

## AN ABSTRACT OF THE DISSERTATION OF

Christian E. Zimmerman for the degree of Doctor of Philosophy in Fisheries Science  
presented on May 5, 2000. Title: Ecological Relation of Sympatric Steelhead and  
Resident Rainbow Trout in the Deschutes River, Oregon.

Redacted for Privacy

Abstract approved: \_\_\_\_\_

Gordon H. Reeves

Sympatric steelhead and resident rainbow trout (*Oncorhynchus mykiss*) are known to exist in many rivers throughout the Pacific Rim. Whether sympatric steelhead and resident rainbow trout are polymorphisms within a single gene pool or two reproductively isolated populations has significant implications concerning the study and conservation of this polytypic species. I examined population structure and use of spawning and rearing habitats by steelhead and resident rainbow trout in the Deschutes River, Oregon. I used otolith microchemistry to determine the maternal origin (steelhead versus resident) of adult steelhead and resident rainbow trout based on Sr/Ca ratios in primordia and freshwater growth regions of otoliths. Only steelhead of steelhead origin and resident rainbow trout of resident origin were encountered. In the Babine River of British Columbia, however, steelhead of resident origin and resident rainbow trout of steelhead origin were present. Temporal and spatial segregation of spawning habitat served to limit breeding between steelhead and resident rainbow trout in the mainstem Deschutes River. The timing of 50% spawning by steelhead occurred 9 to 10 weeks earlier than by resident

rainbow trout. Steelhead spawning sites were deeper and of larger substrate than those used by resident rainbow trout. There was an overlap in the timing of emergence by steelhead and resident rainbow trout fry in the mainstem Deschutes River, but higher levels of aggression and territoriality characterize newly emerged steelhead fry.

Determination of maternal origin based on otolith microchemistry indicated that young-of-year *O. mykiss* in small hydrologically unstable tributaries to the Deschutes River were exclusively the progeny of steelhead. Progeny of resident rainbow trout numerically dominated mainstem-rearing habitats. Based on the degree of segregation between steelhead and resident rainbow trout, the two life history forms act as two separate species in the Deschutes River. This relationship has significant implications concerning the restoration and conservation of steelhead and resident rainbow trout. Where steelhead and resident rainbow trout constitute reproductively isolated populations, conservation of both life history forms within the species cannot be achieved unless both populations are maintained.

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Ecological Relation of Sympatric Steelhead and Resident Rainbow Trout in the  
Deschutes River, Oregon.

By

Christian E. Zimmerman

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Christian E. Zimmerman, Author

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# **Ecological Relation of Sympatric Steelhead and Resident Rainbow Trout in the Deschutes River, Oregon**

## **CHAPTER 1**

### **Introduction**

Many species are characterized by discrete resource polymorphisms (Skúlason and Smith 1995). These polymorphisms manifest in differences in morphological, behavioral, and life-history characteristics and have been observed in a variety of taxa (Skúlason and Smith 1995). In birds, resource polymorphisms are generally related to differences in feeding behavior or shape and size of bill (Goss-Custard and Ditt Durell 1983; Smith 1987) although differences in migratory behavior are also documented (Berthold 1991). Resource polymorphisms are particularly well documented in freshwater fish. Many lake species show adaptations related to benthivory, planktivory, or piscivory (Schluter and McPhail 1993; Taylor and Bentzen 1993; Skúlason et al. 1996). Migratory polymorphisms are also well documented in fish (McDowall 1987).

Migrations are costly and risky strategies but offer benefits including larger size at maturity and higher fecundity (Northcote 1992). Migration is, therefore, a trade-off between the benefits of increased fecundity and the costs of migration. Diadromous migrations between freshwater and ocean habitats are known in 28 families of fish (Gross et al. 1988). Diadromous migrations will only evolve

through natural selection if the migration results in a gain in fitness that exceeds the costs of migration (Gross 1987). Anadromous species are born in freshwater, migrate to the ocean, and return to freshwater to reproduce. Anadromy is more common in higher latitudes where ocean habitats are characterized by higher productivity than freshwater habitats (Gross et al. 1988) and thus result in larger size and higher fecundity. Many species are characterized by coexisting migratory and non-migratory phenotypes, which may result as a trade-off between productivity and difficulty of migration (Wood 1995).

The term "partial migration" describes the phenomenon of populations split into migratory and resident individuals (Jonsson and Jonsson 1993). In birds, for example, the seasonal migration between reproductive sites and wintering grounds may involve only a fraction of the population (Kaitala et al. 1993). Many fish species are similarly divided into resident and migratory morphs. Resident and migratory forms can represent "ecophenotypes" within a single gene pool or they each represent genetically distinct populations. Genetic differentiation between migratory and non-migratory morphs has been demonstrated in the European robin (*Erithacus rubecula*; Biebach 1983), threespine stickleback (*Gasterosteus aculeatus*; Snyder and Dingle 1989), sockeye salmon and kokanee (Foote et al. 1989), brown trout (*Salmo trutta*; Skaala and Nævdal 1989), and Atlantic salmon (Verspoor and Cole 1989). Many studies exist concerning the genetic and ecologic relation of sympatric migratory and non-migratory forms. These studies do not suggest a single explanation concerning the relationship of coexisting life

history forms exists. For example, Nordeng (1983) found that resident and migratory Arctic char arose from a single gene pool and growth rate was the single determining factor whether a fish migrated to sea or not. Sockeye salmon and kokanee within the same lake system are often genetically divergent but show more genetic similarity to one another than to their counterparts in neighboring lake systems (Taylor et al. 1996; Foote et al. 1989) suggesting that divergence between sockeye salmon and kokanee has occurred repeatedly and is evident in differing degrees of divergence. Wood et al. (1999) argued that sockeye salmon and kokanee in Takla Lake, British Columbia should be treated as separate biological species.

The relation of migratory and resident forms of rainbow trout (*O. mykiss*) has long confused biologists. Throughout the range of rainbow trout, populations of resident and migratory populations have been described (Behnke 1992). In many locations, multiple life history forms coexist and the relation of coexisting life history forms is unresolved. This "rainbow trout problem" (sensu Nordeng 1983) is evident in a sense of uncertainty concerning the management of coexisting life history forms of rainbow trout.

Several studies have attempted to identify racial differences between steelhead and resident rainbow trout or among seasonal ecotypes of steelhead. Neave (1944) concluded that hereditary differences existed between resident rainbow trout and steelhead in the Cowichan River, British Columbia based on differences in lateral line scale counts and rearing experiments. Chilcote (1976)



compared steelhead and resident rainbow trout from five locations within the lower Deschutes River, Oregon based on allele frequencies at 13 loci examined with protein electrophoresis. No significant genetic differences were observed with the exception of one headwater population of resident trout isolated above two waterfalls. Chilcote (1976), therefore, concluded that considerable interbreeding and gene flow occurred between Deschutes River steelhead and resident rainbow trout. Currens et al. (1990) reexamined the relationship of rainbow trout populations among locations within the Lower Deschutes River based on allele frequencies at 24 loci examined with protein electrophoresis and meristic analysis. Currens et al. (1990) and Currens (1987) did find genetic distinction between resident rainbow trout and steelhead isolated by barrier falls and suggested that resident rainbow trout may derive from either resident or anadromous forms although some isolation between these forms was detected. The relation between life history forms of *O. mykiss* has not been as thoroughly studied as in Arctic char, brown trout, or sockeye salmon and kokanee. As a result, uncertainty still remains concerning the "rainbow trout problem" and no one can write the "solution to the rainbow trout problem" as Nordeng (1983) was able to do for Arctic char.

The following six chapters summarize studies concerning sympatric steelhead and resident rainbow trout. Chapter 2 examines the contribution of steelhead and resident rainbow trout progeny to the adult spawning population of each life history form based on otolith microchemistry in the Deschutes River in Oregon and the Babine River in British Columbia. Chapter 3 focuses on the timing

and location of spawning by steelhead in and resident rainbow trout in the mainstem Deschutes River. Chapter 4 describes the size of emerging steelhead and resident rainbow trout fry and the timing of emergence and discusses possible ramifications of timing and size at emergence on later life history events. Chapter 5 describes laboratory experiments concerning the behavior and territoriality of newly emerged steelhead and resident rainbow trout from the Deschutes River. Chapter 6 examines the use and segregation of tributary and mainstem Deschutes River rearing habitats by steelhead and resident rainbow trout. Chapter 7 discusses the importance of steelhead and resident rainbow trout population structure on management and conservation of the diversity of life history forms that constitute *O. mykiss*.

## CHAPTER 2

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

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## Abstract

The population structure of sympatric anadromous steelhead and resident rainbow trout (*Oncorhynchus mykiss*) in the Deschutes River, Oregon and Babine River, British Columbia was determined 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 with a wavelength-dispersive electron microprobe. 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 may 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 relation between 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. When multiple life history forms reside sympatrically within the same stream, the situation becomes even more confusing.

Do resident and migratory forms represent "ecophenotypes" within a single gene pool or do they represent genetically distinct populations? Foote et al. (1989) identified three possible explanations for the 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.

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 temporal and spatial segregation may 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 some progeny of resident rainbow trout may migrate to sea and some progeny of steelhead might 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. 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.

Identification of the maternal origin (i.e., life history of the maternal parent: 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) compared otolith nuclear dimensions in steelhead and rainbow trout progeny in the Deschutes River, Oregon and found that nucleus length in steelhead was longer than in resident rainbow trout. Rybock et al. (1975) suggested that the method could be used on unknown juveniles to discriminate steelhead from resident rainbow trout. Currens et al. (1988) attempted to recreate the study, again in the Deschutes River, and found that the method did not reliably distinguish steelhead and resident rainbow trout.

Otolith microchemistry can be used to identify maternal origin based on examination of the ratio of strontium (Sr) and calcium (Ca). 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 ratio of Sr/Ca in the

environment (Kalish 1990). The ratio of Sr/Ca is generally greater in seawater compared to freshwater (Kalish 1990). Therefore, analysis 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. 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. In this study, Sr/Ca ratios in the primordia and freshwater growth regions were used to describe the maternal origin of adult steelhead and resident rainbow trout in the Deschutes River, Oregon and the Babine River weir area, British Columbia.

## Materials and Methods

### Otolith collection

Sagittal otoliths were collected from adult rainbow trout and steelhead in the Deschutes River, Oregon (44° 40' N 120° 57" W) and the Babine River weir area, British Columbia (54° 40' N 126° 00" W) (Fig. 2.1). Otoliths were collected from wild adult steelhead (n = 20) in the Deschutes River returning to the Pelton Fish Trap at river km 160 and from carcasses encountered during spawning surveys. Adult rainbow trout (n = 38) were collected from a 3 km segment of the riverbank 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.

Classification of adults as steelhead and resident rainbow was based on size and appearance. 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 steelhead lengths range from 48 cm to 80 cm with more than 90% of the population being greater than 54 cm. 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).



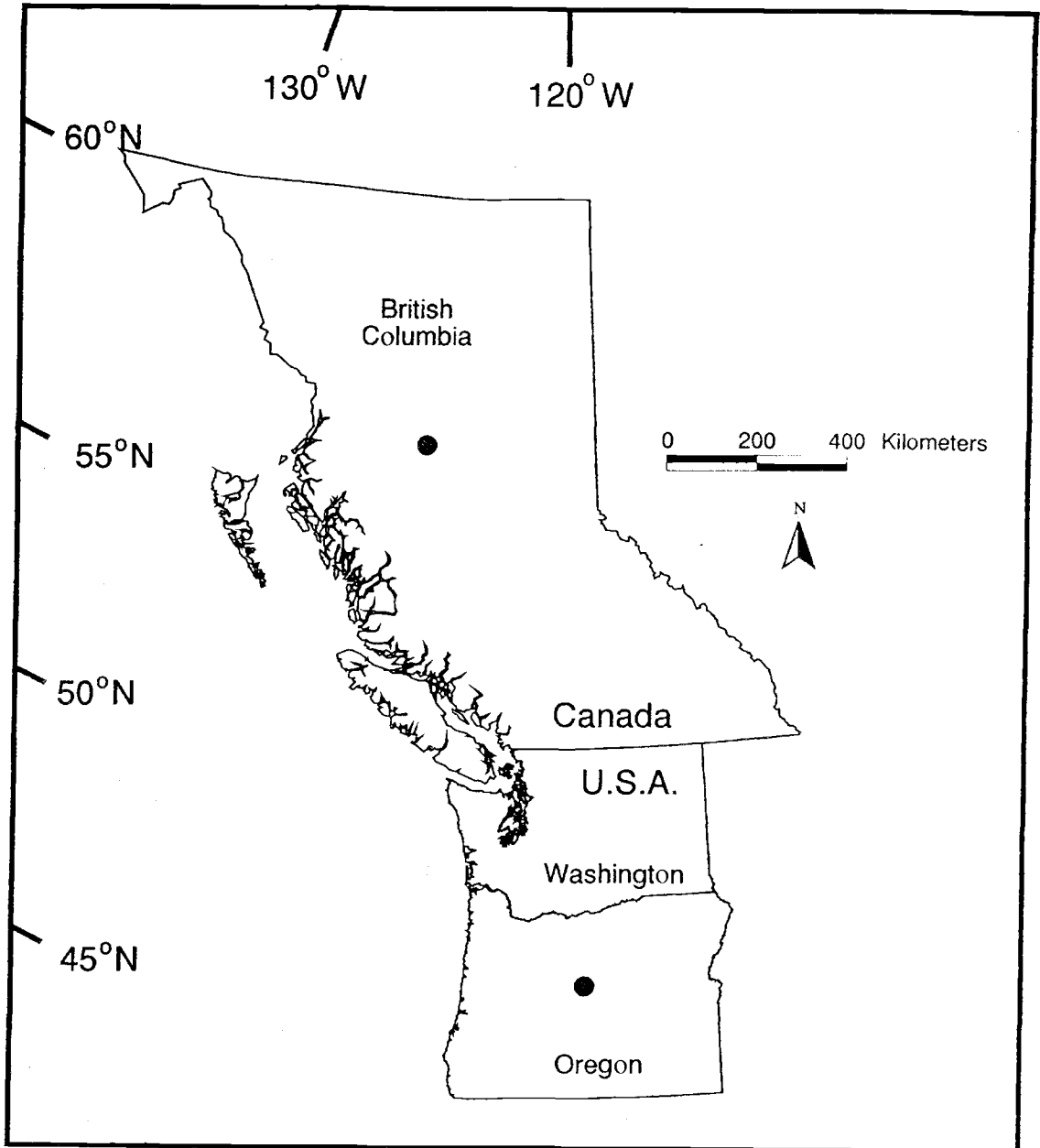


Figure 2.1. Location of otolith sampling locations, Babine River, British Columbia and Deschutes River, Oregon.

Babine River steelhead otoliths ( $n = 24$ ) were collected from mortalities encountered at the Babine Lake salmon counting weir; resident rainbow trout ( $n = 9$ ) were collected from the stream in the vicinity of the weir. All resident rainbow trout from the Babine River were age 4 or 5 and ranged in length from 350 to 495 mm. Although most steelhead in the Babine River smolt at age 3, a small proportion smolt at age 4 and 5 (Narver 1969). The back calculated lengths-at-age of steelhead at age 4 and 5 ranged from 179 to 246 mm (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 with 1200-grit sandpaper in the sagittal plane to the level of the nucleus. The mounting medium was heated and the otolith turned sulcus side-up. The otolith was then ground with 1200-grit and 2000-grit sandpaper in the sagittal plane to the level of the primordia 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 400  $\text{\AA}$  carbon layer.

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). Sr was measured using the TAP crystal and Ca was measured using the PET crystal.

Otolith regions were classified as primordia, freshwater growth region, and saltwater growth region based on growth rates inferred from banding patterns. 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 (4 to 12 per fish) and transects of at least 10 points in both the freshwater growth region in all fish and the 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 one-tailed t-test with  $\alpha = 0.05$ .

## Results

Life history transects of steelhead were similar to those described for anadromous salmonids by Kalish (1990), with lower Sr/Ca in the freshwater growth regions and increased Sr/Ca in saltwater growth regions (Fig. 2.2a and 2.2b). Life history transects of resident rainbow were characterized by constant low Sr/Ca (Fig. 2.2c and 2.2e). 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 (Fig. 2.2d).

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 ( $P < 0.0001$ ) in the primordia compared to the freshwater growth region indicating that at least the maternal parent of each fish was a steelhead. None of the 38 resident rainbow trout otoliths from the Deschutes River had significantly higher Sr/Ca ( $P > 0.05$ ; Range 0.16 – 0.49) in the primordia than in the freshwater growth region indicating that at least the maternal parent of each fish was a resident rainbow trout. The relation between individual life history and the life history of the maternal parent of fish in the Babine River was less consistent than in the Deschutes River. Of the 24 steelhead otoliths from the Babine River weir area examined, all but one had significantly higher Sr/Ca ( $P < 0.05$ ; Range  $<0.001 - 0.02$ ) in the primordia compared to the freshwater growth region indicating steelhead maternal origin. The Sr/Ca in the primordia of one Babine River

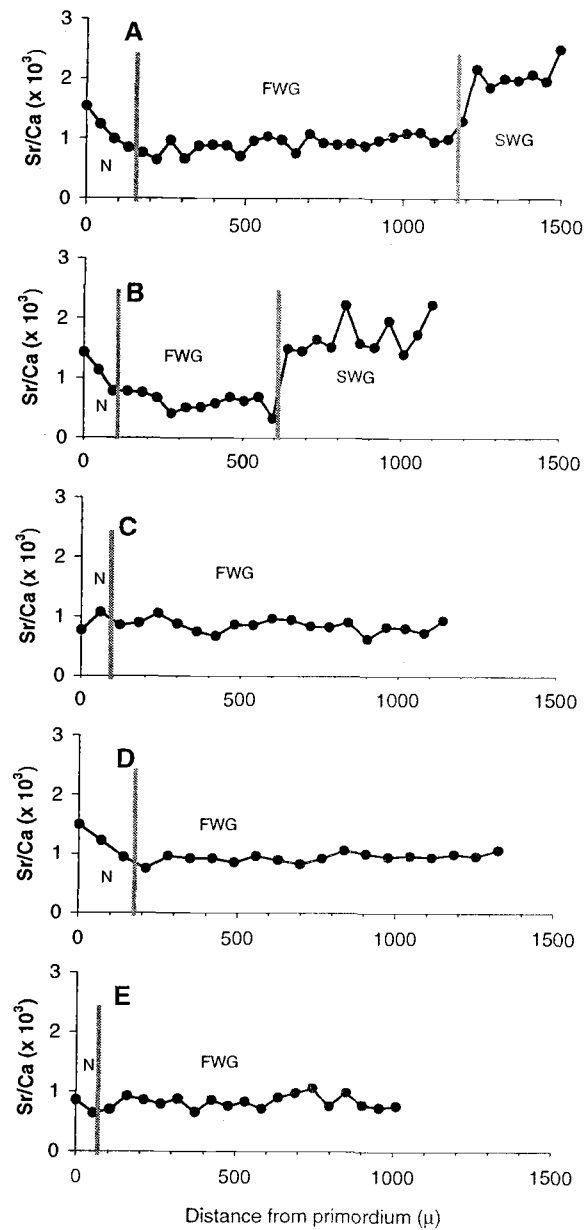


Figure 2.2. Transects of otolith Sr/Ca measured from a single primordium to the otolith edge. Each point represents a single measurement. (A) Deschutes River adult steelhead; (B) Babine River adult steelhead; (C) Deschutes River adult rainbow trout; (D) Babine River adult rainbow trout whose maternal 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.

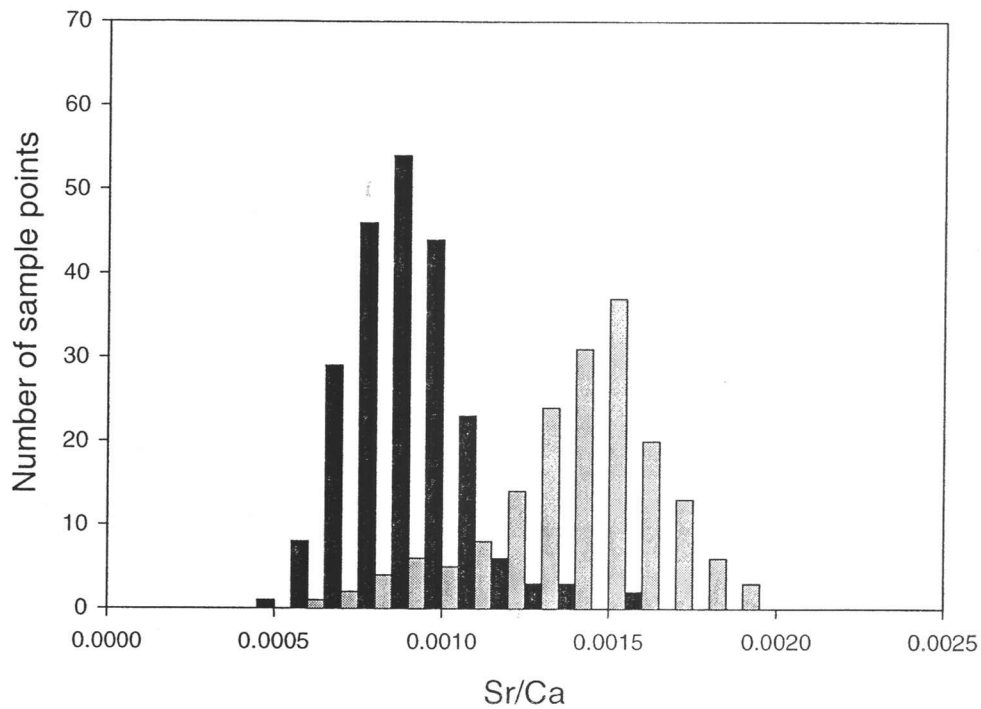


Figure 2.3. Frequency distribution of Sr/Ca in primordia of resident rainbow trout (black bars) and steelhead (gray bars) from the Deschutes River, Oregon.

steelhead was not significantly higher ( $t = 1.46$ ,  $P = 0.09$ ) than the freshwater growth region indicating that the maternal parent was a resident rainbow trout.

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 ( $P < 0.001$ ). This suggests that maternal parents of two fish were steelhead.

The remaining seven resident rainbow trout did not have significant differences between Sr/Ca in the primordia or freshwater growth regions ( $P > 0.05$ ; Range 0.09 – 0.4), indicating that the maternal parents were resident rainbow trout.

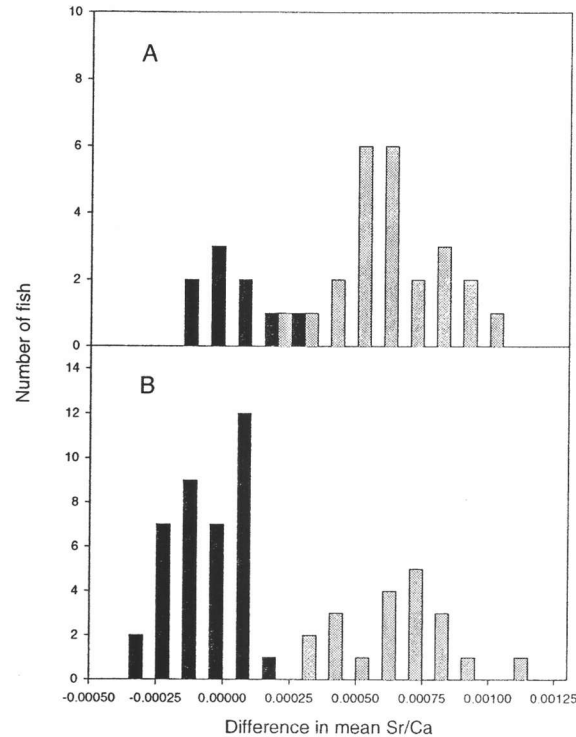


Figure 2.4. Frequency distribution of the difference between mean primordia Sr/Ca and mean freshwater growth region Sr/Ca for adult resident rainbow trout (black bars) and adult steelhead (gray bars) in (A) the Babine River, British Columbia and (B) the Deschutes River, Oregon.

The distribution of Sr/Ca in primordia sample points in steelhead and rainbow trout adults from the Deschutes River was bimodal and overlapping (Fig. 2.3).

Similarly, the distribution of differences between mean Sr/Ca in the primordia and mean Sr/Ca in the freshwater growth region were bimodal in both the Babine and Deschutes samples (Fig. 2.4). In the Babine River sample, there was a slight overlap in differences due to the occurrence of resident rainbow trout of steelhead origin and steelhead of resident rainbow trout origin (Fig. 2.4a). There was no overlap in the Deschutes River samples (Fig. 2.4b).

## Discussion

All adult steelhead from the Deschutes River were progeny of steelhead females and all resident rainbow trout were progeny of resident rainbow trout. 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, one of the steelhead appeared to have had a resident maternal parent and two of the resident rainbow trout were the progeny of a steelhead maternal parent. These patterns suggest that there are differences between the Deschutes and Babine Rivers concerning the degree of segregation between steelhead and resident rainbow trout.

Identification of maternal origin based on Sr/Ca ratios can be confounded by high Sr/Ca ratios in freshwaters. Rieman et al. (1994) cautioned that the utility of otolith microchemistry is highly dependent on the variation in chemistry of freshwaters. Reiman et al. (1994) reported Sr/Ca ranging from  $<0.0012$  to  $0.0061$  for three lakes and a hatchery. The  $0.0061$  measurement from Alturas Lake precluded use of Sr/Ca to determine maternal origin of sockeye salmon (*O. nerka*) in that system. The Sr/Ca ratio in freshwater growth regions and primordia of fish from Alturas Lake were similar to measurements in the primordia of known anadromous fish from other systems. As a result, Rieman et al. (1994) suggested the analysis of water chemistry in future application of otolith microchemistry. Sr/Ca ratios in the Deschutes River ranged from  $0.0016$  to  $0.0030$  in 13 quarterly samples collected between April 1983 and June 1986 (Alexander et al. 1996).



Assuming that these samples represent the typical variation for the Deschutes River, Sr/Ca levels in the Deschutes River are low enough to allow use of otolith microchemistry in the determination of maternal origin in steelhead and resident rainbow trout. Future research concerning the relationship of environmental Sr/Ca and otolith Sr/Ca in controlled conditions is warranted to refine the utility of otolith microchemistry.

Although there is an overlap in the distribution of Sr/Ca ratios in individual sampling locations within the primordia of steelhead and resident rainbow trout, this does not preclude the identification between the two life history forms (Fig. 2.3). Rather, it suggests that a single point sampled in a single primordium of a fish cannot discriminate life history. It is for this reason, I sampled as many primordia as possible within each fish for comparison with the freshwater growth region.

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 (unpublished data) observed only two instances in 4,302 observations in the Deschutes River where steelhead and rainbow trout spawned together.

Resident populations can give rise to anadromous juveniles (Northcote 1992). Rieman et al. (1994) found juveniles of both kokanee (*O. nerka*) and sockeye origin in samples of emigrants (presumed smolts) leaving Redfish Lake,

Idaho. However, of the five adult sockeye salmon that returned to Redfish Lake in 1991, all had a sockeye maternal parent. Since 1991, adult sockeye of kokanee maternal origin have been confirmed at Redfish Lake (Bruce Rieman, pers. comm.). In presumed steelhead smolts collected from the estuary of a small central California coastal stream, juveniles of both steelhead and resident rainbow trout maternal origin were present (Zimmerman, unpublished data). This observation suggests that resident rainbow trout 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.

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. Although these results do not unequivocally determined the relationship of

steelhead and resident rainbow trout, they do suggest that there may be variation among locations in this relationship.

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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 - 15 % of the total rainbow trout spawning occurred during the period when steelhead spawned. The timing of fifty-percent 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.

## 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 char (*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 lead 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 as the progeny of resident and migratory spawners could contribute to either life history form. Identifying the extent to which migratory forms contribute to the spawning population of resident forms and vice versa is required to determine reproductive isolation.

Analysis of otolith microchemistry provides the means to determine whether adult spawners are the progeny of migratory or non-migratory forms. If migratory and non-migratory trout represent ecophenotypes within a single gene pool, migratory adults of resident maternal origin and resident trout of migratory maternal origin would be commonly encountered. If the two life history forms are reproductively isolated, migratory trout of resident trout maternal origin and

residents of migratory trout maternal origin would not be present. Otolith microchemistry can be used to identify maternal origin based on examination of the ratio of strontium (Sr) and calcium (Ca). 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, analysis 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.

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 site**

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 (Fig. 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 RK 160 and the Trout Creek campground at RK 139 (Fig. 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 fish. 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.

### **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,

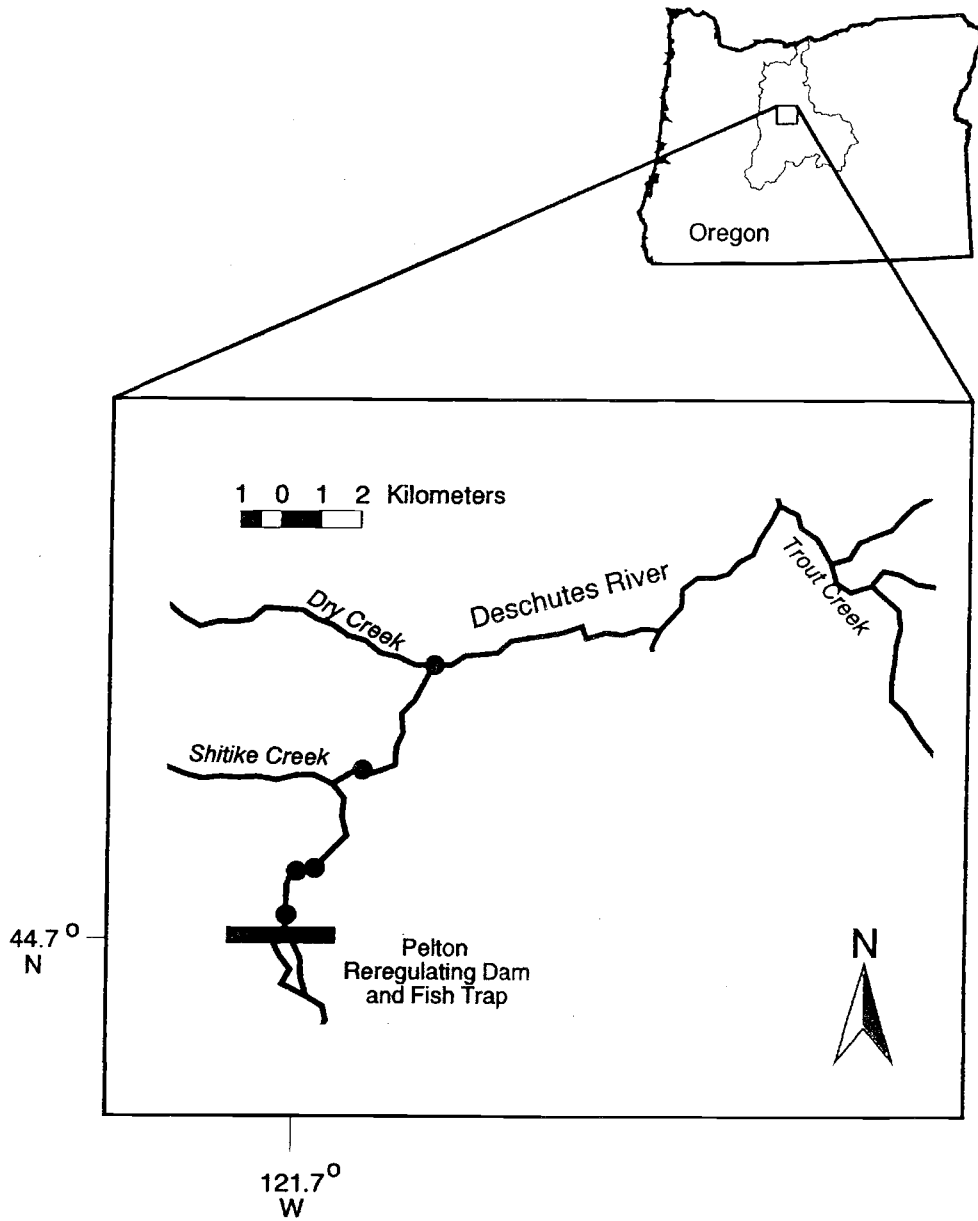


Figure 3.1. Location of study area for spawning surveys, Deschutes River, Oregon. Study sites are identified with solid dots.

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 (Fig. 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

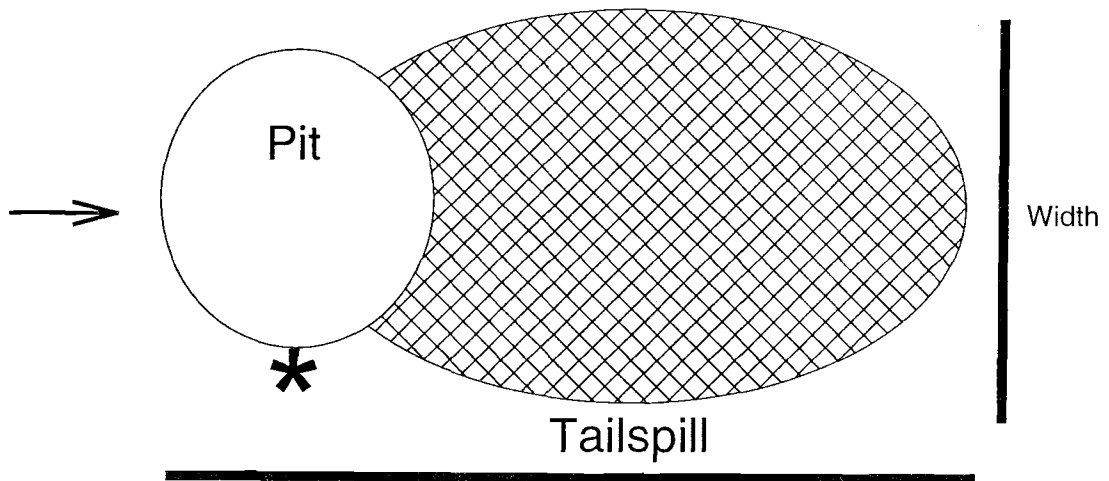


Figure 3.2. Plan form view of a redd illustrating length and width measurements. Asterisk represents point where depth and velocity measurements were taken.

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 (Fig. 3.2).

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.



### **Determination of population structure based on otolith microchemistry**

Sagittal 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 from a 3 km segment of the riverbank 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 we were able to ensure that we were comparing adult steelhead and resident rainbow trout.

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 with 1200-grit sandpaper in the sagittal plane to the level of the nucleus. The mounting medium was heated and the otolith turned sulcus side-up. The otolith was then ground with 1200-grit and 2000-grit sandpaper in the sagittal plane to the level of the primordia 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 400  $\text{\AA}$  carbon layer.

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). Sr was measured using the TAP crystal and Ca was measured using the PET crystal.

Otolith regions were classified as primordia, freshwater growth region, and saltwater growth region based on growth rates inferred from banding patterns. 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. 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  $\alpha = 0.05$ .

## 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 fifty-percent spawning by steelhead occurred during week of year 14, 16, and 14 in 1995, 1996, and 1997, respectively (Fig. 3.3). The time of fifty-percent spawning by resident rainbow trout occurred during week of year 23 in 1995 and 24 in 1996 and 1997 (Fig. 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
	<b>Total</b>	48	1430	21	1504	58	1241

\* = no survey due to high flows

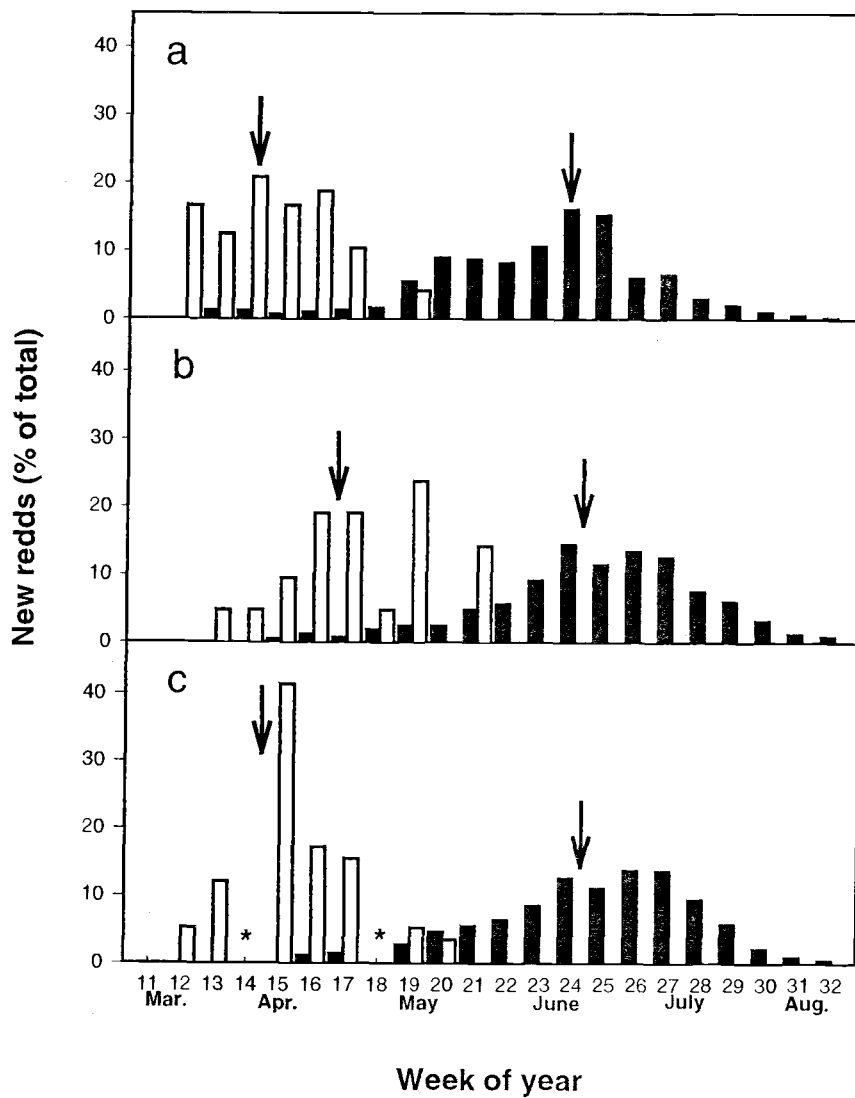


Figure 3.3. Percent of total redds observed by week of year, Deschutes River, Oregon, (a) in 1995, (b) in 1996, and (c) in 1997. Clear bars are steelhead redds, and solid bars are resident rainbow trout redds. Arrows indicate timing of fifty-percent spawning, and asterisks indicate lack of data due to high flows.

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

### 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).

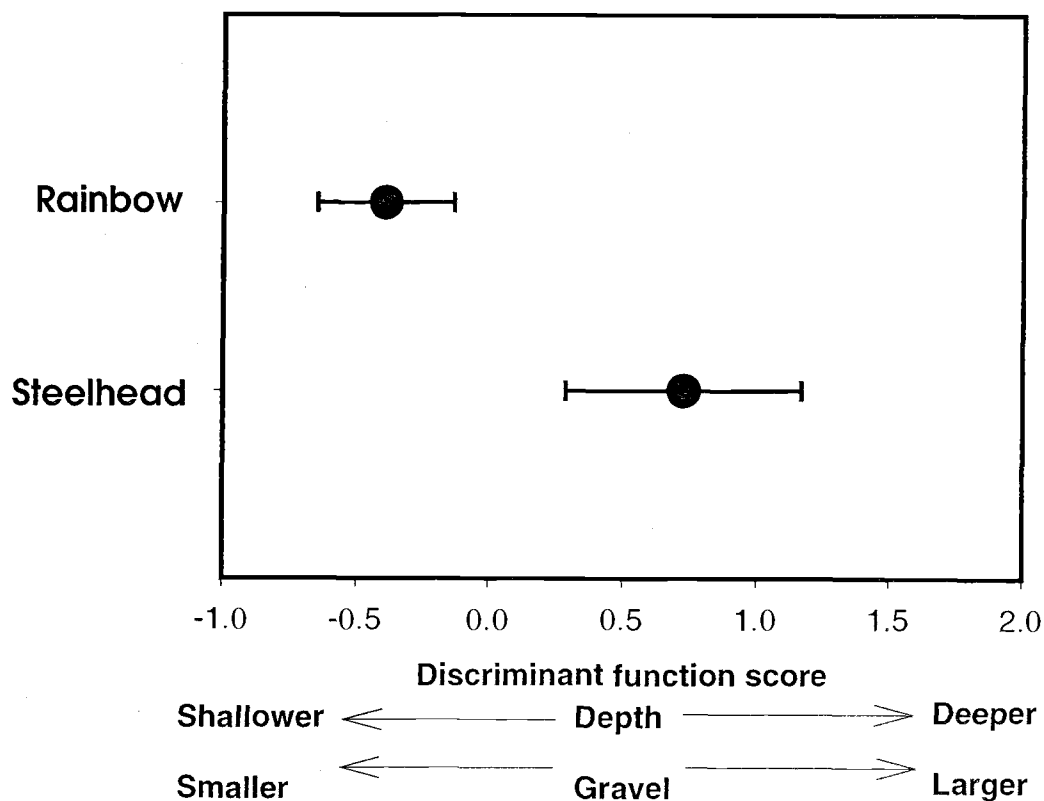


Figure 3.4. Means and 95% confidence intervals on the discriminant function for microhabitat characters used by steelhead and resident rainbow trout in the Deschutes River, Oregon.

Step-wise discriminant function analysis indicated that depth and substrate size contributed significantly to separation of steelhead and resident rainbow trout redds (Fig. 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.

### **Heritability of life history**

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 (all  $P < 0.0001$ ) indicating that at least the maternal parent of each fish was a steelhead. None of the 38 resident rainbow trout otoliths had significantly higher Sr/Ca in the primordia than in the freshwater growth region (all  $P > 0.05$ ) indicating that at least the maternal parent of each fish was a resident rainbow trout. These results indicate that life history (steelhead vs. resident) is inherited and juveniles of one life history form do not contribute to the recruitment of adults of the alternate life history form.

### **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. 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; Fig. 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 lead 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 char 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 char, 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) for rainbow trout in 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.

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## CHAPTER 4

# Timing of Emergence and Size of Fry at Emergence of Sympatric 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 sympatric 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. The resulting embryos and alevins develop within the gravel until they emerge into the water column as free-swimming fry with little or no visible yolk remaining. The duration of the inter-gravel period is a function of egg size and water temperature (Beacham and Murray 1990).

Following emergence from the gravel, steelhead and rainbow trout fry establish feeding territories that they aggressively defend (Slaney and Northcote 1974). Timing of emergence and size of fry at emergence may influence the social interactions among fry establishing territories. The size of fry at emergence, for example, has been shown to influence the outcome of competitive interactions (Mason and Chapman 1965; Chandler and Bjornn 1988), with larger fry dominating. The timing of emergence may also have impacts on competitive interactions related to size

and territory acquisition. Fry that emerge first have a theoretical advantage in obtaining optimum habitat because they not only arrive first, but they may also 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) may encounter harsher environments (i.e., temperatures and flows) upon emergence (Leider et al. 1986).

The relation between sympatric steelhead and resident rainbow trout is uncertain. Zimmerman and Reeves (in review) described the temporal and spatial distribution of spawning by steelhead and resident rainbow trout in the Deschutes River, Oregon. Although, there was an overlap in the timing of spawning by steelhead and resident rainbow trout, differential microhabitat use served to segregate the two life history forms. Steelhead spawning occurred from mid-March through May and resident rainbow trout spawning occurred from mid-March through August. The median timing of steelhead spawning was 9 -- 10 weeks earlier than the median timing of resident rainbow trout spawning. Given the overlap in steelhead and resident rainbow trout spawning during mid-March through May, the potential for competition between newly emerged steelhead and resident rainbow trout fry exists. In this study, we describe the timing of emergence and size of fry at emergence of sympatric steelhead and resident rainbow trout in the mainstem Deschutes River, Oregon.

## 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 (Fig. 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.

Steelhead and resident rainbow trout redds were identified during weekly spawning surveys during March through June of 1995 and 1996. Only redds that could positively be identified as either steelhead or resident rainbow trout were included in this study. Identification was based on the size and appearance of spawning adult fish at the redd. 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 steelhead lengths range from 48 cm to 80 cm with more than 90% of the population being greater than 54 cm. 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). When a redd was encountered in an area that was conducive to trap construction it 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. Eighteen traps were set during the two years of the study.

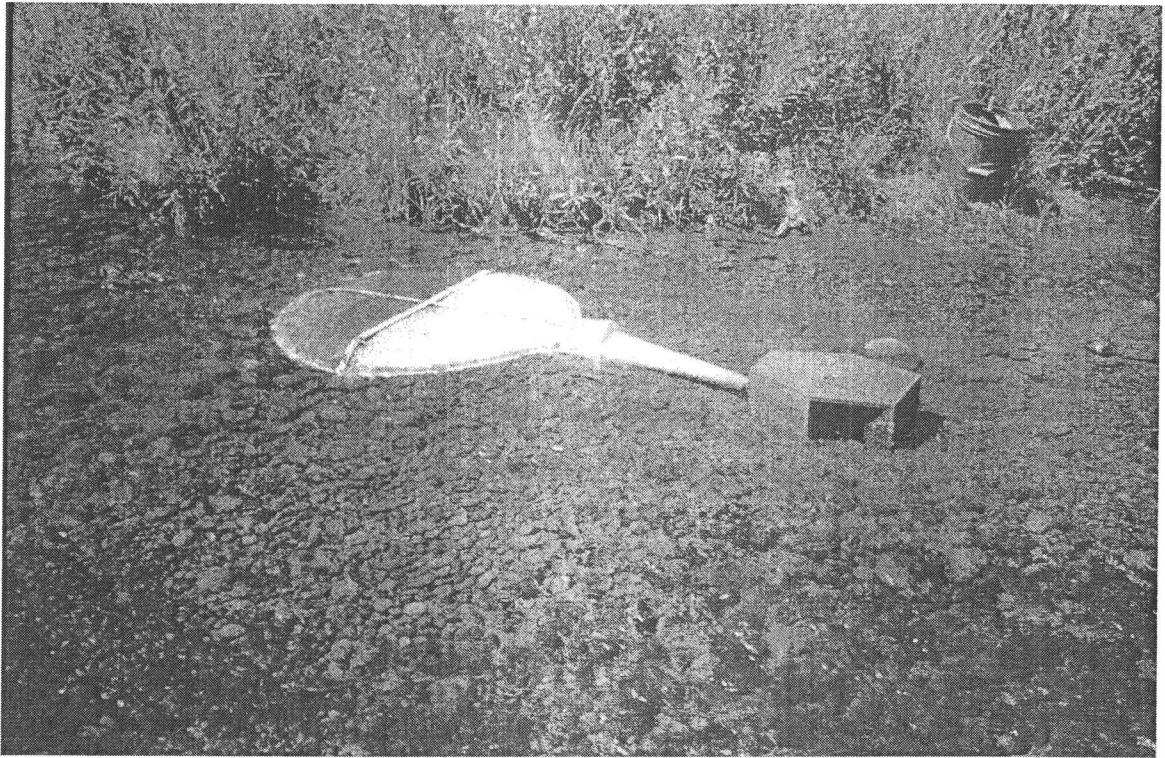


Figure 4.1. Emergence trap constructed over a resident rainbow trout redd, Deschutes River, Oregon.

After the initiation of emergence, traps were visited at least every other day. All fry captured were measured to the nearest millimeter and released. The timing and duration of emergence was plotted to compare the timing of emergence between steelhead and rainbow trout. The length of steelhead and rainbow trout fry was tested for significant difference using a two-tailed t-test.

## Results and Discussion

Emerging fry were collected in 11 of the 18 traps that were set. There was an overlap in the timing of emergence by steelhead and resident rainbow trout emergence during 1995 (Fig. 4.2) that was similar to the overlap in timing of spawning reported by Zimmerman and Reeves (in review). The timing of emergence was only plotted for redds sampled in 1995 with greater than 20 fry captures. Too few redds were sampled in 1996 to accurately describe timing of emergence.

There is an overlap in the timing of emergence by steelhead and resident rainbow trout in the Deschutes River with steelhead and resident rainbow trout emergence occurring simultaneously. Steelhead spawning in the Deschutes River occurs from mid-March through May and resident rainbow trout spawning occurs from mid-March through August (Zimmerman and Reeves in review). As a result, the timing of resident rainbow trout emergence occurs over a longer period than steelhead emergence. The redds that were examined in this study represented redds constructed during the overlap in spawning by steelhead and resident rainbow trout with the exception of one rainbow trout redd that was constructed on 28 June 1995. Emergence from that redd occurred from the end of August through the first week of September (Fig. 4.2). It is likely, therefore, that rainbow trout emergence continues through October.

The emergence traps collected a total of 326 rainbow trout fry and 310 steelhead fry from 5 steelhead and 6 rainbow trout redds during the two years sampled (Table 4.1). The mean length of steelhead fry was 28.03 mm (s.d. = 1.47 mm; range =



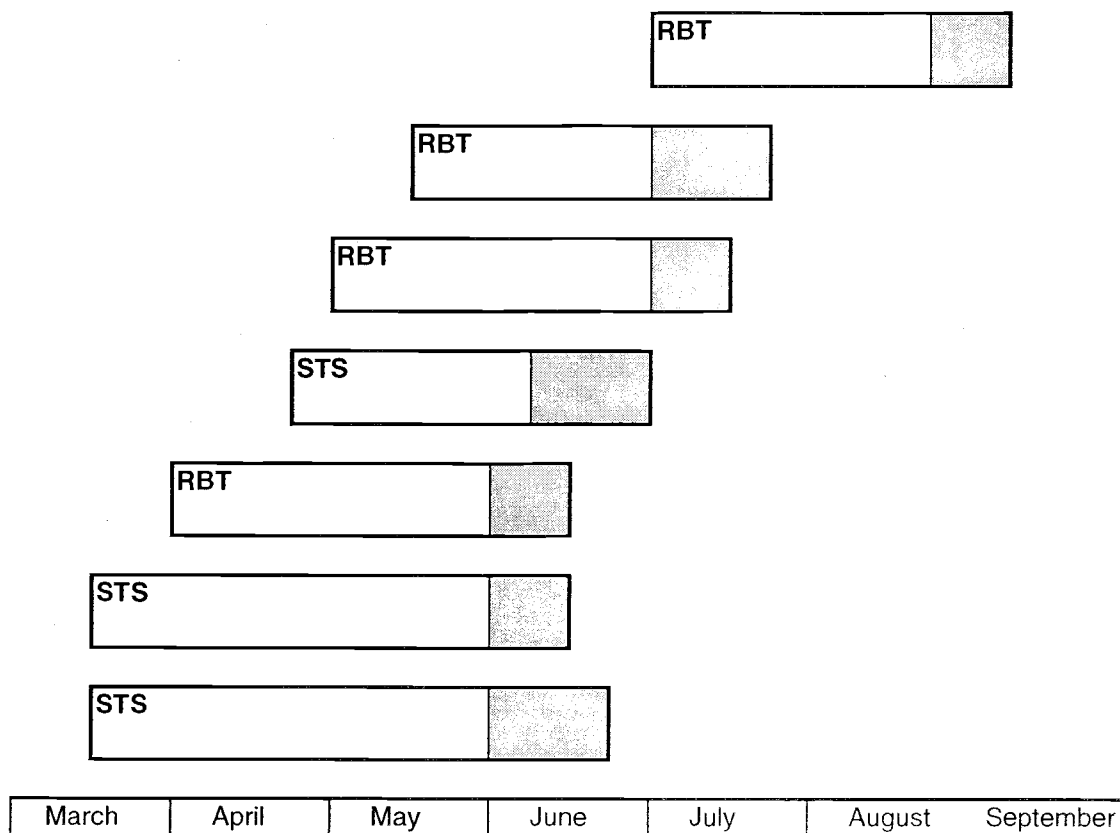


Figure 4.2. Timing of incubation and emergence for steelhead (STS) and resident rainbow trout (RBT) from seven redds in the Deschutes River, Oregon, 1995. The clear portion of the box represents incubation and the solid portion represents emergence of fry from the redd.

Table 4.1. Redds of steelhead (STS) and resident rainbow trout (RBT) sampled, date redd constructed, life-history form, number of fry captured, and mean length of fry, Deschutes River, Oregon.

Date Spawned	Life History	Fry Captured	Mean Length
			± s.d. (mm)
22 March 1995	STS	179	28.2 ± 0.96
22 March 1995	STS	4	28.5 ± 0.56
28 March 1995	RBT	85	28.1 ± 0.87
06 April 1995	STS	32	29.6 ± 0.72
19 April 1995	STS	20	26.9 ± 1.00
02 May 1995	RBT	39	28.6 ± 0.72
09 May 1995	RBT	145	27.1 ± 0.76
28 June 1995	RBT	5	26.8 ± 0.45
13 May 1996	STS	99	27.1 ± 1.73
10 May 1996	RBT	41	25.7 ± 0.87
13 May 1996	RBT	5	27.5 ± 1.51

22 – 33 mm) and the mean length of rainbow trout fry was 27.39 mm (s.d. = 1.42; range = 24 – 31 mm). The mean length of steelhead and resident rainbow trout fry were significantly different (one-tailed  $t = -6.63$ ;  $P < 0.0001$ ). In spite of this statistical difference in mean lengths, the length frequency distributions of steelhead and resident rainbow trout fry are similar and overlapping (Fig. 4.3). This suggests that there is no consistent competitive advantage to either steelhead or resident rainbow trout fry based on length at emergence.

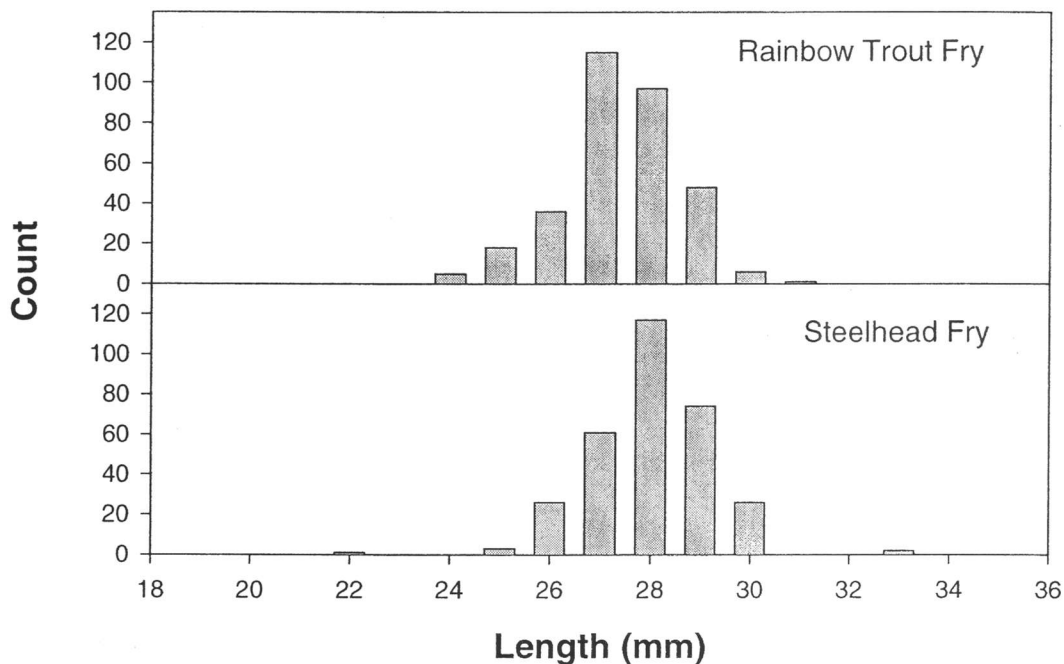


Figure 4.3. Length frequency of emerging fry from 6 resident rainbow trout and 5 steelhead redds, Deschutes River, Oregon, 1995 and 1996.

In most cases, we collected only a small percentage of fry from each redd compared to potential production based on the fecundity of rainbow trout and steelhead. Although, this would preclude analyses of survival or production, it does provide a representative sample of fry size and emergence timing. It is likely that fry moved laterally through the gravel and emerged outside the trap (Garcia de Leaniz et al. 1993). Previous attempts to trap emerging fry in the Deschutes River were unsuccessful due to 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 overlap in the length of steelhead and resident rainbow trout fry precludes a consistent size advantage to fry of either life history form as they compete for territories following emergence. We assumed that steelhead eggs would be larger than resident rainbow trout eggs and would, hence, produce larger fry. Olofsson and Mosegaard (1999) examined egg size in sympatric migratory and non-migratory brown trout (*Salmo trutta*) and found that resident trout had larger eggs when sympatric with migratory trout. If such an egg-size relationship exists between sympatric steelhead and resident rainbow trout in the Deschutes River, it is likely that competitive advantage as a result of life history type does not exist. Rather, fry size may be the result of some other variable such as female length. Further analysis concerning the relationship of female size to egg size is needed to further understand the size of newly emerging steelhead and resident rainbow trout fry.

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## CHAPTER 5

**Variation in Agonistic Behavior and Territoriality Exhibited by  
Sympatric Steelhead and Resident Rainbow Trout (*Oncorhynchus  
mykiss*) Fry Immediately Following Emergence**

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## **Abstract**

Behavior and territoriality of newly emerged fry of steelhead and resident rainbow trout (*Oncorhynchus mykiss*) was compared in laboratory stream channels. Steelhead and resident rainbow trout fry from the Deschutes River, Oregon were introduced as emerging fry from redds within artificial stream channels and monitored for 18 days. Three treatments were examined: steelhead alone, steelhead and resident rainbow trout together, and resident rainbow trout alone. Fry were allowed to emigrate freely from the channels into traps at the downstream end of each channel segment. Trials with only steelhead had higher levels of aggression and lower densities of fish at the conclusion of the 18-day experimental period.

## **Introduction**

Upon emergence from the gravel, juvenile salmonids such as steelhead and rainbow trout (*Oncorhynchus mykiss*) fry, establish and defend territories (Chapman 1966). During the period immediately following emergence, mortality related to competition for territory is high (McFadden 1969). Fry that 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 (Chapman 1962). Elliot (1989) referred to the period directly following emergence as a "critical time" during which much of the initial population regulation occurred.

Agonistic and territorial behavior in salmonids is variable and sometimes population specific. Olsén and Karlsson (1991) described differences in agonistic



behavior between two allopatric populations of Arctic char (*Salvelinus alpinus*). One population was more territorial while the other formed shoals of less aggressive individuals. Swain and Holtby (1989) compared morphology and behavior of juvenile coho salmon (*O. kisutch*) in a lake and a tributary stream. The stream-rearing coho were more aggressive and characterized by a body shape that optimized burst swimming rather than prolonged swimming performance in comparison to the lake rearing juveniles.

Differences in aggressive behavior and territoriality may play an important role in the relationship of migratory and non-migratory salmonids. Hutchinson and Iwata (1997) found that aggression is positively correlated with length of stream residence (i.e., species with longer juvenile stages exhibit higher levels of aggression). 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. The adaptive significance of life history specific behavior exhibited by sympatric anadromous and non-anadromous salmonids is uncertain. In locations with reproductively isolated life history forms, variation in behavior and territoriality may play an important role in competition between juveniles of each life history form and segregation in rearing habitats.

In this study, we examined territoriality, agonistic behavior, and alevin to fry recruitment dynamics of steelhead and resident rainbow trout in laboratory stream aquaria. Steelhead and resident rainbow trout are sympatric in the Deschutes River, Oregon and the relationship of the two life history forms in this river is unresolved.

Resolving this relationship requires an understanding of habitat use and interactions between all life history stages.

## Materials and Methods

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 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 delay development and 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 (Fig. 5.1). 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 were regulated independently in each channel. Current velocity was maintained by a Plexiglas paddle wheel at  $10 \text{ cm}\cdot\text{s}^{-1}$ . The photoperiod was maintained by a timer that provided 15 h of

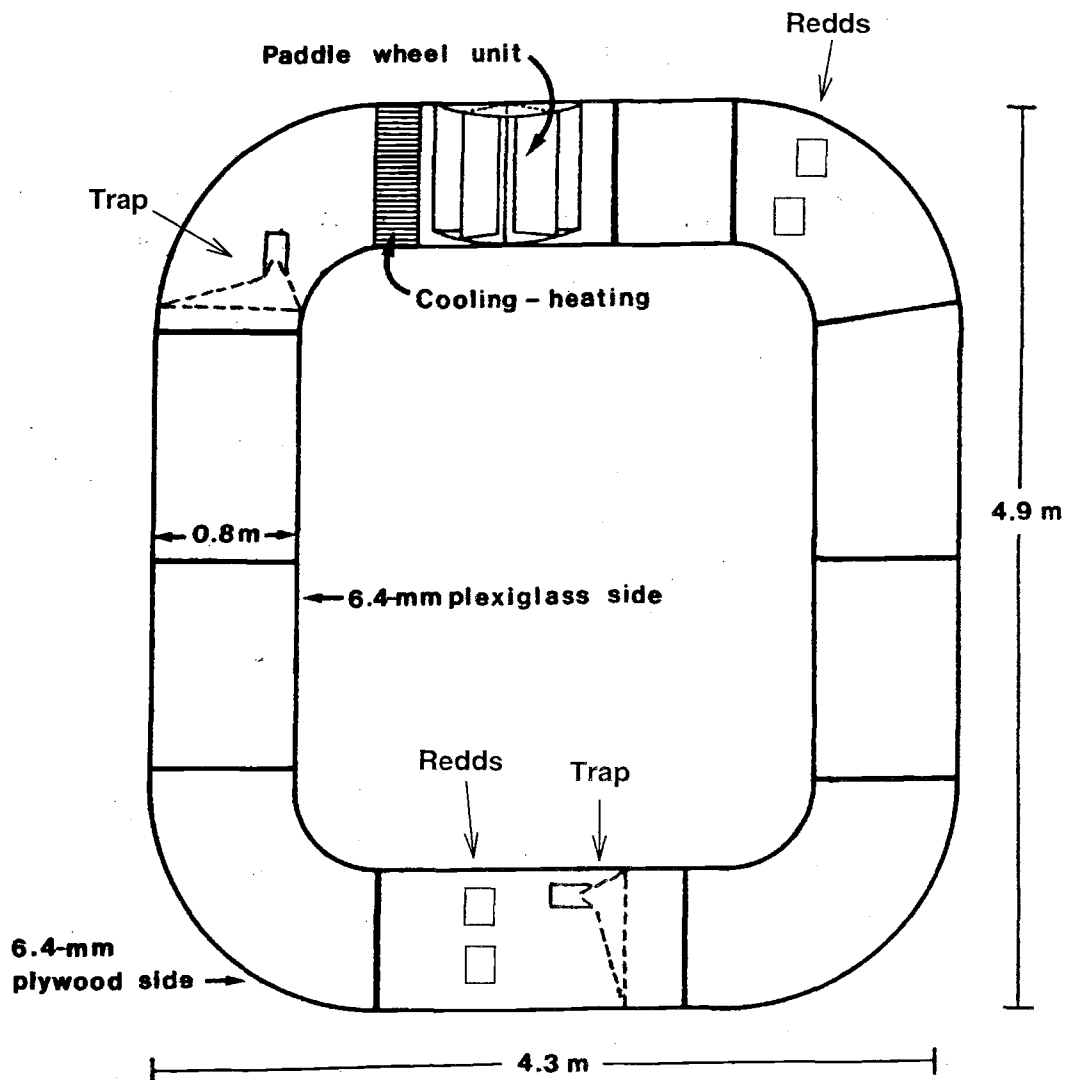


Figure 5.1. Plan view of experimental channels.

light and 9 h of darkness. The light phase consisted of 1.5 h morning where lights gradually increased from zero to full intensity, 12 h of full intensity, and a 1.5 h evening where intensity gradually dimmed to zero. Nine 60-W incandescent bulbs

spaced at equal intervals around the channels were the sole source of light. Each stream channel was divided into two compartments and each compartment 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 3-4 days before the fish were introduced. Channel water 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 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 these fry was achieved by placing the fish in a solution of  $50 \text{ mg}\cdot\text{l}^{-1}$  of alizarin complexone for 4 h and the other fish from that treatment 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. An additional 30 fry from both steelhead and resident rainbow trout were collected at the time of sorting to represent the mean length and weight of fry at the initiation of the experiment. After marking, the fry were introduced to the channels in plastic mesh boxes with lids. The fry were allowed to acclimatize for 24 h before the start of the experiment. After the 24 h acclimatization period, the lid was removed from the first box and after 48 h the lid was removed from the second box. The determination of early (first box) and later (second box) emergers was included to test the effects of emergence timing.

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. 1988). The PVC pipe is perforated with graduated holes along its length and allows for food to emerge from throughout the length of the substrate rather than concentrated at one feeding station.

Test periods were 18 days. On each day, the fry in each migratory 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 alizarin 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.

A paired two-sample t-test was used to test the null hypothesis that the numbers of early fish versus late fish remaining in the channels did not differ. This test included all treatments. To test the null hypothesis that the number of steelhead and rainbow trout remaining did not differ, a paired two-sample t-test was conducted for the mixed steelhead and rainbow trout treatments only.

Rates of aggressive interactions were quantified during the second experiment. After emigration from all channel segments reached less than three individuals per day, observations of levels of aggression were conducted. Immediately following feeding, an observer randomly chose one fish and counted all agonistic encounters

between that fish and other fish. Agonistic encounters included chasing and nipping (Dill 1977). One-way analysis of variance was used to test the null hypothesis that the number of aggressive interactions displayed by individual fish did not differ among the treatments.

## Results

In all treatments containing only steelhead and steelhead with resident rainbow trout, the number of fry remaining at the conclusion of the trial was lower than in the rainbow only treatment (one-way ANOVA;  $F_{2,5} = 10.08$ ;  $P = 0.02$ )(Fig. 5.2).

Emigration rates during both experiments were similar. Initially, emigration rates were high, but within 8 days of the start of the experiments dropped to less than 3 fish per day. In all cases, emigration from the channels ceased prior to the end of the experimental period.

There was no difference in the number of early versus late emergers remaining at the end of the experimental period ( $t = -0.46$ ;  $p = 0.32$ ;  $n = 8$ ). The number of steelhead or resident rainbow trout fry remaining at the end of the trial in the mixed treatments was not significantly different ( $t = 0$ ;  $p = 0.5$ ;  $n = 4$ ). There was not a consistent pattern in the ratio of steelhead or resident fry numerically dominating at the conclusion of the experiment in the mixed treatments (Table 5.1).

Table 5.1. Experimental design, number of steelhead (S) and resident rainbow trout (R) fry stocked in channel, and summarized statistics concerning fry remaining in channels at conclusion of 18-day trial. \* = significantly different from size ( $p < 0.05$ ).

Trial	Group	Stocked Number	Otolith Mark	Number in Channel	End-of-test statistics					
					Mean Length (mm)	Mean Weight (g)	Fish Density fry/m <sup>2</sup>	Biomass Density g/m <sup>2</sup>	Total Biomass	Fish Ratio S:R
1	S	150	N	3	26.3	0.104	0.5	0.202	1.13	
	S	150	Y	13	28.4*	0.087	2.3	0.056	0.31	
	Total	300		16	27.7	0.090	2.8	0.257	1.44	
1	R	150	Y	35	26.3*	0.083	6.2	0.536	3.00	
	R	150	N	36	25.8*	0.087	6.4	0.546	3.06	
	Total	300		71	26.1	0.085	12.6	1.082	6.06	
1	S	150	Y	2	29.5*	0.112	0.4	0.039	0.22	
	R	150	N	7	27.3*	0.095	1.3	0.119	0.66	
	Total	300		9	27.8	0.098	1.7	0.159	0.88	0.3 : 1
1	R	150	Y	8	26.3*	0.087	1.4	0.148	0.83	
	S	150	N	8	28.4*	0.104	1.4	0.124	0.70	1 : 1
	Total	300		16	27.4	0.095	2.8	0.273	1.53	
2	S	125	N	7	28.6*	0.102	1.3	0.127	0.71	
	S	125	Y	6	28.1*	0.091	0.9	0.098	0.55	
	Total	250		13	28.3	0.097	2.2	0.225	1.26	
2	R	125	Y	13	27.4*	0.078	2.3	0.020	1.15	
	R	125	N	32	27.1*	0.077	5.7	0.474	2.66	
	Total	250		45	27.2	0.077	8.0	0.679	3.81	
2	S	125	N	22	28.5*	0.105	4.0	0.414	2.32	
	R	125	Y	9	28.4*	0.093	1.7	0.150	0.84	
	Total	250		32	28.5	0.102	5.7	0.564	3.16	2.4 : 1
2	R	125	N	13	27.1*	0.098	2.3	0.228	1.28	
	S	125	Y	5	28.9*	0.110	0.9	0.098	0.55	
	Total	250		18	27.6	0.102	3.2	0.326	1.82	0.4 : 1

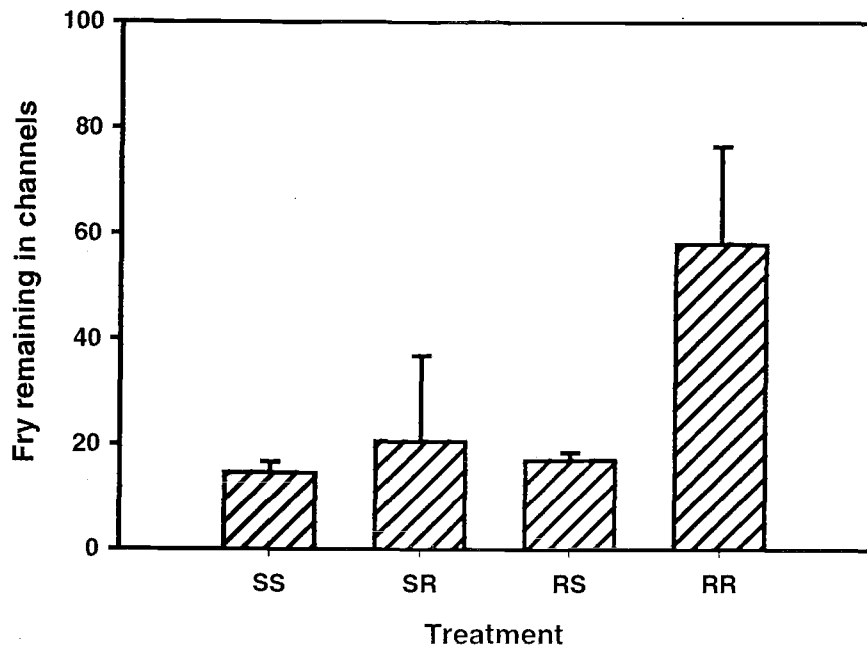


Figure 5.2. Mean number of fry remaining at the conclusion of the experiments for each treatment. S = steelhead, R = resident rainbow trout. The sequence of the letters indicates order of emergence into channel.

The mean length and weight of steelhead and resident rainbow trout fry was significantly different at the beginning of both trials ( $p < 0.05$ ). In the first trial, steelhead fry had a mean length ( $\pm$  SD) of  $26.6 \pm 0.93$  mm and a mean weight ( $\pm$  SD) of  $0.076 \pm 0.007$  g. Resident rainbow trout fry had a mean length ( $\pm$  SD) of  $24.2 \pm 0.69$  mm and a mean weight ( $\pm$  SD) of  $0.72 \pm 0.004$  g. In the second trial, steelhead fry had a mean length ( $\pm$  SD) of  $26.4 \pm 0.73$  mm and a mean weight ( $\pm$  SD) of  $0.075 \pm 0.007$  g. Resident rainbow trout fry had a mean length ( $\pm$  SD) of  $24.4 \pm 0.72$  mm and a mean weight ( $\pm$  SD) of  $0.72 \pm 0.006$  g. At the conclusion of the experiments, the mean length and weight of fry remaining were significantly longer than the reference



group from the start of the experiment (Table 5.1). The total fry biomass in each treatment at the conclusion of the experiment was correlated to the number of fry remaining ( $r = 0.99$ ;  $p < 0.001$ ).

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. The number of aggressive interactions exhibited by an individual fish in 10 min. was not the same in all treatments ( $F_{3,60} = 6.06$ ,  $p = 0.0011$ ). Fisher's least significant difference procedure indicated that rates of aggression in the rainbow trout only treatment were significantly different from the other treatments ( $P < 0.05$ ) and there were no differences between the other treatments (Fig. 5.3). 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 interaction per 10 min (Fig. 5.3).

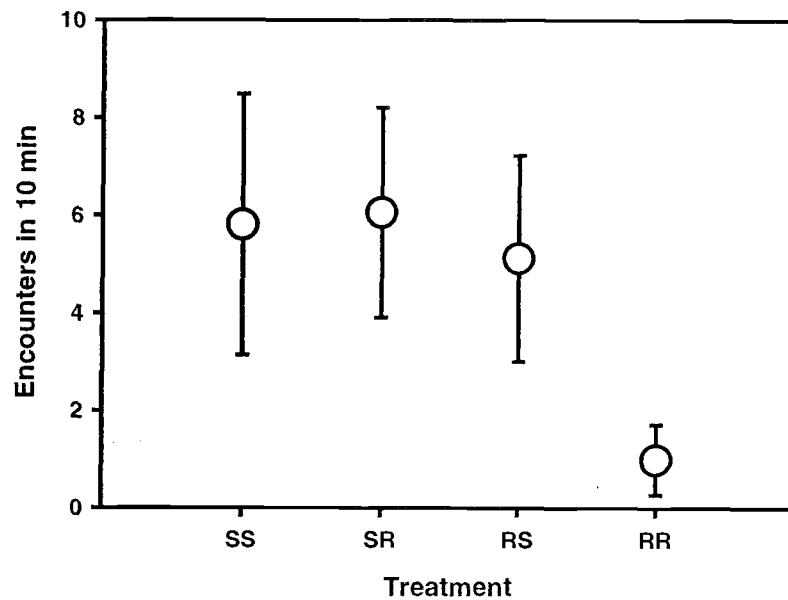


Figure 5.3. Mean and 95% confidence intervals of behavioral interactions exhibited by individual fry in each treatment during the second experiment. S = steelhead, R = resident rainbow trout, and the order indicates sequence of emergence into channel.

## Discussion

Treatments containing only resident rainbow trout fry exhibited lower levels of aggression and higher densities at the conclusion of the experiment than did those containing steelhead fry. These results suggest that there are innate differences between the two life history forms that manifest in differential habitat use and recruitment dynamics of newly emerged fry.

Contrary to the results of Hutchinson and Iwata (1997), we found that resident rainbow trout showed significantly lower levels of aggression than did steelhead. Hutchinson and Iwata (1997) examined aggression in several species of salmonids and concluded that aggression was correlated with length of stream residence. Steelhead, for example, with a juvenile stream rearing stage that lasts up to 4 years had much higher levels of aggression than chum salmon (*O. keta*) which is characterized by little to no stream residence. Hutchinson and Iwata (1997) examined levels of aggression exhibited by juvenile salmonids in small plastic troughs with no current. The resident rainbow trout were from an experimental hatchery stock in Japan that was derived from an inland California stock. The number of generations this stock was removed from the wild was not reported so it is difficult to interpret the results for wild populations. In this study, we examined aggression and recruitment dynamics of wild progeny in a more natural stream-like environment. We hesitate to extrapolate our results beyond steelhead and resident rainbow trout from the Deschutes River. Further work on steelhead and resident rainbow trout from other localities is needed to derive patterns of aggression like those reported by Hutchinson and Iwata (1997).

Our results indicate that resident rainbow trout fry cannot be used as surrogates for steelhead in the study of habitat use or population dynamics. Where steelhead and resident rainbow trout are sympatric the juveniles are indistinguishable and it seems intuitively reasonable to use resident juveniles as surrogates for steelhead in systems with declining steelhead runs.

During both experiments, rainbow trout fry seemed to use the pool-like habitats and remained in the water column when steelhead were not present. Steelhead fry, however, remained close to the substrate in the riffle-like units. In spite of these apparent differences in habitat use by the two life history forms, habitat segregation was not likely occurring. If steelhead and resident rainbow trout fry were segregating habitat the number of fry remaining in the channel in the mixed treatments should be equal to the number of fry remaining in both the steelhead and rainbow trout only treatments combined. This, however, can only really be tested in natural conditions. In observations of fry in tributaries of the Deschutes River, large schools of non-aggressive fry are regularly observed in slow moving marginal habitats and individual territorial fry are observed in faster flowing riffle-like habitats (Zimmerman, unpublished data). It is likely, that larger natural streams with a diversity of microhabitats might provide opportunity for segregation between newly emerged steelhead and resident rainbow trout fry.

There are many studies examining interspecific competition in salmonids (e.g., Hartman 1965; Everest and Chapman 1972). Segregation among habitats often serves to limit interactions between species (Nilsson 1967). Everest and Chapman (1972) concluded that populations of chinook salmon (*O. tshawytscha*) and steelhead in sympatry would use available habitat more fully and lead to higher production than would populations of either species in allopatry. Steelhead and chinook salmon juveniles used similar habitats but at different times due to differences in the timing of spawning and emergence (Everest and Chapman 1972).

There are also many studies examining intraspecific competition in salmonids (e.g., Chapman 1962; Elliot 1989; Titus and Mosegaard 1991). Intraspecific competition plays a potentially important role in the density-dependent regulation of population size. Given our understanding of inter- and intra-specific competition, how should we treat competition between life history morphs of the same species? The answer to this question is dependent on the degree of reproductive isolation between life history morphs. Wood et al. (1999) suggested that sockeye salmon and kokanee (the anadromous and non-anadromous morphs of *O. nerka*) act as different biological species in Takla Lake, British Columbia. Sockeye salmon and kokanee in Takla Lake are reproductively isolated and genetically distinct. As age 0 juveniles, sockeye salmon and kokanee showed no detectible difference in distribution and food habits were virtually identical although the proportion of sockeye and kokanee juveniles in the two arms of the lake was related to the distribution of spawning by the two forms (Wood et al. 1999).

Whether steelhead and resident rainbow trout in the Deschutes River constitute biological species is beyond the scope of this study. The juveniles, however, exhibit significantly different behavior and recruitment dynamics. As a result, studies and management concerning behavior or habitat use by steelhead and resident rainbow trout fry should consider the potential for differences between the two life history forms of the same species.

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## CHAPTER 6

**Utilization of Mainstem and Tributary Habitats by Steelhead and  
Resident Rainbow Trout (*Oncorhynchus mykiss*) in the Deschutes  
River, Oregon**

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## Abstract

The distribution of the progeny of steelhead and resident rainbow trout (*Oncorhynchus mykiss*) in mainstem and intermittent tributary rearing habitats was compared in the Deschutes River, Oregon. Otolith microchemical analysis of Sr/Ca ratios in the primordia and first summer growth region was used to identify progeny of steelhead and resident rainbow trout. Significantly higher Sr/Ca in the primordia characterized steelhead progeny. The relative proportion of steelhead and resident rainbow trout progeny differed in mainstem Deschutes River and tributary rearing habitats. Mainstem rearing habitats were almost exclusively used by the progeny of resident rainbow trout and the lower portions of tributaries exhibiting intermittency and high water temperatures were used exclusively by steelhead progeny. The upper portion of one tributary contained only progeny of resident rainbow trout upstream of a barrier to steelhead migration suggesting that resident populations were present in the headwaters of that stream. Growth was greater in tributary habitats due to warmer water temperatures. Intermittent tributaries provide important spawning and rearing habitat for steelhead in spite of the risks associated with spawning in streams characterized by harsh environmental conditions. Differential habitat use by steelhead and resident rainbow trout may play an important role in the segregation of the two life history forms.

## Introduction

Intermittent tributaries are often discounted as important habitat for fish due to their ephemeral nature. They may, however, serve as important spawning and nursery habitats for some species. Intermittent tributaries can be important habitat for steelhead and resident rainbow trout (*Oncorhynchus mykiss*). Everest (1973) reported that many tributaries of the Rogue River, Oregon were utilized by spawning steelhead in winter but were completely dry by summer. Similarly, Erman and Hawthorne (1976) reported disproportionate use of an intermittent tributary in a high Sierra stream in California. Erman and Hawthorne (1976) suggested that use of this tributary was related to earlier peak flows resulting from snow melt and a lack of competing brook trout (*Salvelinus fontinalis*). Downstream movement of fry from this tributary was highly correlated with discharge and large numbers of fry emigrated from the stream before it was dry (Erman and Leidy 1975). Everest (1973) and Faudskar (1980) suggested that downstream movement of steelhead fry from intermittent tributaries in the Rogue River was related to increasing intraspecific interactions and decreasing habitat area.

Rainbow trout are a polytypic species and exist in populations of resident rainbow trout, adfluvial and fluvial rainbow trout, and anadromous steelhead (Behnke 1992; Scott and Crossman 1973). In many locations, multiple life history forms coexist within the same watershed. The relation of these sympatric life history forms is unresolved.

The distribution of life history forms throughout a watershed may play an important role in the structure of multiple life history forms. For example, anadromous and resident threespine stickleback (*Gasterosteus aculeatus*) populations in the Navarro River, California segregated among habitats (Snyder and Dingle 1990). The freshwater resident population migrated less than 5 km and spawned in small tributaries. The anadromous population migrated at least 10 km between the estuary and lower reaches of the mainstem Navarro River to spawn. Rearing experiments indicated that life history (freshwater vs. anadromous) was genetically based (Snyder and Dingle 1990). Similarly, seasonal ecotypes of chinook salmon (*O. tshawytscha*) segregate between mainstem and tributary habitats. In the Deschutes River of Oregon, for example, spring run chinook salmon utilize spring-fed tributary streams and fall run chinook salmon utilize mainstem spawning habitats (Lindsay et al. 1989). Segregation between mainstem and tributary habitats serves to limit gene flow between the two populations. Differential use among locations within a watershed by different ecotypes of the same species such as that exhibited by threespine stickleback and chinook salmon has not been described for sympatric steelhead and resident rainbow trout.

In this study, we examined the proportion of steelhead and resident rainbow trout juveniles in mainstem rearing habitats exhibiting perennial flow and tributaries characterized by intermittent flows and high water temperatures. We were interested in the role of intermittent tributaries as habitat for steelhead and resident rainbow trout. Studies concerning steelhead and resident rainbow trout juveniles are

complicated by the inability to differentiate juveniles of steelhead and rainbow trout based on gross morphology or coloration. The progeny of anadromous and resident salmonids can be determined based on otolith microchemistry (Kalish 1990; Rieman et al. 1994; Radtke 1995). We used otolith microchemistry to identify the progeny of steelhead and resident rainbow trout in tributary and mainstem rearing habitats. We tested the null hypotheses that the proportion of steelhead progeny and resident rainbow trout progeny would be equally distributed throughout all habitats and the size of young-of-year *O. mykiss* would be the same in tributary and mainstem-rearing habitats.

## **Materials and Methods**

### **Site description**

The Deschutes River, a mid-Columbia River tributary located in north central Oregon, drains a watershed of approximately 27,200 km<sup>2</sup> (Fig. 6.1). The western portion of the basin is primarily spring fed and mean monthly discharge near its confluence with the Columbia River ranges from 124 m<sup>2</sup>·s<sup>-1</sup> in August to 212 m<sup>2</sup>·s<sup>-1</sup> in February (1957 – 1997: United States Geological Survey Data). There are only four perennial tributaries along the lower 160 km and many intermittent tributaries. Anadromous salmonids once inhabited much of the basin, but since 1968 have been limited to the lower 160 km downstream of the Pelton-Round Butte dam complex. The Deschutes River currently supports populations of spring and fall chinook salmon, steelhead, rainbow trout, mountain whitefish (*Prosopium williamsoni*), bull trout (*S.*

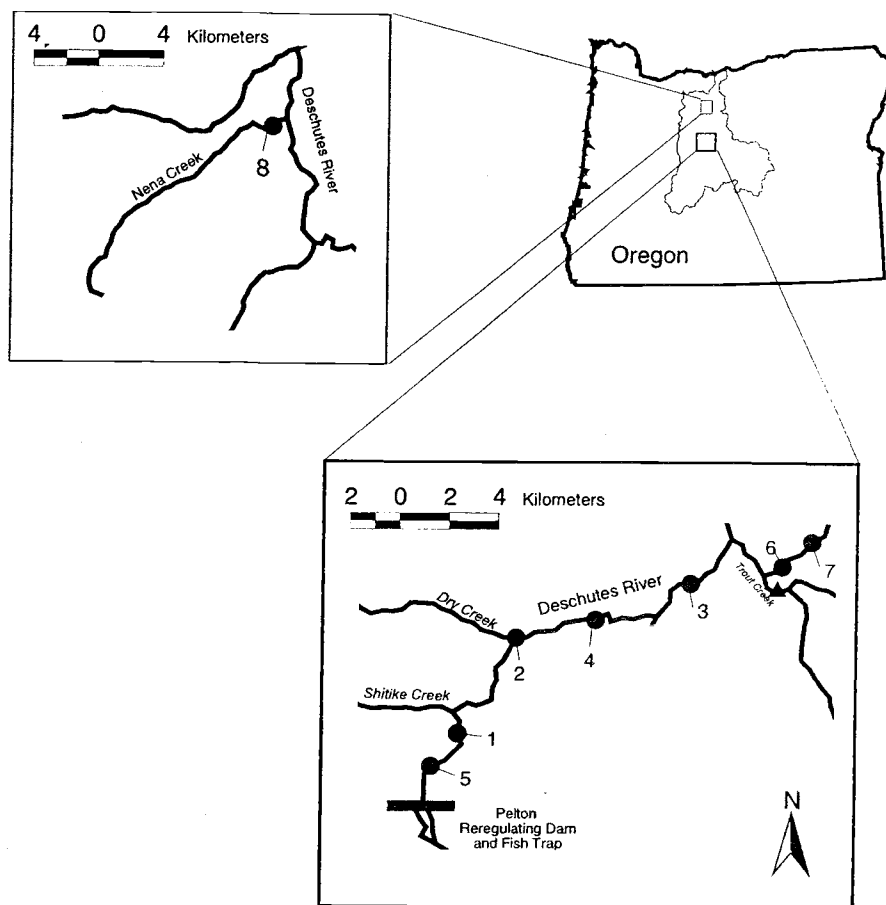


Figure 6.1. Location of sampling sites, Deschutes River, Oregon. Study sites are: 1 – 5 mainstem, 6 = Tenmile Creek below Falls, 7 = Tenmile Creek above Falls, and 8 = Nena Creek.

*confluentus*), northern pikeminnow (*Ptychocheilus oregonensis*), suckers (*Catostomus* spp.), speckled dace (*Rhinichthys osculus*), and sculpins (*Cottus* spp).

Tenmile Creek is a tributary to Trout Creek and encompasses a watershed of 5.7 km<sup>2</sup> (Fig. 6.1). The stream is approximately 18 km long. A falls consisting of three plunge pools separated by several steep drops is located approximately 2 km upstream from the confluence with Trout Creek. Although the falls have been modified to allow passage of fish, passage is dependent on flow conditions, which may not occur in all years. Several portions of the stream are intermittent including the lower 200 m. Summer water temperatures in Tenmile Creek ranged from 18 to 24°C. Nena Creek is a tributary to the Deschutes River located 93 km upstream from the confluence of the Deschutes River and the Columbia River. The Nena Creek basin encompasses 11.5 km<sup>2</sup> and the stream is approximately 20 km long (Fig. 6.1). Like Tenmile Creek, the lower portion of the stream is intermittent. A small waterfall approximately 1 km upstream from the confluence with the Deschutes River prevents upstream migration. Mainstem rearing sites were located in the 21 kilometers of mainstem river between the Pelton Reregulating Dam at river km 160 and the Trout Creek campground at river km 139.

### **Juvenile sampling**

Juvenile rearing habitats in the mainstem Deschutes River were electrofished in May, July, September, and November of 1995. Juvenile rearing habitats included edge habitat and side-channels. Snorkel surveys indicated that these habitats were the

primary rearing habitats for juvenile *O. mykiss*. All fish encountered were measured and weighed. One side-channel was selected during each survey period and all juvenile *O. mykiss* were collected for otolith analysis. We measured (fork length) and weighed each fish, removed sagittal otoliths, and preserved each fish in alcohol. A different side-channel was chosen for otolith collection during each survey period so the composition of juveniles would represent the natural mixture of steelhead and resident rainbow trout progeny.

On 29 May 1996 and 2 June 1996, we conducted an electrofishing survey of Tenmile Creek and at several sites on the mainstem to compare lengths of young-of-year *O. mykiss*. On Tenmile Creek, fish were collected in all habitats present in the lowermost 1 km beginning at the confluence of Tenmile and Trout Creeks. All fish encountered were measured (fork length), weighed, and released. Seven young-of-year *O. mykiss* killed during electrofishing were collected for otolith analysis. Several mainstem habitats were sampled in the same manner on 29 May 1996 and 31 July 1996. The size distribution of young-of-year *O. mykiss* was compared by plotting length frequencies during each survey.

In 1998, we collected *O. mykiss* from below and above Tenmile Creek falls and from the lowermost 200 m of Nena Creek. We measured (fork length) and weighed each fish, removed sagittal otoliths, and preserved each fish in alcohol.

### Otolith preparation and microchemical analysis

One sagittal otolith from each fish was mounted sulcus side down with Crystal Bond 509 on a microscope cover slip attached to a standard microscope slide. The otolith was then ground with 1200-grit sandpaper in the sagittal plane to the level of the nucleus. The mounting medium was heated and the otolith turned sulcus side-up. The otolith was then ground with 1200-grit and 2000-grit sandpaper in the sagittal plane to the level of the primordia and polished with a slurry of 0.05  $\mu\text{m}$  alumina paste. The cover slip 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 400 Å carbon layer.

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). Sr was measured using the TAP crystal and Ca was measured using the PET crystal.

Maternal origin was determined by comparing Sr/Ca in the primordia with Sr/Ca in the summer growth region outside of the nucleus. A fish was determined to be of anadromous maternal origin if the Sr/Ca ratio in the primordia was significantly



higher than that in the first summer growth region based on an unpaired one-tailed t-test with  $\alpha = 0.05$ .

## Results

### Proportion of steelhead and resident rainbow trout progeny

In 1995, a total of 40 yearling and 173 young-of-year *O. mykiss* juveniles were collected from mainstem rearing habitats during bimonthly surveys (Table 6.1). All young-of-year were progeny of resident rainbow trout females, and all but two of the yearling *O. mykiss* were progeny of resident rainbow trout females (Table 6.1). All *O. mykiss* juveniles collected upstream of the falls on Tenmile Creek were the progeny of resident rainbow trout females (Table 6.1). In contrast, all but one juvenile *O. mykiss* collected below the Tenmile Creek falls were progeny of steelhead females. Similarly, all *O. mykiss* collected in the lowermost 200 m of Nena Creek were progeny of steelhead females (Table 6.1).

The comparison of Sr/Ca in the primordia and within the first summer of otolith growth provided an unambiguous discrimination of maternal origin. Significance of all comparisons with primordia Sr/Ca greater than Sr/Ca in the otolith growth during the first summer was less than 0.001 (unpaired one-tailed t-test for each fish). The distribution of Sr/Ca of all sampling points among fish in the primordia and summer growth for each sampling area was either unimodal or bimodal with little overlap (Fig. 6.2). In *O. mykiss* collected from mainstem rearing habitats, Sr/Ca measurements in primordia and first summer growth region were overlapping with a

Table 6.1. Proportion of steelhead (STS) and resident rainbow trout (RBT), mean fork length, and mean weight of *O. mykiss* collected in mainstem (M) and tributary (T) habitats in the Deschutes River, Oregon.

Date	Location	Habitat	Age Class	N	Mean Length (mm)	Mean Weight (g)	STS	RBT
1 June 1995	Mainstem 1	M	1	10	103	15.8	0	1.0
27 June 1995	Mainstem 2	M	0	23	31	0.2	0	1.0
28 July 1995	Mainstem 3	M	1	10	132	39.0	0.1	0.9
			0	61	41	0.8	0	1.0
25 Sept 1995	Mainstem 4	M	1	10	137	18.8	0.1	0.9
			0	41	51	1.6	0	1.0
29 Nov 1995	Mainstem 5	M	1	10	115	18.8	0	1.0
			0	48	60	2.6	0	1.0
2 June 1996	Tenmile Below Falls	T	0	7	38	0.43	1.0	0
24 April 1998	Tenmile Above Falls	T	2	5	153	27.8	0	1.0
28 Oct 1998		T	0	10	86	6.5	0	1.0
12 June 1998	Tenmile Below Falls	T	0	3	37	0.32	1.0	0
10 July 1998		T	0	10	69	3.3	0.9	0.1
28 Oct 1998		T	0	5	79	4.9	1.0	0
10 July 1998	Nena Creek	T	0	9	73	2.7	1.0	0

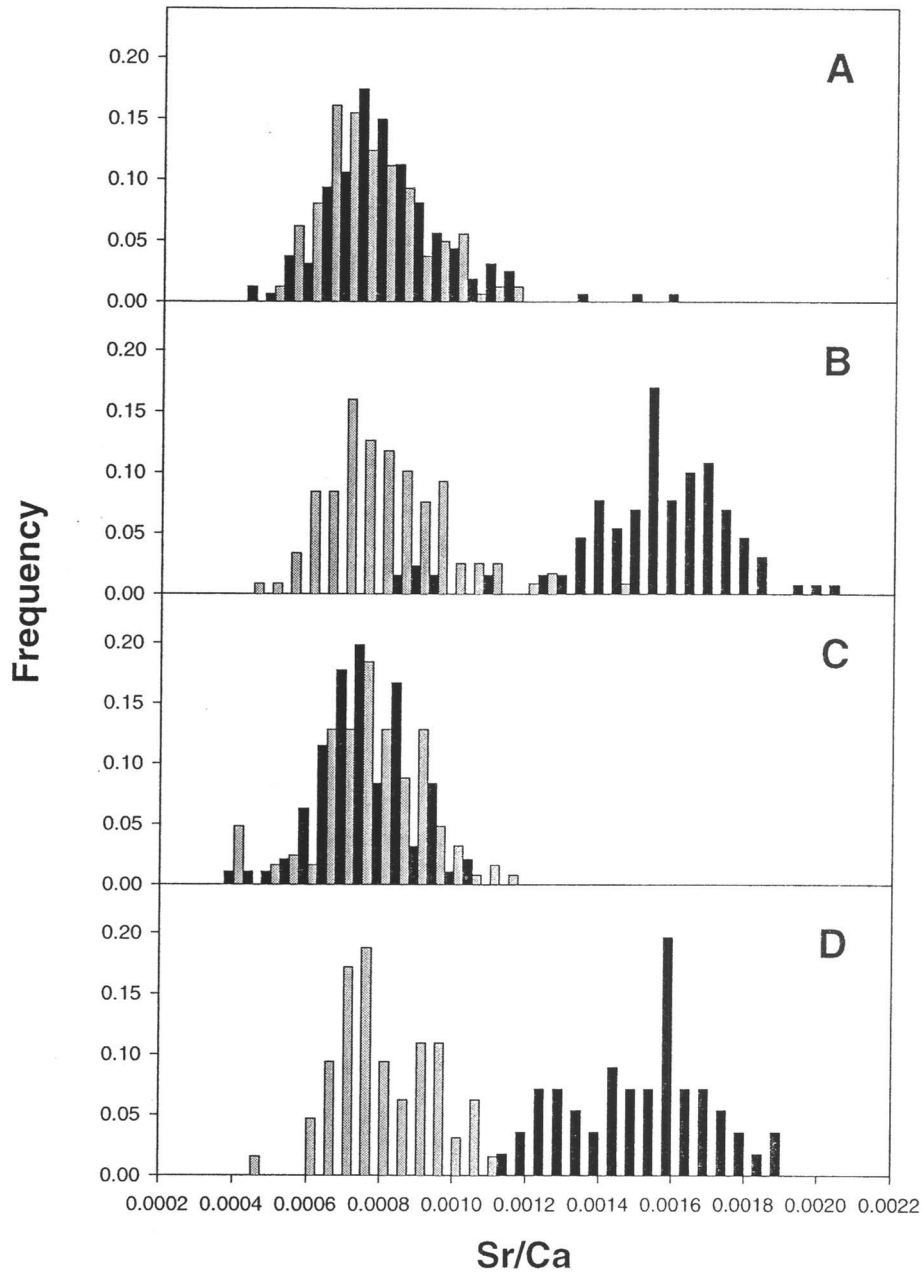


Figure 6.2. Distribution of Sr/Ca in primordia (black bars) and summer growth region (gray bars) in juvenile *O. mykiss* collected from (A) mainstem Deschutes River, (B) Tennile Creek below falls, (C) Tennile Creek above falls, and (D) Nena Creek.

small number of higher Sr/Ca in primordia corresponding to the two yearling steelhead progeny (Fig. 6.2a). Sr/Ca measurements in the primordia and first summer growth in juveniles collected from below the falls on Tenmile Creek and in lower Nena Creek were bimodal and not overlapping with the exception of the few low Sr/Ca primordia measurements associated with the single progeny of resident rainbow trout collected in Tenmile Creek below the falls (Fig. 6.2b and 6.2d). Primordia and first summer growth region Sr/Ca measurements in *O. mykiss* collected above the falls on Tenmile Creek were low and unimodal indicating that no steelhead progeny were present (Fig. 6.2c). The size distribution of fish collected for otolith analysis during bimonthly electrofishing surveys was similar to the size distribution of fish sampled in all mainstem-rearing habitats (Fig. 6.3).

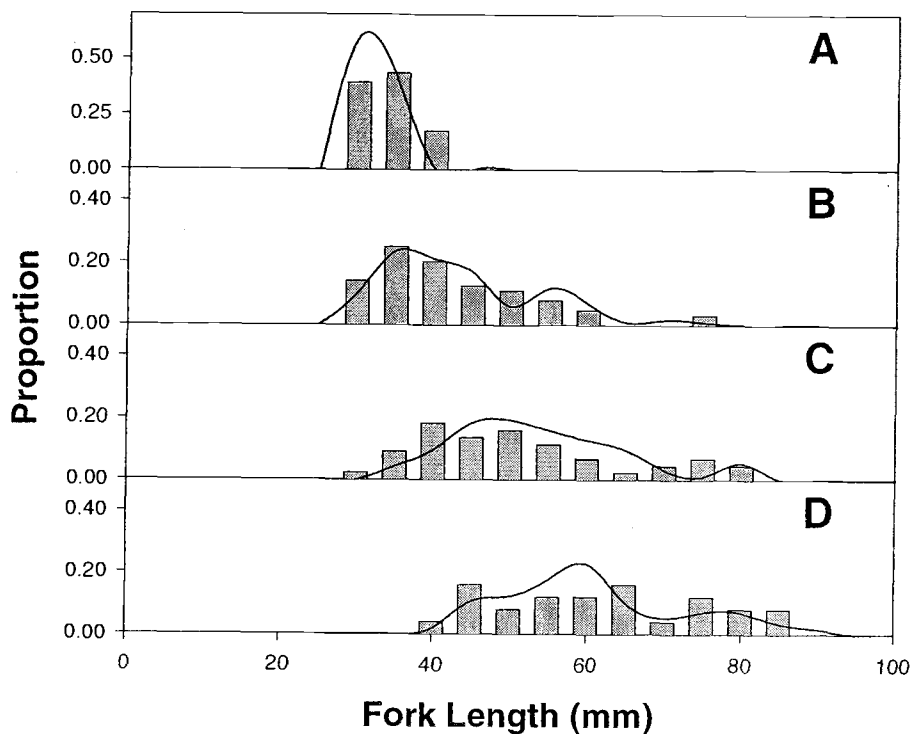


Figure 6.3. Length frequency of *O. mykiss* fry in rearing habitats (line) and of fry collected for otolith analysis (bars) in (A) June 1995, (B) July 1995, (C) September 1995, and (D) November 1995, mainstem sites, Deschutes River, Oregon.

#### Size of young-of-year *O. mykiss* in tributaries and mainstem rearing habitats

Young-of-year *O. mykiss* in Tenmile Creek were significantly larger than fry in the mainstem. Steelhead fry electrofished from Tenmile Creek on 2 June 1996 were significantly larger than fry electrofished in the mainstem Deschutes River on 19 May 1996 (one-tailed  $t = 7.02$ ;  $P < 0.0001$ ) (Fig. 6.4). The mean length ( $\pm$  S.D) of fry in Tenmile Creek was  $50 \text{ mm} \pm 7.7 \text{ mm}$  with a range of 42 to 66 mm (Fig. 6.4). On 29 May 1996, fry in the mainstem had a mean length ( $\pm$  S.D) of  $34 \text{ mm} \pm 5.7 \text{ mm}$  and a

range of 26 to 41 mm. Fry in the mainstem did not reach lengths comparable to those seen in Tenmile Creek on 2 June 1996 until the end of July when fry in the mainstem had a mean length ( $\pm$  S.D) of 41 mm  $\pm$  5.7 mm with a range of 27 mm to 76 mm (Fig. 6.4).

## **Discussion**

Although intermittent flow and high water temperatures characterize many of the tributaries to the Deschutes River, they serve as important habitats for steelhead. Tenmile Creek below the falls and Nena Creek were used exclusively by steelhead in spite of the risks associated with spawning in streams characterized by seasonally low or intermittent flows. Previous studies have described the importance of such tributaries for steelhead and resident rainbow trout (Everest 1973; Erman and Leidy 1975; Erman and Hawthorne 1976) but differential habitat use by sympatric life history forms has not previously been demonstrated. Steelhead and resident rainbow trout may constitute reproductively isolated populations in the Deschutes River and exhibit spatial and temporal segregation in spawning habitat use within the mainstem (Zimmerman and Reeves in review). Differential use of tributary and mainstem spawning and rearing habitats by steelhead and resident rainbow trout may further serve to segregate the two populations.

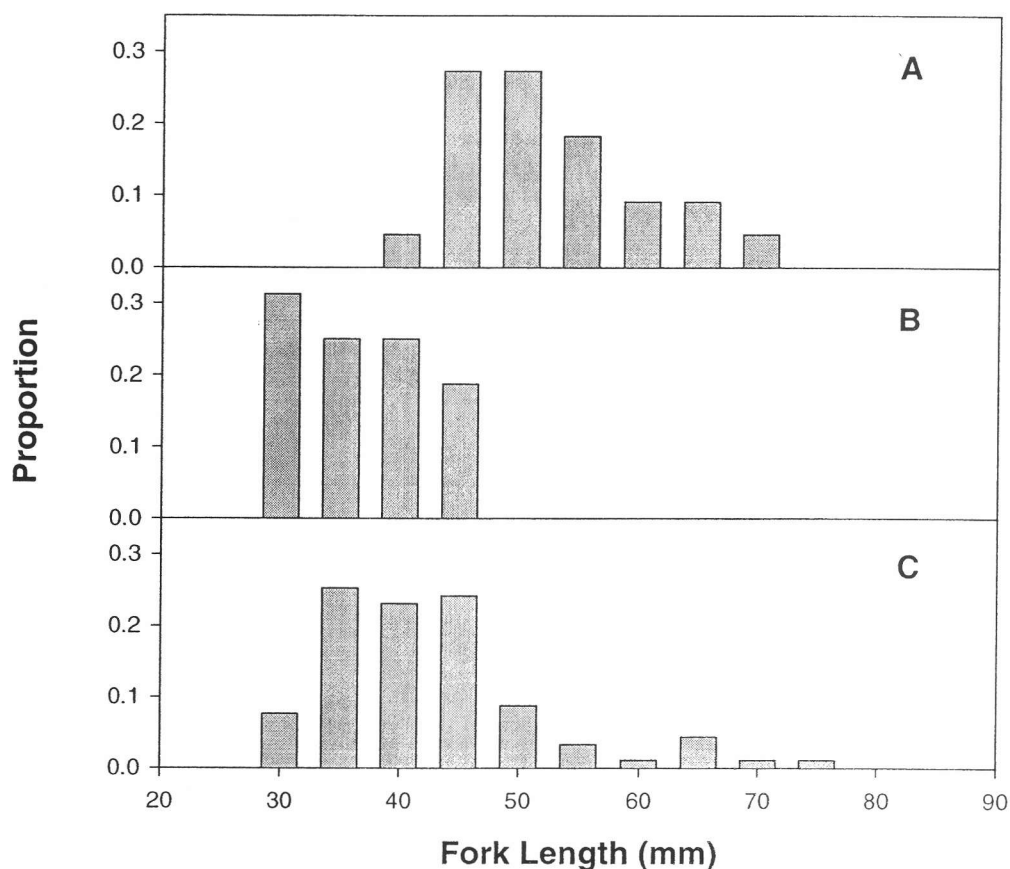


Figure 6.4. Length frequency of young-of-year *O. mykiss* in (A) Tenmile Creek on 2 June 1996, (B) mainstem Deschutes River on 29 May 1996, and (C) mainstem Deschutes River on 31 July 1996.

The distribution of spawning by steelhead and resident rainbow trout may play an important role in the distribution of juveniles of each life history form. Wood et al. (1999) examined diet and competition between progeny reproductively isolated and genetically distinct sockeye salmon and kokanee in Takla Lake, British Columbia. Sockeye salmon progeny were predominant in one arm of the lake and kokanee progeny were predominant in another arm and this pattern was attributed to the

distribution of spawning adults. Steelhead spawning in Tenmile Creek was restricted to the area downstream of the falls. Total number of steelhead redds encountered were 7, 2, and 2 in 1996, 1997, and 1998, respectively. In 1998, both steelhead redds were located in the lowermost 150 m of the stream. Steelhead carcasses were observed in 1996 and were associated with a redd just below the falls. No resident rainbow trout redds nor adult resident rainbow trout were observed in the lower 4.5 km of Tenmile Creek in any of the three years studied. Based on the occurrence of resident rainbow trout progeny above the falls, it appears likely that resident rainbow trout populations are present in the upper portion of the Tenmile Creek watershed. The lower sections of tributaries such as Tenmile Creek and Nena Creek are probably not used by resident rainbow trout due to timing of flows and higher water temperatures. The lower portions of Shitike Creek, a spring-fed tributary on the western side of the Deschutes River (Fig. 6.1), are extensively used by resident rainbow trout (Zimmerman, unpublished data). These resident rainbow trout migrate upstream from the mainstem Deschutes River in late May, June, and July. This timing of fluvial migration by resident rainbow trout occurs as flows are extremely low in tributaries such as Tenmile Creek and Nena Creek.

Differences in growth between tributary and mainstem-rearing habitats may play an important role in subsequent behavioral interactions. Water temperatures in the lower portion of Tenmile Creek were consistently higher than in the mainstem Deschutes River and lead to greater growth by juveniles in tributary habitats. Given the importance of size of fry in determining the outcome of competitive interactions in



steelhead (Chandler and Bjornn 1988), it is likely that the fry emigrating from Tenmile Creek would have a competitive advantage against the smaller steelhead and rainbow trout fry inhabiting the mainstem.

Steelhead and resident rainbow trout segregate rearing habitats in the Deschutes River. Steelhead, spawning in tributary habitats not used by resident rainbow trout, may benefit from larger fry than steelhead and resident rainbow trout spawning in the mainstem Deschutes River. This advantage comes at some costs. Fry that do not emigrate from desiccating tributary habitats or locate cooler pool habitats to over-summer may experience high mortality. On the other hand, fry that experience greater growth in tributaries and emigrate as flow drops may experience greater competitive advantage and higher survival to smolt than juveniles that spend their whole life in mainstem-rearing habitats. Analysis of back-calculated length of smolts of steelhead from the Keogh River, British Columbia indicates that smolt-to-adult survival is positively correlated to smolt size (Ward et al. 1989; Ward and Slaney 1989). The effect of accelerated growth in tributary habitats on maturation, smolting, and smolt-to-adult survival deserves further study in the Deschutes River. Further work based on otolith growth patterns or some other means of assessing growth in juvenile *O. mykiss* is needed to assess the importance of tributaries in the relation of steelhead and resident rainbow trout in the Deschutes River.

It is not clear how the current pattern of habitat use by steelhead and resident rainbow trout evolved in the Deschutes River. The role that segregation among tributaries and the mainstem plays in the dynamics and maintenance of population

structure is unclear and deserves further examination. Segregation between life history types within watersheds is possible and may provide important means of reproductive isolation and selection.

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## CHAPTER 7

### Conclusion

In the preceding chapters, I have described several studies concerning sympatric steelhead and resident rainbow trout. I examined life history-related or racial differences between steelhead and resident rainbow trout in an effort to better understand the relation between the two life history forms. These results provide information concerning life history of adults and interactions between the two forms. Based on the contribution of steelhead and resident rainbow trout progeny to the adult spawning population of each life history form, steelhead and resident rainbow trout in the Deschutes River constitute reproductively isolated populations (Chapter 2). Progeny of the alternative life history form were not observed in the adult spawning population of either steelhead or resident rainbow trout. Reproductive isolation between life history forms was not evident in the Babine River. This suggests that there is not a single explanation of the structuring of anadromous and non-anadromous *O. mykiss* but rather, it is likely to be specific to location.

Segregation of spawning habitat serves to limit gene flow between steelhead and resident rainbow trout in the Deschutes River (Chapter 3). Although, there was a small proportion of the total rainbow trout population spawning concurrent with steelhead spawning, use of different microhabitats served to isolate the two forms spawning at the same time. Neither steelhead nor resident rainbow trout fry have a

competitive advantage due to earlier emergence or larger size at emergence (Chapter 4), although, the two life history forms exhibit very different behavior and levels of territoriality (Chapter 5). Examination of the proportion of steelhead and resident rainbow trout progeny in tributary and mainstem rearing habitats indicated that there was segregation among habitats (Chapter 6). Given the degree of segregation of spawning and rearing habitats and the divergence of behavior following emergence, steelhead and resident rainbow trout in the Deschutes River are very different morphs of the same species.

Results of these studies show that the two life history forms should, in essence, be considered as separate biological species in the Deschutes River. Reproductively isolated morphs that exhibit fixed differences in life history would be diagnosed as separate species under some species concepts (e.g., Mayden and Wood 1995). I do not suggest that there should be a change in taxonomic status for steelhead and resident rainbow trout, but rather that the two life history forms *act* as different species in the Deschutes River. Hence, conservation and study should be conducted in a manner that recognizes the inherent differences between these reproductively isolated populations.

The evolution of diadromy is related to productivity of freshwater and marine environments (Gross 1987; Gross et al. 1988). In temperate latitudes, oceans are more productive than freshwater habitats and anadromous species predominate those exhibiting diadromy (Gross et al. 1988). On the other hand, in tropical regions, catadromous species predominate those exhibiting diadromy due to greater

productivity in freshwater habitats compared to tropical oceans (Gross et al. 1988). Gross (1987) argued that diadromous life histories will evolve through natural selection only if the migration results in a gain in fitness that exceeds the costs of migration. Wood (1995) presented a model that combined the role of productivity in freshwaters and difficulty of migration to describe the occurrence of anadromous and non-anadromous populations of sockeye salmon. As productivity of freshwaters increases the occurrence of resident forms increases and as difficulty of migration increases that occurrence of anadromous forms decreases (Wood 1995). Within an intermediate range of productivity and migration difficulty sockeye salmon and residual forms (non-migratory) sockeye salmon are expected. At greater productivity, and higher difficulty of migration reproductively isolated populations of anadromous sockeye salmon and non-anadromous kokanee are expected (Wood 1995).

The model presented by Wood (1995) for sockeye salmon is probably applicable to steelhead and resident rainbow trout. Rivers, such as the Deschutes River, which are characterized by stable flows, high productivity, and moderate distance from the ocean are likely to contain reproductively isolated steelhead and resident rainbow trout populations. The occurrence of reproductively isolated resident rainbow trout populations is probably driven by the high productivity and stability of environment that leads to high fitness without migration to the ocean. Geologic events, which served to isolate resident rainbow trout in the Deschutes River with later recolonization by steelhead, are likely to have reinforced selection of a reproductively isolated resident population (as discussed in Chapter 3). The Babine River probably

falls within the upper range of residualism and coexistence of resident and anadromous forms. Hence, progeny of both steelhead and resident females are present in the adult populations of both steelhead and resident rainbow trout. Lower productivity and low difficulty of migration is common in coastal stream throughout the range of *O. mykiss* and would, thus, explain the occurrence of only steelhead in these systems without a resident or large residual component.

In some cases, the presence of both steelhead and resident rainbow trout in a river system may play an important role in the persistence of *O. mykiss* in that system. Segregation into resident and migratory life history morphs can act as a buffer against extinction in species inhabiting unstable environments. A species that covers a wide range of aquatic environments by partitioning into resident and migratory forms may be in a better position for long-term survival where conditions are dynamic and unpredictable (Northcote 1992). Life history variation may, therefore, provide an important mechanism for preserving small populations of salmonids in marginal habitats. Saunders and Schom (1985) examined the high variability of life history parameters in Atlantic salmon. Atlantic salmon exhibit variable ages at maturity and may spawn more than once. Saunders and Schom (1985) concluded that this variability in life histories might act as a safeguard against loss of small populations living in harsh conditions (i.e., small streams prone to large annual variations in discharge). As a result of the mixture of age classes in the spawning population, the effective spawning population may be potentially larger, and the level of inbreeding relatively low.



In some *O. mykiss* populations, it is probable that the presence of both resident and migratory components of a population serves to spread the risk of extinction. If unpredictable environmental conditions lead to high mortality or complete loss of one component of the population, maintenance of the species in that location is ensured by the other component. For example, drought conditions could lead to extirpation of fish within a watershed. The anadromous component of that population is under a different set of environmental conditions in the ocean during the period of drought. Thus, the species is not completely extirpated from the stream. Nielsen et al. (1997) suggest that southern California streams that are no longer connected to the ocean due to water withdrawal may serve as refugia for residual *O. mykiss* that have recent anadromous lineage but are now non-anadromous. Restoration of steelhead is expected from these populations with improvements to the freshwater habitat and reconnection to the sea. Where steelhead and resident rainbow trout are reproductively isolated, such as in the Deschutes River, restoration of steelhead from resident populations is not likely. Conservation and restoration of steelhead and resident rainbow trout is critically tied to the relation between life history forms. Recognition of this relationship and further investigation is needed if we are to maintain the range of life history found in *O. mykiss*.

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