout, we measured water depth, water velocity over redd, and estimated gravel size in the tailspill of redds. For this portion of the study, a redd was identified as either a steelhead or resident rainbow trout redd based on the presence of actively spawning fish or single females holding in the water column over the redd, and only redds that could be positively

identified to life history type were included. All positively identified steelhead redds were measured, and a stratified sample of positively identified resident rainbow trout redds were measured. A total of 28 steelhead redds and 52 resident rainbow trout redds were examined over the three years of the study. We measured water depth and velocity at the upstream edge of the redd pit (Figure 3-2). Water depth was measured to the nearest 1 cm with a wading staff. We measured water velocity at 60% of water depth to the nearest  $1 \text{ cm}\cdot\text{s}^{-1}$  using an electromagnetic current meter. Size of gravel in the tailspill was estimated by measuring the predominant size of material in the surface layer of the tailspill. To confirm that the use of redd size was appropriate in the identification of unknown redds, the length of each positively identified redd was measured from the upstream edge of the pit to the most downstream edge of the tailspill, and the width of the redd was measured at the widest cross section perpendicular to the flow (Figure 3-2).



**Figure 3-2.** Plan form view of a redd illustrating length and width measurements. Asterisk represents point where depth and velocity measurements were taken.

One-way analysis of variance was used to determine the significance of differences in mean characteristics of steelhead and rainbow trout redds. Step-wise discriminant function analysis was performed to describe the association of depth, water velocity, and substrate size in the selection of redd sites by the two life history forms.

## RESULTS

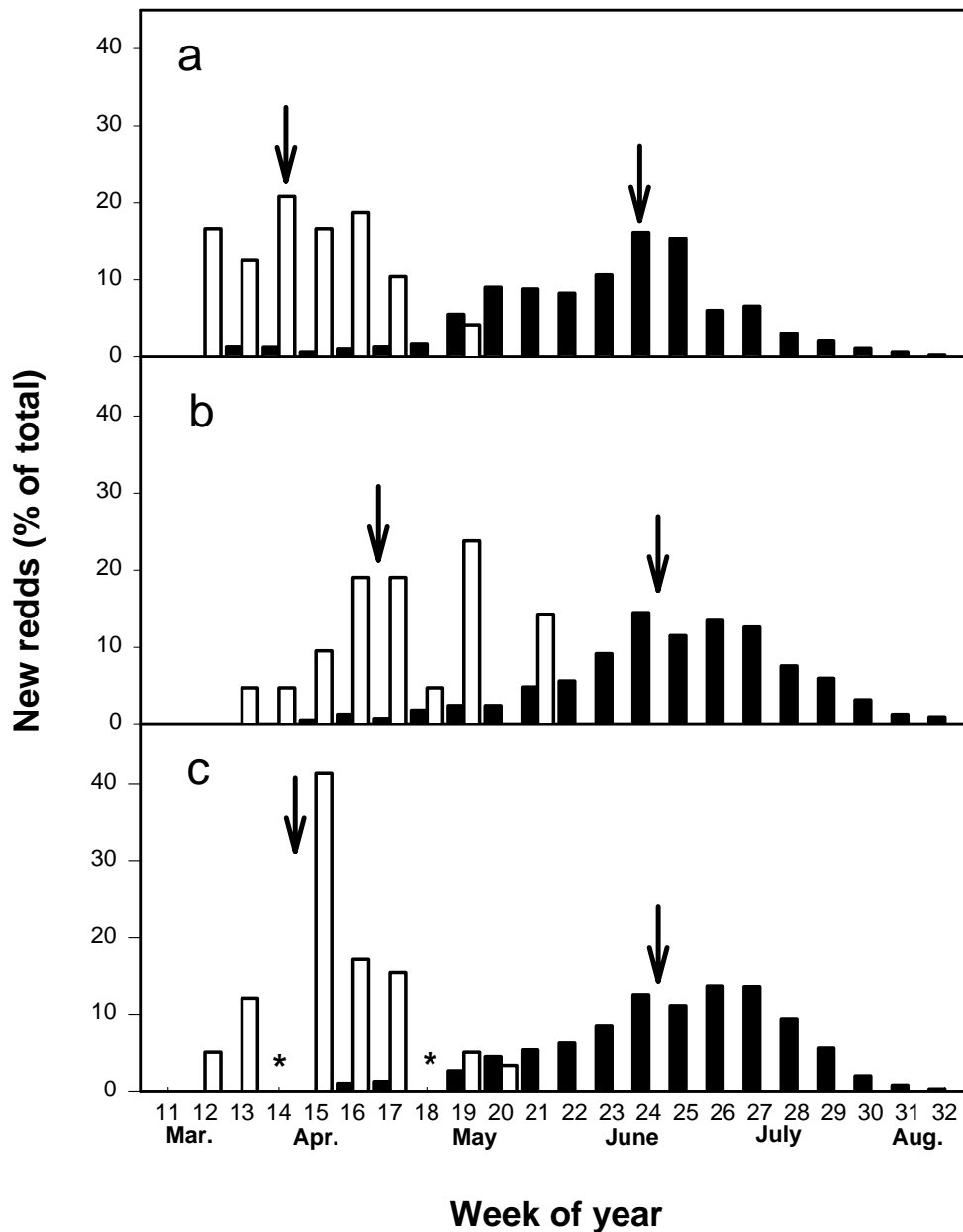
### Timing and Duration of Spawning

The total numbers of steelhead redds observed ranged from 21 to 58 in the five study sites (Table 3-1). Total numbers of rainbow trout redds ranged from 1241 to 1504 (Table 3-1). Steelhead and resident rainbow trout spawning began about the same time, but the spawning period was shorter for steelhead than it was for resident rainbow trout. Steelhead spawning occurred between the middle of March and the end of May, and trout spawning occurred between the end of March and the end of August. Only 9 to 15% of the total resident rainbow trout redds were observed during the period of steelhead spawning. The time of 50% spawning by steelhead occurred during week of year 14, 16, and 14 in 1995, 1996, and 1997, respectively (Figure 3-3). The time of 50% spawning by resident rainbow trout occurred during week of year 23 in 1995 and 24 in 1996 and 1997 (Figure 3-3). The distribution in time of steelhead and rainbow trout spawning was significantly different in all three years (Kolmogorov-Smirnov two-sample test;  $P < 0.0001$ ).

**Table 3-1.** Number of new redds identified by week in five study sites, Deschutes River.

	Week of Year	1995		1996		1997	
		Steelhead Redds	Rainbow Redds	Steelhead Redds	Rainbow Redds	Steelhead Redds	Rainbow Redds
<b>March</b>	11	0	0	0	0	0	0
	12	8	0	0	0	3	0
	13	6	18	1	2	7	0
<b>April</b>	14	10	17	1	2	*	*
	15	8	8	2	7	24	0
	16	9	14	4	18	10	14
	17	5	18	4	10	9	17
	18	0	23	1	28	*	*
<b>May</b>	19	2	79	5	37	3	34
	20		129	0	37	2	57
	21		126	3	73		68
	22		118		85		79
<b>June</b>	23		152		138		106
	24		231		218		157
	25		219		173		138
	26		86		203		171
<b>July</b>	27		94		190		170
	28		43		114		117
	29		29		90		71
	30		15		48		26
<b>August</b>	31		8		18		11
	32		3		13		5
	33		0		0		0
Total		48	1430	21	1504	58	1241

\* = no survey due to high flows



**Figure 3-3.** Percent of total redds observed by week of year, Deschutes River, Oregon, (a) in 1995, (b) in 1996, and (c) in 1997. Clear bars are steelhead redds, and solid bars are resident rainbow trout redds. Arrows indicate timing of 50% spawning, and asterisks indicate lack of data due to high flows.

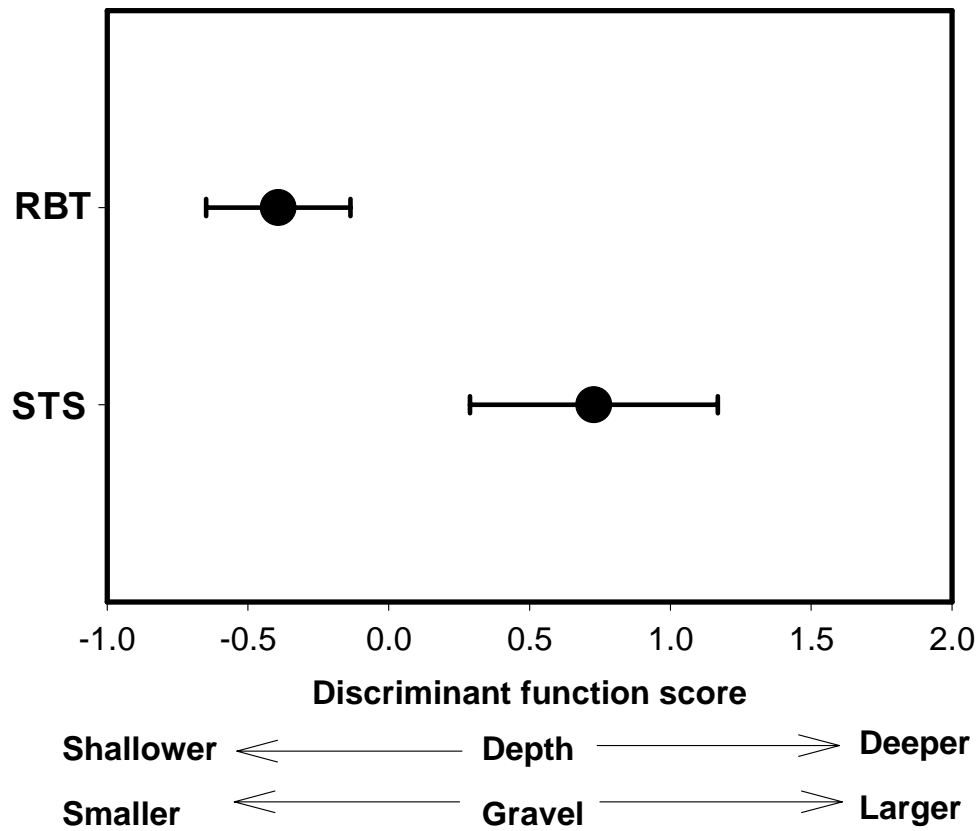
## Microhabitat Measurements

Steelhead and rainbow trout spawned in areas with different features. Steelhead redds were significantly larger than rainbow trout redds ( $P < 0.001$ ). Steelhead redds were in deeper water ( $P < 0.001$ ) and had larger substrate ( $P < 0.001$ ) than rainbow trout redds (Table 3-2). However, there was no difference ( $P > 0.05$ ) in the water velocity over steelhead or rainbow trout redds (Table 3-2).

**Table 3-2.** Mean characteristics (standard error) and one-way analysis of variance of 28 steelhead and 52 rainbow trout redds, Deschutes River, Oregon.

Variable	Steelhead	Rainbow	F-ratio	P-value
Depth (cm) adjacent to pit	54.07 (2.74)	42.58 (1.89)	3.51	0.0007
Mean velocity (cm·s <sup>-1</sup> ) adjacent to pit	71.43 (3.41)	63.35 (2.51)	1.43	N.S.
Gravel Size (mm) in tailspill	32.50 (1.98)	25.10 (1.11)	3.53	0.0007
Redd Length (m)	2.08 (0.14)	1.50 (0.05)	4.77	0.00001
Redd Width (m)	1.18 (0.11)	0.83 (0.03)	3.81	0.0003

Step-wise discriminant function analysis indicated that depth and substrate size contributed significantly to separation of steelhead and resident rainbow trout redds (Figure 3-4). One-way analysis of variance indicated significant differences between steelhead and resident rainbow trout for the first discriminant function ( $F_{1,78} = 22.866$ ,  $P < 0.0001$ ). The first discriminant function accounted for 100% of the variation. Wilks'  $\lambda$ , a measure of the function's discriminating power, was 0.7733 ( $P < 0.001$ ). Depth and gravel size in the tailspill was positively correlated ( $P < 0.01$ ) with the discriminant scores. Reclassification of redds by the discriminant function correctly identified 64% of steelhead redds and 72% of resident rainbow trout redds.



**Figure 3-4.** Means and 95% confidence intervals on the discriminant function for microhabitat characters used by steelhead and resident rainbow trout in the Deschutes River, Oregon.

## DISCUSSION

Given the temporal and spatial distribution (as measured by microhabitat characteristics) of spawning by steelhead and resident rainbow trout, we conclude that steelhead and resident rainbow trout in the Deschutes River constitute reproductively isolated populations. There is a weak overlap in the timing of spawning but spatial segregation appears to reinforce reproductive isolation. If steelhead gave rise to resident morphs and vice versa, we could not conclude that reproductive isolation was evident.

Zimmerman (in prep.), using otolith microchemistry, has confirmed that the adult population of steelhead does not include individuals of resident rainbow trout maternal origin and the adult population of resident rainbow trout does not include individuals of steelhead maternal origin.

Reproductive isolation among sympatric life history morphs of the same species has been described for kokanee (Kurenkov 1978), brown trout (Baglinière et al. 1989; Skaala and Nævdal 1989), and Atlantic salmon (Verspoor and Cole 1989). The two forms of kokanee described by Kurenkov (1978) were reproductively isolated within a single lake. Spawning by the two populations was spatially and temporally segregated, and the two populations exhibited trophic and morphologic differences. In locations where spawning by the two forms was spatially overlapping, there was a temporal segregation of spawning. Baglinière et al. (1989) also described spatial segregation of spawning by anadromous and resident brown trout based on the location of spawning locations and the distribution of tagged fish.

In addition to temporal and spatial segregation of spawning, assortative mating has the potential to reinforce the limitation of gene flow between life history forms of a species if the forms are of different sizes. Foote and Larkin (1988) determined that assortative mating served to reproductively isolate sockeye salmon and kokanee (*O. nerka*). During this study, only two instances of spawning activity between steelhead and resident rainbow trout were observed. Both instances occurred on the same day, one week after any other steelhead were observed spawning in the study sites. Steelhead adults captured in the Pelton Fish Trap (located at the Reregulating Dam; Figure 3-1) were released back into the river after sitting in the trap for at

least three weeks. One day after being released in the river, they were observed spawning with rainbow trout. Generally, steelhead spawning occurred at night and resident rainbow trout spawning occurred during the day.

Reproductive isolation between life history forms has been described in other fish families. For example, Snyder and Dingle (1990) investigated threespine stickleback (*Gasterosteus aculeatus*) populations from the Navarro River, California. This species was divided into a freshwater resident population that migrated <5 km and spawned in small tributaries. An anadromous population migrated between the estuary and spawned in lower reaches of the mainstem Navarro River. Rearing experiments indicated that life history (freshwater resident vs. anadromous) was genetically based. Taylor and Bentzen (1993) used molecular genetic evidence to determine reproductive isolation between sympatric “normal-sized” and “dwarf-sized” rainbow smelt (*Osmerus mordax*) in a New Brunswick lake. Taylor and Bentzen (1993) argued that, given the molecular evidence of reproductive isolation coupled with strong morphological and ecological differences, the two forms of smelt were behaving as distinct species. Bernatchez et al. (1996) described a similar reproductive isolation among whitefish (*Coregonus clupeaformis*) trophic ecotypes in Yukon lakes. Bernatchez et al. (1996) suggested that the molecular data corroborated previous genetic and ecological studies demonstrating reproductive isolation between sympatric trophic ecotypes of whitefish.

Reproductive isolation may lead to genetic divergence among sympatric populations under different selection regimes. The selective pressure experienced by anadromous and nonanadromous individuals are probably very different and would be expected to lead to genetic differences between the two forms (Foote et al. 1989). There has been very little work done to examine the relationship of sympatric steelhead and resident rainbow trout, and results of the few studies vary. Neave (1944) examined steelhead and rainbow trout from the Cowichan River in British Columbia and identified significant differences in meristic characters. These differences were maintained in experimental conditions, leading Neave to conclude that the differences were hereditary and the two life history forms (steelhead and resident rainbow trout) should be treated as two different species. On the other hand, Savvaitova et al. (1997) concluded that the three life history forms (resident, estuary migrating, and anadromous) of rainbow trout present in the Utkholok River of western Kamchatka represented one interbreeding population. Given the

disparity in results among locations, it is likely that the population structure is not species specific but, rather, dictated by a combination of environment conditions, phylogeny, and genetics.

Many studies examining reproductive isolation among life history forms of the same species, however, have inferred reproductive isolation based solely on genetic analyses or conjecture. Verspoor and Cole (1989), for example speculated that temporal and spatial segregation of spawning lead to genetic differentiation between resident and anadromous populations of Atlantic salmon in Newfoundland, Canada. On the other hand, Ryman et al. (1979) found little detectable genetic differentiation between brown trout populations that were assumed to be reproductively isolated. Although reproductive isolation may have led to or maintained the differences observed by Verspoor and Cole (1989), occurrence of isolation should be independently corroborated. Use of indirect measures of reproductive isolation among life history forms should not be considered the final arbiter. Spatial and temporal segregation or assortative mating should also be used to identify the presence and degree of reproductive isolation.

The present population structure of *O. mykiss* in the Deschutes River may have derived in two ways. First, multiple life history forms may be derived in sympatry. Skúlason et al. (1996) describe four morphs of Arctic charr from Thingvallavatn in Iceland exhibiting trophic specialization including benthivory, piscivory, and planctivory. Skúlason and Smith (1995) suggest that such polymorphism can lead to divergence of populations. In their analysis of the role of resource polymorphism in speciation, they include behavioral polymorphism such as residency and anadromy. In any case, divergence of populations requires reproductive isolation between sympatric morphs. In the Arctic charr, reproductive isolation occurred as a result of spatial and temporal segregation of spawning between morphs (Skúlason et al. 1996).

Alternatively, the present population structure may be the result multiple invasions of the Deschutes River basin by *O. mykiss*. This scenario is supported by the genetic evidence presented by Currens et al. (1990) of rainbow trout the Deschutes River in Oregon. Currens et al. (1990) identified significant differences in rainbow trout above and below barriers and suggested these differences were likely the result of multiple invasions of the Deschutes Basin by

different populations of *O. mykiss*. Currens (1997) suggests that the genetic structure of *O. mykiss* in the Pacific Northwest is the result of isolation and recolonization of new habitats from different refugia since Pleistocene ice receded. Such isolation and recolonization may have occurred repeatedly in the Deschutes Basin. Recent geologic evidence suggests that within the last 30,000 years, multiple large landslides created temporary impoundments in the Deschutes Basin that may have persisted several hundred years (Gordon Grant, USFS PNW Research Station, Corvallis, Oregon, pers. comm.). These impoundments may have isolated populations of *O. mykiss* with later recolonization by anadromous populations. In those populations that were isolated above the impoundment, selective pressures may have selected against migrants. Following breaching of the impoundment, it is likely that anadromous populations would have recolonized the basin. Such a scenario provides a possible explanation of the multiple life history forms with reproductive isolation observed in the Deschutes River.

The population structure of steelhead and resident rainbow trout in the Deschutes River, Oregon is characterized by reproductively isolated populations. We do not suggest that rainbow trout and steelhead populations are reproductively isolated in all locations. Rather, we have described one situation in one location. Further research is warranted throughout the range of steelhead to document the population structure in other populations.

Describing the degree of reproductive isolation between sympatric life history forms of the same species is critical in the definition of units of conservation and management (Waples 1995). Whether sympatric life history forms are managed as single populations exhibiting polymorphism or as reproductively isolated populations has profound implications in decisions related to protection and recovery of species. For example, in considering the status of coastal cutthroat trout in the North Umpqua River in Oregon, the resident and sea-run forms were treated as one single unit (Waples 1995) under the assumption that both life history forms could give rise to the other. This would not be appropriate for Deschutes River steelhead and resident rainbow trout, which, given the segregation of spawning habitat and potential reproductive isolation, should be treated as two species. As a result, there is little chance that resident rainbow trout can contribute to the recovery of steelhead in the Deschutes River. In locations where steelhead and resident rainbow trout are not reproductively isolated, recovery of one life history form of the population from the other life history form may be a possible conservation strategy.

## ACKNOWLEDGMENTS

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**Chapter 4: Timing of Emergence and Size of Fry at  
Emergence of Steelhead and Resident Rainbow Trout  
(*Oncorhynchus mykiss*) in the Deschutes River, Oregon.**

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## ABSTRACT

The timing of emergence and size of fry at emergence was determined for steelhead and resident rainbow trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon. Traps placed over redds of known origin were used to capture fry emerging from the gravel. There was an overlap in the timing of steelhead and resident rainbow trout emergence. There was no apparent size difference between newly emerged steelhead and resident rainbow trout.

## INTRODUCTION

Steelhead and resident rainbow trout (*Oncorhynchus mykiss*), like other salmonids, spawn in gravel nests constructed by the female in streams and rivers. In the Deschutes River, Oregon, steelhead spawning occurs from mid-March through mid-May, and resident rainbow trout spawning occurs from mid-March through mid-August (Zimmerman and Reeves 1999a). In spite of this overlap in the timing of spawning by steelhead and resident rainbow trout in the Deschutes River, Zimmerman and Reeves (1999a) concluded that spatial and temporal segregation led to reproductive isolation between the two life history forms.

The size of fry at emergence may influence the outcome of competitive interactions (Mason and Chapman 1965; Chandler and Bjornn 1988) with larger fry dominating. Fry that emerge first have a theoretical advantage in obtaining optimum habitat because they not only arrive first, but have a size advantage by the time later fry emerge (Mason and Chapman 1965; Chandler and Bjornn 1988). On the other hand, fish that spawn early (and hence produce early emerging fry) could encounter harsher environments (i.e., temperatures and flows) upon emergence (Leider et al. 1986).

The timing of emergence and size at emergence is unknown for steelhead and rainbow trout in the Deschutes River. Previous attempts to trap emerging fry in the Deschutes River were unsuccessful because of trap design and algal growth (Aney et al. 1967). Aney et al. (1967) did not attempt to trap fry from natural redds, and in 18 artificial redds constructed under emergence traps, only 9 emergent fry were collected.

The purpose of this study was to describe the timing of emergence and size of fry at emergence of steelhead and resident rainbow trout in the mainstem Deschutes River between the Pelton Reregulating Dam and the Trout Creek Campground. Understanding the dynamics of emergence timing and behavior of newly emerged fry provides important information concerning interactions and habitat use by juvenile steelhead and resident rainbow trout.

## METHODS

Emergence traps were constructed according to the plans of Porter (1973) and consisted of a metal frame with a canvas and net liner that terminates in a live-box (Figure 4-1). The metal frame and fabric liner is placed over the suspected location of the egg pocket and all emerging fry are contained by the fabric and diverted into the live-box.



**Figure 4-1.** Redd trap as constructed over a resident rainbow trout redd.

Redd traps are difficult to construct in high velocity flows or deeper water. Therefore, during weekly spawning surveys, when redds were encountered in areas that were conducive to trap construction, the redd was flagged and a trap was installed the following day. Traps were installed as soon as possible to limit superimposition by other fish. The traps were then visited at least once every three days to clean algae from the net and monitor for the beginning of emergence. After the initiation of emergence, traps were visited at least every other day. All fry captured were measured to the nearest millimeter and released, with the exception of the first four fry, which were collected for otolith analysis to confirm origin of the redd (steelhead v. rainbow trout). Dead fry and fry killed in the process of netting from the live-box were also collected.

The timing and duration of emergence were plotted to compare the timing of emergence between steelhead and rainbow trout. The size of fry was compared using one-way analysis of variance.

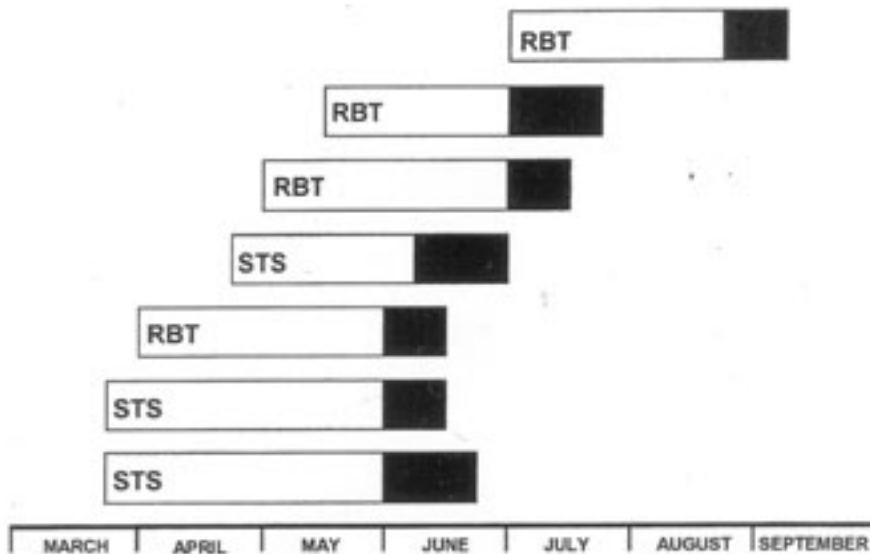
## RESULTS

Emerging fry were collected in 10 of the 18 traps constructed in 1995 and 1996 (Table 4-1). There was a significant overlap in the timing of emergence during 1995 (Figure 4-2), which was similar to the overlap in timing of spawning between steelhead and rainbow trout.

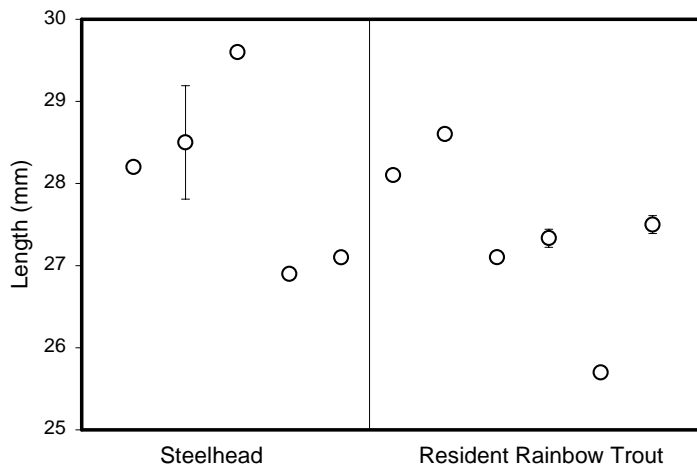
There were significant differences among traps in the length of emerging fry during 1995 ( $F_{7,508} = 58.349$ ;  $p < 0.0001$ ). It does not appear, however, that there is a difference in length between steelhead and rainbow trout (Figure 4-3).

**Table 4-1.** Location of emergence traps (river mile and side of river), date redd constructed, life-history form, number of fry captured, and mean size of fry, Deschutes River, Oregon.

Location	Date Spawned	Life History	Fry Captured	Mean Length (mm)
94.2L	22 March 1995	STS	179	28.2
94.2L	22 March 1995	STS	4	28.5
99.0R	28 March 1995	RBT	85	28.1
99.0R	06 April 1995	STS	32	29.6
94.2L	19 April 1995	STS	20	26.9
94.9R	02 May 1995	RBT	39	28.6
94.2L	09 May 1995	RBT	145	27.1
99.0R	13 May 1996	STS	99	27.1
96.4R	10 May 1996	RBT	41	25.7
96.4R	13 May 1996	RBT	5	27.5



**Figure 4-2.** Timing of incubation and emergence for steelhead (STS) and resident rainbow trout (RBT) from seven redds in 1995 in the Deschutes River, Oregon. The clear portion of the box represents incubation, and the solid portion represents emergence of fry from the redd.



**Figure 4-3.** Length and 95% confidence intervals of fry captured from steelhead and resident rainbow trout redds in the Deschutes River, Oregon, in 1995 and 1996.

## DISCUSSION

There is an overlap in the timing of emergence by steelhead and resident rainbow trout in the Deschutes River between Trout Creek and the Pelton Reregulating Dam. This overlap is similar to the overlap in the timing of spawning by steelhead and resident rainbow trout reported by Zimmerman and Reeves (1999a). We assumed that steelhead, which typically have larger eggs, would produce larger emerging fry. In laboratory experiments using steelhead and resident rainbow trout gametes from the Deschutes River, we did find that steelhead were slightly larger (Zimmerman and Reeves 1999b). The largest mean size of fry were from a steelhead redd, and the smallest were from a resident rainbow trout redd (Figure 4-3).

Given the overlap in timing of emergence and size of emerging fry, there is no competitive advantage due to prior residence or greater size to either steelhead or resident

rainbow trout. Steelhead fry from intermittent tributaries such as Tenmile Creek experience greater growth than those in the mainstem and may, therefore, experience a competitive advantage as they shift from tributary environments to the mainstem (Zimmerman 1999). In addition, innate differences in the behavior of recently emerged steelhead and resident rainbow trout may play an important role in the dynamics of juvenile habitat use (Zimmerman and Reeves 1999b).

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Zimmerman, C.E., and Reeves, G.H. 1999b. Behavior of steelhead and resident rainbow trout (*Oncorhynchus mykiss*) immediately following emergence. Report prepared for Portland General Electric, Portland, Oregon.

**Chapter 5: Differential Recruitment of Steelhead and Resident Rainbow Trout (*Oncorhynchus mykiss*) Fry Immediately Following Emergence**

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## ABSTRACT

Territoriality and levels of aggression were determined for sympatric steelhead and resident rainbow trout (*Oncorhynchus mykiss*) from the Deschutes River, Oregon. Steelhead and resident rainbow trout fry were introduced as emerging fry from redds within artificial stream channels. Three treatments were examined: steelhead alone, steelhead and resident rainbow trout, and resident rainbow trout alone. Treatments containing steelhead were characterized by higher levels of aggression, higher initial rates of emigration, and lower densities of fish at the conclusion of the 20-day experimental trials.

## INTRODUCTION

Territorial behavior plays an important role in population dynamics (Gordon 1997). Upon emergence from the gravel, juvenile salmonids such as steelhead and rainbow trout (*Oncorhynchus mykiss*) fry establish and defend territories (Chapman 1962). Elliot (1989) referred to the period directly following emergence as a “critical time” during which much of the initial population regulation occurred. This regulation is the result of territoriality of juvenile stream salmonids, which is mediated through aggressive behavior (Titus 1990). Fry which are unable to establish feeding stations drift downstream and may find another spot to establish a feeding territory or may be lost from the system.

Behavior in salmonids is variable and sometimes population specific. Olsén and Karlsson (1991) described differences in agonistic behavior between two allopatric populations of arctic charr (*Salvelinus alpinus*). One population was more territorial while the other formed shoals of less aggressive individuals. Swain and Holtby (1989) found that stream and lake rearing coho salmon (*Oncorhynchus kisutch*) exhibited both morphological and behavioral differences. The stream-rearing coho were more aggressive and characterized by a body shape that optimized burst swimming rather than prolonged swimming performance.

Differences in aggressive behavior and territoriality may play an important role in the relationship of migratory and non-migratory salmonids. Hutchinson and Iwata (1997) suggest

that aggression is positively correlated with length of stream residence. Hutchinson and Iwata (1997) characterized both steelhead and resident rainbow trout with high levels of aggression but found that resident rainbow trout were more aggressive than steelhead juveniles.

Steelhead and resident rainbow trout are sympatric in the lower Deschutes River, Oregon. Zimmerman (1999) suggested that steelhead and resident rainbow trout in the Deschutes River are reproductively isolated and should be treated as two species for management purposes. Zimmerman and Reeves (1999) described the spatial and temporal segregation in spawning by the two life history forms. In spite of this segregation, there is an overlap in the timing of emergence by steelhead and resident rainbow trout fry (Zimmerman and Reeves 1999). The purpose of this study was to compare behaviorally mediated population dynamics of newly emerged steelhead and resident rainbow trout.

## METHODS

The experimental fish were the progeny of wild steelhead and resident rainbow trout from the Deschutes River, Oregon. Eggs and milt were collected from wild steelhead and rainbow trout at the Pelton Fish Trap, located at river kilometer 160. The eggs and milt were transported to the Round Butte Hatchery in plastic bags, mixed, treated with iodine, and placed in incubation trays according to the standard hatchery procedures. The fertilized eggs from each life-history form (steelhead and rainbow trout) were divided into two groups and incubated separately. One group was incubated at ambient temperature and one in chilled water to allow for two experimental trials.

When the fry reached a size corresponding to emergence size, they were transported to Corvallis. Tests were conducted in two artificial streams (Reeves et al. 1983) located at the Forestry Sciences Laboratory. Each stream is oval, measuring 4.3 x 4.9 m on the sides, 0.76 m wide, and 0.61 m deep. The channels are set one above the other on metal frames. Black plastic curtains encircle the channels to restrict outside light and disturbance. Water temperature, duration and intensity of photoperiod, filtration, current velocity, and ultraviolet (UV) sterilization are regulated independently in each channel. Current velocity was maintained by a Plexiglas paddle wheel at 10 cm/s. The photoperiod was maintained by a timer that provided

15 h of light and 9 h of darkness. The light phase consisted of a 1.5-h morning during which lights gradually increased from zero to full intensity, 12 h of full intensity, and a 1.5-h evening during which intensity gradually dimmed to zero. Nine 60-W incandescent bulbs spaced at equal intervals around the channels were the sole source of light. Each channel segment was bounded on the downstream end by a Plexiglas trap, which trapped all fry emigrating from that channel segment. The channels were filled with deionized water 3 to 4 days before the fish were introduced and was continuously passed through a sand filter and UV sterilizer. Channels were drained, sterilized, and refilled between tests.

In Corvallis, the fry were divided into groups of 150 individuals and randomly allocated to experimental treatments (Table 5-1). In each treatment, one group was chosen by the flip of a coin to receive an alizarin complexone mark on the otolith. Immersion marking of fry was achieved by placing the fish in a solution of 50 mg/l of alizarin complexone for 4 h and the other fish in a water bath under identical conditions. A test batch of 20 fry was included in one marking tank to determine the proportion of fry showing the mark. After marking, the fry were introduced to the channels in plastic mesh boxes with lids. After 24 h, the lid was removed from the first box and after 48 h the lid was removed from the second box.

Frozen euphausiids were the sole food source. Daily rations were equal to 5% of the biomass of fry present in the channel. Food was delivered to each channel segment via a 2.5-cm-diameter PVC pipe that ran in a zigzag pattern along the entire area available to fish (Reeves et al. 1983).

Test periods were 20 days. On each day, the fry in each trap were removed and placed in alcohol. At the conclusion of the experiment, all fry remaining in the channel were removed. All fry were weighed, measured, and otoliths removed and examined for alizarine complexone marks. The number of fry remaining in the channel was assumed to reflect overall territoriality within each treatment under the assumption that each channel segment could only support a limited number of territories.

Rates of aggressive interactions were quantified during the second experiment. After emigration from all channel segments reached less than three individuals per day, an observer

randomly chose one fish immediately following feeding and counted all agonistic encounters between that fish and other fish. Agonistic encounters included chasing and nipping (Dill 1977).

**Table 5-1.** Experimental protocol for laboratory stream experiments. Shading indicates group receiving mark.

**Experiment I**

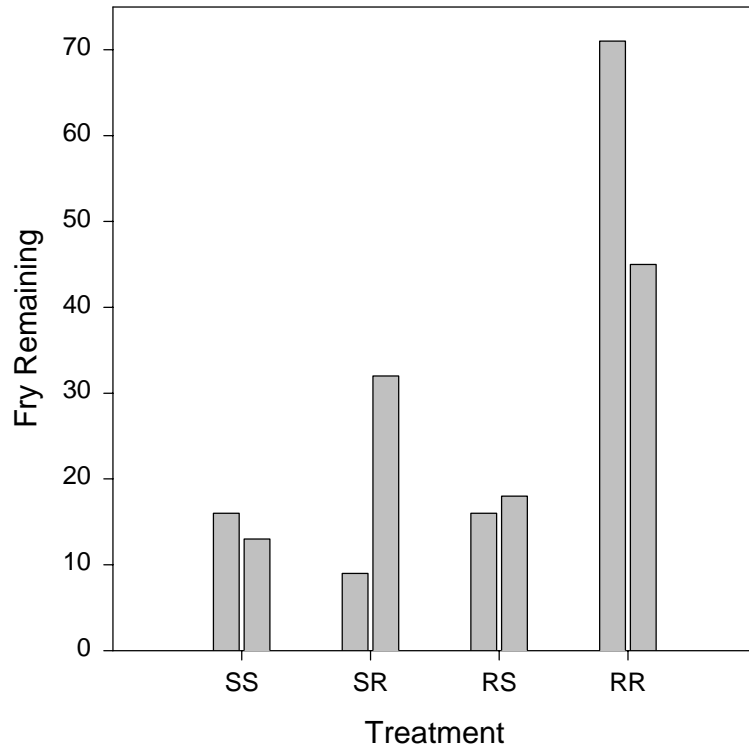
Cell	1st Introduction	2nd Introduction	Fry Remaining
1	Steelhead	Steelhead	16
2	Steelhead	Rainbow	9
3	Rainbow	Steelhead	16
4	Rainbow	Rainbow	71

**Experiment II**

Cell	1st Introduction	2nd Introduction	Fry Remaining
1	Rainbow	Rainbow	45
2	Steelhead	Steelhead	13
3	Rainbow	Steelhead	18
4	Steelhead	Rainbow	32

**RESULTS AND DISCUSSION**

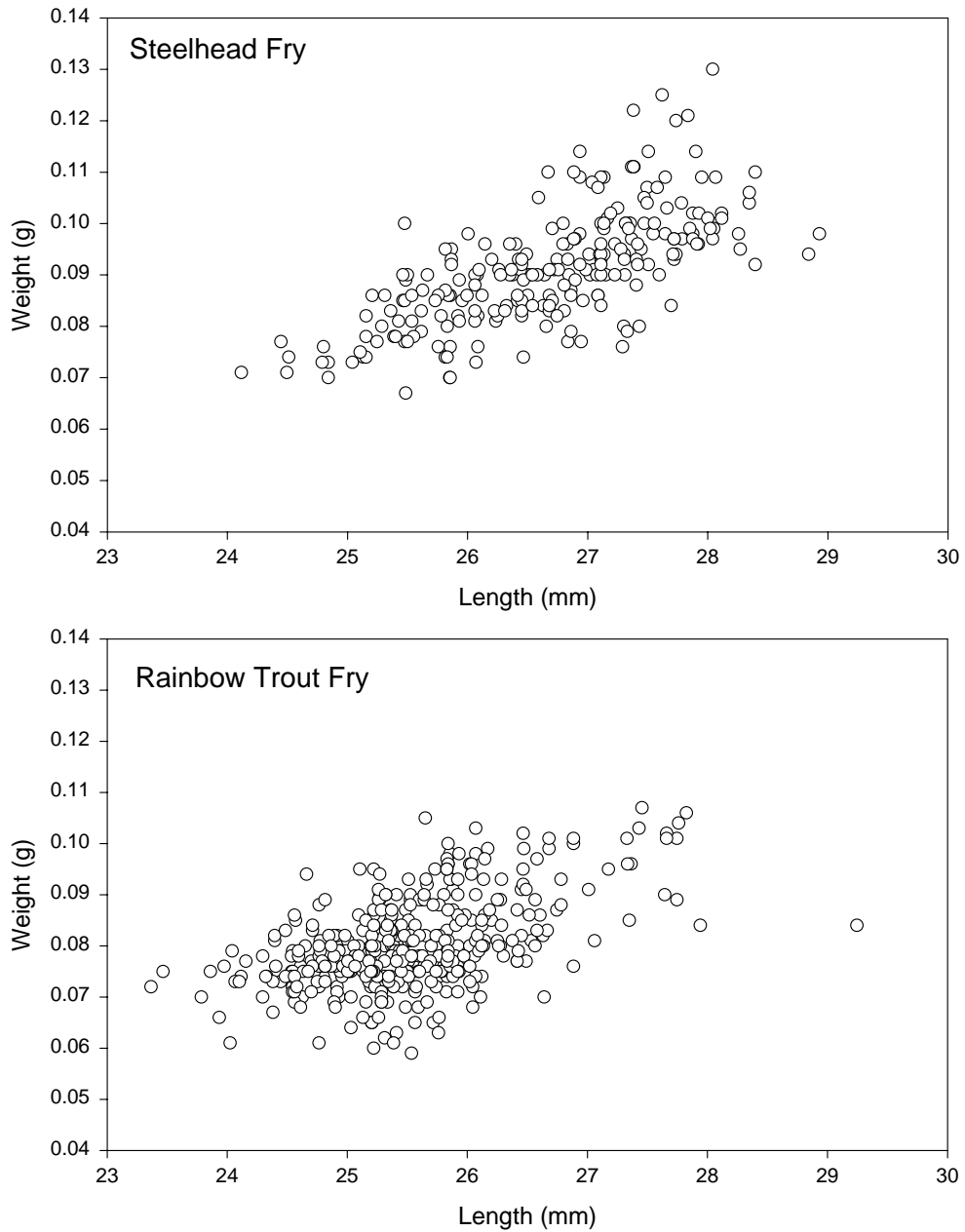
In all treatments containing steelhead, the number of fry remaining at the conclusion of the trial was much lower than in the rainbow only treatment (Figure 5-1). In treatments containing steelhead, fry were observed maintaining territories and exhibited aggressive behavior. In rainbow trout only treatments, the fry schooled in pool-like (slower water) habitats and showed no aggression. In treatments that contained steelhead, mean rates of aggression exhibited by individual fish ranged from 5.12 to 6.06 interactions per 10 min. The mean rate of aggressive interactions in the rainbow only treatment was 1.0 interactions per 10 min.



**Figure 5-1.** Number of fry remaining in channels at conclusion of the first (first bar) and second (second bar) experiment. The treatments are: SS steelhead followed by steelhead, SR steelhead followed by rainbow, RS rainbow followed by steelhead, and RR rainbow followed by rainbow.

The proportion of steelhead and resident rainbow trout fry remaining at the end of the trial in the mixed treatments was not consistently dominated by either life history form. Ratios of steelhead and rainbow trout fry were: 1:1, 2:7, 22:9, and 5:13.

In the first experiment, the mean length of all steelhead was 26.69 mm (s.d. = 0.85, n = 240) and the mean length of all rainbow trout was 25.51 mm (s.d. = 0.57, n = 420). The mean lengths and mean weights of the two life history forms were significantly different (two-tailed t-test,  $P < 0.001$ ) but there was an overlap in both weight and length (Figure 5-2).



**Figure 5-2.** Length and weight relationship of steelhead and resident rainbow trout fry at the conclusion of the first experiment.

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