

Anthropogenic hybridization of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) with rainbow trout (*O. mykiss*)

by

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A Professional Paper

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ABSTRACT

The range and abundance of genetically pure westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) has greatly decreased as a result of the introduction of, and hybridization with, rainbow trout (*O. mykiss*). By examining the ecology, physiology and the phylogenetic relationship, between these two closely related fishes, the characterization and mechanisms of hybridization can be better understood. Derived from the same ancestor these two taxa are morphologically and genetically very similar. Occurring both in sympatry and allopatrically they have similar ecological and physiological requirements. Although in sympatry interspecific reproductive isolation mechanisms limit introgression, they are inversely affected by anthropogenic rainbow trout stocking density. Increasing introductions result in a complete breakdown of pre-zygotic and post-zygotic selection leading to the formation of hybrid swarms. Introgression then spreads both in a stepping stone and continental island invasion pattern. The only viable management alternative, isolation via upstream migration barriers, can increase the risk of extinction due to demographic and environmental stochasticity, as well as reducing genetic diversity. Relegated to isolated headwater streams, less than 10% of historical westslope cutthroat trout populations remain genetically pure. Given continued human mediated introductions and the lack of effective conservation strategies, it is unlikely that westslope cutthroat trout will retain its genetic integrity as unique subspecies of cutthroat trout.

ACKNOWLEDGEMENTS

This professional paper is the result of a lifelong passion for nature, trout and the lotic ecosystems in which they live. The more I study and learn, trying to understand the way in which natural processes govern and have formed our surroundings, the more firmly I am reassured the presence of the great engineer. I unequivocally believe that God our Father, his son Jesus Christ and the Holy Spirit have created all things on earth for man.

And God blessed them. And God said to them, “Be fruitful and multiply and fill the earth and subdue it, and have dominion over the fish of the sea and the birds of the heavens and over every living thing that moves on the earth.” Gen 1:28

Furthermore, I truly believe that humans are capable of amazing things, after all the LORD said it himself, “...this is only the beginning of what they will do. And nothing that they propose to do will now be impossible for them.” (Gen 11:6). Yet “it is not in man who walketh to guide his steps (Jeremiah 10:23). There are not words to express enough humility or thankfulness to justify such love that his blessings have bestowed upon me, yet I will continue to give him all of the glory and honor.

I want to thank my mom (Bonnie) for instilling in me the knowledge and faith I know to be true and always loving and supporting me; never being afraid to tell me when I am not honoring God. To my Pap - Junior, who passed away during my time in graduate school, I say thank you for introducing me to the world outdoors and sparking an interest in all of nature. You are deeply missed. I also must thank my brother and his wife, David and Kim Hawkins for their unwavering support of me throughout a very trying time in my life and for them opening their home to me when I no longer had one.

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Introduction

Anthropogenic activities continue to influence natural occurring ecological processes in unforeseen ways. The introduction of non-native freshwater fishes displaces and disrupts local communities (Moyle & Light, 1996), usually leading to a decline and eventual extirpation of native taxon. Biological invasions and extinctions are considered natural processes of community development (Moyle & Light, 1996) and are essential to speciation and adaptation (Barton & Hewitt, 1985). For fishes that are capable of interspecific breeding, hybridization allows for the natural flow of genes (introgression; Moyle & Light, 1996; Allendorf *et al.*, 2001). Human-mediated introgressive hybridization alters locally adapted gene complexes, degrading ecological adaptations and possibly resulting in extinction (Allendorf *et al.*, 2001). Hybridization is most common in fishes (Leary *et al.*, 1995; Allendorf *et al.*, 2001) where external fertilization and similar mating behavior provide the opportunity for crossbreeding. Limited spawning habitat and differential abundance of parental species can further magnify the level of introgression.

Normally occurring in a natural hybrid zone, Clarke *et al.* (1998) described natural introgression as “molecular leakage, the convergence of neutral and mutually advantageous genes in two species through occasional hybridization”. Natural introgression occurs as a result of hybridization between sympatric species that evolved together or through secondary contact between allopatric species (those evolving independently of one another). Although there is gene flow between these species, both taxon retain their genetic integrity. This maintenance of uniqueness has been attributed to reproductive isolating mechanisms involving pre-zygotic and post-zygotic selection processes (Ostberg & Rodriguez, 2006). Differences in the timing and location of spawning, as well as assortative mating, are considered pre-zygotic selection mechanisms (Docker *et al.*, 2003; Ostberg & Rodriguez, 2006; Kozfkay *et al.*, 2007). Post-zygotic selection can include reduced hybrid fitness, lower juvenile survival and disorientation in homing behavior (Campton & Utter, 1985; Muhlfeld *et al.*, 2009a). Historical distributions can overlap or converge creating a naturally occurring hybrid zone where parental types can either remain stable or evolve into a new species (Allendorf *et al.*, 2001). Maintenance of individual

uniqueness is attributable in part to sexual selection and the natural selection associated with environmental differences (Barton & Hewitt, 1985; Allendorf *et al.*, 2001). Speciation is the result of naturally occurring gene flow (introgression), whereby natural hybrid taxa become distinct organisms (Dowling *et al.*, 1993; Dowling & Secor, 1997). Allendorf *et al.* (2001) best conceptualized a framework on how to categorize hybridization (Figure 1).

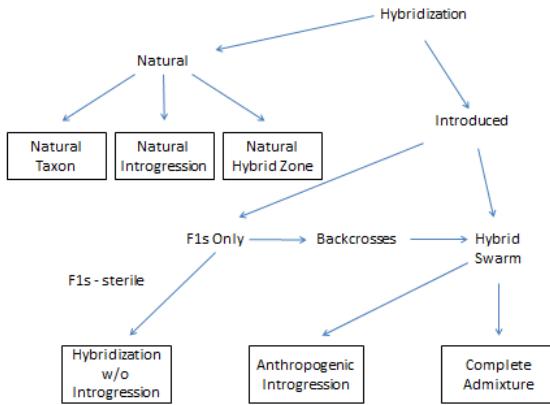


Figure 1. Conceptual diagram providing a framework to categorize hybridization. F1 represents first generation hybrids. Modified from Allendorf *et al.*, 2001.

Hybridization can occur without introgression when two species evolve allopatrically and come into contact secondarily. Whether naturally or through human-mediated introduction the resulting progeny are sterile and may not live to maturity (Allendorf *et al.*, 2001). Alternately, anthropogenic introgressive hybridization is the spread of hybrid progeny of native species and human-mediated invasive taxa. Hybrid swarms develop and continue to spread and backcross with parental stocks (Ostberg & Rodriguez, 2006; Boyer *et al.*, 2008; Muhlfeld *et al.*, 200b). Left unabated, these hybrid swarms can result in a complete admixture (Allendorf *et al.*, 2001) or genomic extinction (Allendorf & Leary, 1988).

In combination with over fishing (Behnke, 1979; MacPhee, 1966; Thurow & Bjornn, 1978) and habitat degradation and reduction (Rieman & Apperson, 1989), biodiversity of fishes is threatened worldwide by invasive species (Molye & Light, 1996; Mack *et al.*, 2000). Leading to various levels of conservation status (Table 1; Wilson & Turner, 2009) the geographic range and abundance of numerous

members of the subfamily Salmoninae (trout and salmon) have decreased in recent years. Hybridization has been considered to be the greatest threat to conservation biology for many freshwater fishes of North America (Allendorf & Leary, 1988; Muhlfeld *et al.*, 2009b). Consequently, the introduction and subsequent hybridization of non-native rainbow trout (*Oncorhynchus mykiss*) with native cutthroat trout (*Oncorhynchus clarki*) has led to threatened and endangered statuses and, in some cases, extinction of multiple cutthroat trout subspecies (Behnke, 1992).

Table 1. Historical distribution (United States) and Federal and State Agency conservation status of species and subspecies of *Oncorhynchus*. Modified from Wilson & Turner, 2009.

Scientific name	Common name	Current status ^{a,b,e}											
		AK	AZ	CA	CO	ID	MT	NM	NV	OR	UT	WA	WY
<i>Oncorhynchus gorbuscha</i>	pink salmon	+	-	-	-	-	-	-	-	-	-	PS	-
<i>O. keta</i>	chum salmon	+	-	-	-	-	-	-	-	T	-	T	-
<i>O. kisutch</i>	Coho salmon	+	-	T, E	-	-	-	-	-	T	-	T	-
<i>O. nerka</i>	sockeye salmon	+	-	-	-	E	-	-	-	+	-	T, E	-
<i>O. tshawytscha</i>	Chinook salmon	+	-	T, E	-	T	-	-	-	T	-	T, E	-
<i>O. clarkii alvordensis</i>	Alvord cutthroat trout	-	-	-	-	-	-	-	X	X	-	-	-
<i>O. c. bouvieri</i>	Yellowstone cutthroat trout	-	-	-	-	S	SC	-	+	-	+	-	+
<i>O. c. clarki</i>	coastal cutthroat trout	+	-	SC	-	-	-	-	-	S	-	PS	-
<i>O. c. henshawi</i>	Lahonton cutthroat trout	-	-	T	-	-	-	-	T	T	T	-	-
<i>O. c. lewisi</i>	westslope cutthroat trout	-	-	-	-	S	SC	-	-	+	-	PS	+
<i>O. c. macdonaldi</i>	yellowfin cutthroat trout	-	-	-	X	-	-	-	-	-	-	-	-
<i>O. c. pleuriticus</i>	Colorado River cutthroat trout	-	+	-	SC	-	-	+	-	-	CAS	-	+
<i>O. c. stomias</i>	greenback cutthroat trout	-	-	-	T	-	-	-	-	-	-	-	+
<i>O. c. utah</i>	Bonneville cutthroat trout	-	-	-	-	S	-	-	+	-	CAS	-	+
<i>O. c. virginalis</i>	Rio Grande cutthroat trout	-	-	-	SC ^e	-	-	SC ^e	-	-	-	-	-
<i>O. gilae apache</i>	Apache trout	-	T	-	-	-	-	-	-	-	-	-	-
<i>O. g. gilae</i>	Gila trout	-	T	-	-	-	-	T	-	-	-	-	-
<i>O. mykiss</i>	rainbow trout	+	-	T, E	-	T	-	-	-	T	-	T	-

^aT, threatened; E, endangered; SC, species of special concern; S, sensitive; CAS, conservation agreement species; PS, priority species; X, extinct.

^b(+), part of historical natural distribution; (-) not part of natural distribution

^eEndangered species candidate as of May 2008

Cutthroat trout are the most diverse trout species in North America and have the broadest historical distribution of any native stream dwelling trout in the western hemisphere (Colorado Department of Natural Resources, [CODNR], 2012). Due to the rugged and generally isolated topography of their range, fourteen recognized subspecies have developed (Behnke, 1992). Considered a species of special concern throughout most of its range, westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; WCT) occupy only 59% (54,600 km) of their historical lotic environments (Shepard *et al.*, 2005). Shepard (2003) proposed that due to introgressive hybridization with invasive rainbow trout (*O. mykiss*; RBT), genetically pure WCT now occupy approximately 6% of their historical range. Unfortunately

genetically pure populations are generally relegated to smaller, isolated headwater stream habitats (Williams *et al.*, 2009).

To help the reader better understand why and how anthropogenic introgressive hybridization is occurring between WCT and RBT, this paper will outline the phylogenetic relationship among the subfamily Salmoninae and identify the morphological differences and genetic distances between the two fishes. Additionally, the discussion will include the geographic distribution and ecology of westslope cutthroat trout and rainbow trout. Special emphasis will be made to address the current knowledge regarding the nature and mechanisms underlying introgression in both sympatric and allopatric populations. Furthermore, by discussing the current status of WCT populations within Glacier National Park, MT, conservation considerations will be presented addressing the best management strategies which limit anthropogenic introgressive hybridization.

Phylogeny and divergence of cutthroat trout

Since its inception in 1758 by Linnaeus, phylogenetic controversy has surrounded the group of fishes he termed *Salmo*. Although phenotypic phylogenies based on physically observable traits are inexpensive and can be obtained from both extant and fossil taxa, it is difficult to build and identify morphological datasets, taking lifetimes to compile (Conway, 2012). Genotypic investigations using DNA and allozymes to determine phylogenetic relationship allow for the examination of large numbers of characters which can be obtained within a few days (Conway, 2012). These analyses are very expensive and can normally only be obtained for extant species and specimens that have not been degraded by preservatives. The family Salmonidae provides a prime example where a wide range of investigations into both phenotypic and genotypic cladistics relationships have been established based on meristic, osteological, morphological, and molecular data.

Morphological Data

Stearley and Smith (1993) assessed 119 different morphological characteristics on 33 extant and 4 fossil taxonomic units to estimate the most parsimonious tree for Salmonidae. Three subfamilies – Coregoninae (whitefishes), Thymallinae (graylings) and Salmoninae (lenok, mekous, belvica, huchen,

taimen, chars, trout and salmon) – comprise the family Salmonidae. Within the subfamily Salmoninae they classified *Brachymystax*, *Salmothymus*, *Acantholingua* and *Platysalmo* as archaic trout combining them together with the extinct *Eosalmo* to form the sister group to all other modern salmonines (Figure 2). Stearley and Smith (1993) hypothesized that the clade below the archaic trout (which they termed Eusalmonina) is comprised of the two monophyletic groups: Salvelini (*Hucho* and *Salvelinus*; Node 19, Figure 2) and Salmonini (*Salmo* and *Oncorhynchus*; Node 22, Figure 2).

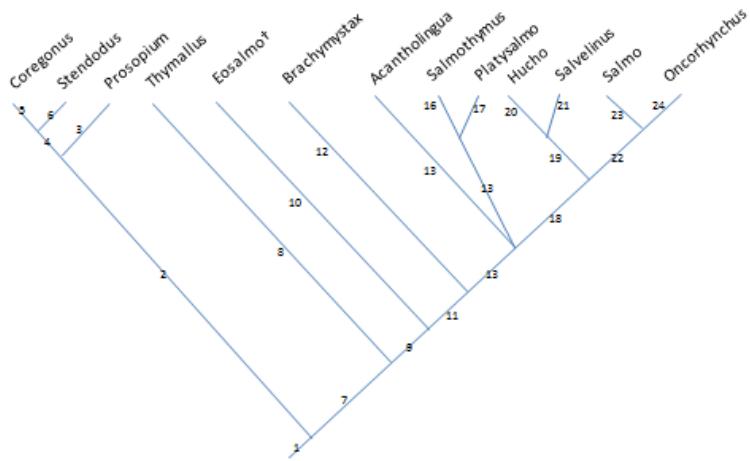


Figure 2. Cladogram of phylogenetic relationships within Salmonidae based on morphological characteristics. Character suites supporting nodes 1-24 are described in Table 2 by Stearley & Smith, 1993. The taxon known only as fossils is indicated by a dagger. Modified from Stearley & Smith, 1993.

Their argument is based on the observation that the ancestral morphological state in *Brachymystax* included a transverse tooth row (item tt, Figure 3) on the head of a short vomer (Node 9, Figure 2) which remained in *Hucho* (Node 20) but evolved in the other fishes of Salmoninae. Exhibiting a posterior extension, the vomerine shaft developed longitudinal teeth anteriorly displaying a “T-shaped” pattern within *Acantholingua*. This seemed to be reduced to an “I” pattern with the loss of the terminal ends of the transverse tooth row in *Salmothymus*, *Platysalmo* (Node 15) and all modern trout and salmon except chars (*Salvelinus*; Node 22). *Salvelinus* displayed the plesiomorphic “T” pattern of teeth but

instead of the teeth being supported by the shaft of the vomer a vomerine crest developed ventrally, anchored to the head of the vomer (Node 21, Figure 2; Figure 3).

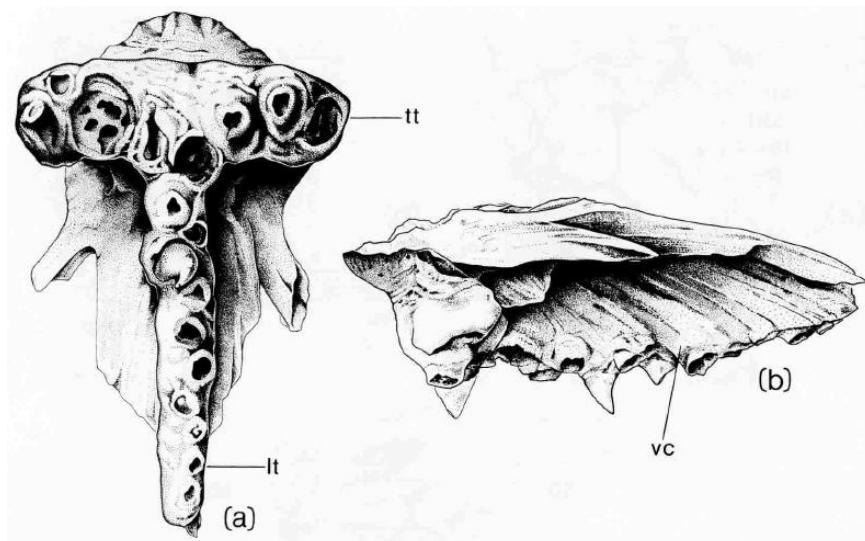


Figure 3. Vomer of *Salvelinus larsoni*;: (a) ventral view, anterior up; (b) left lateral view. Abbreviations: lt, longitudinal tooth row; tt, transverse tooth row; vc, vomerine crest supporting longitudinal tooth row. Stearley, RF, & Smith, GR. (1993). "Phylogeny of the Pacific Trouts and Salmons (*Oncorhynchus*) and genera of the Family Salmonidae. *Transactions of the American Fisheries Society*, 122(1), 1-33. Reprinted with permission of American Fisheries Society (<http://www.fisheries.org>).

Several morphological characteristics unite *Salmo* (Atlantic salmon and trout) and *Oncorhynchus* (Pacific salmon and trout) leading Stearley and Smith to group them together (Figure 4). As discussed above, the anterior transverse tooth row on an elongated vomer is reduced in Atlantic and Pacific trout and salmon. The maxillae are also elongated but arched and ovate-to-round in cross section (Stearley & Smith, 1993). Sexually dimorphic traits for breeding males include an anterior extension of the vomer and the presence of a kype on the dentary (Morton, 1965).

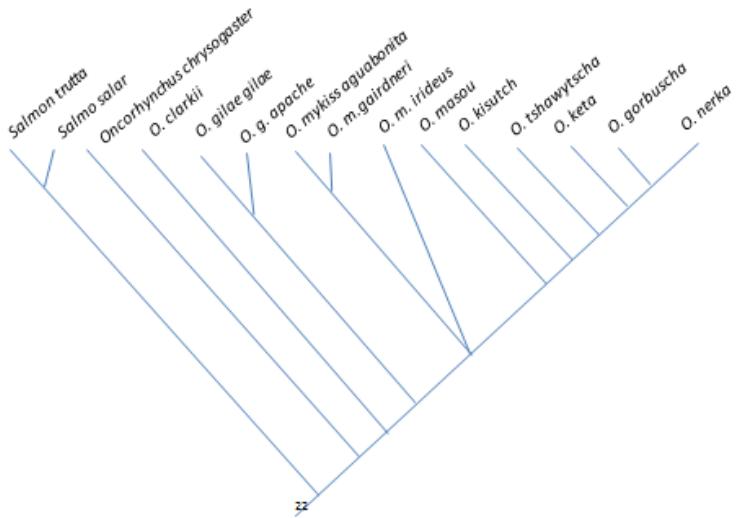


Figure 4. Consensus cladogram of relationship of *Salmo* and *Oncorhynchus* based on morphological characteristics. Character suite supporting node 22 is described in Stearley & Smith, 1993. Modified from Stearley & Smith, 1993.

Historically thought to be part of *Salmo*, C.T. Regan (1914) was the first to truly recognize osteologically that Pacific trout (rainbow trout, cutthroat trout, Mexican golden trout, Gila trout, etc.) should be in a separate natural group from their relatives in the Atlantic. Various studies in the form of meristic counts (Rounsefell, 1962), osteological examinations (Vladykov, 1963; Behnke, 1972; Cavender & Miller, 1982) and molecular data (Berg and Ferris 1984) supported the inclusion of Pacific trout in the genus *Oncorhynchus* and not *Salmo*, yet most were reluctant to place them together in a single monophyletic group (Stearley & Smith, 1989). Stearley and Smith (1993) recognized thirteen synapomorphies that are unique to Pacific trout and salmon. The most diagnostic characteristic for *Oncorhynchus* identified by Regan (1914) was a definitive posterior notch in the dermethylmoid (Figure 5). The dermethylmoid being an exoskeletal bone within the neocranium, which, when paired with the endoskeletal mesothmoid bone, is collectively known as the ethmoid.

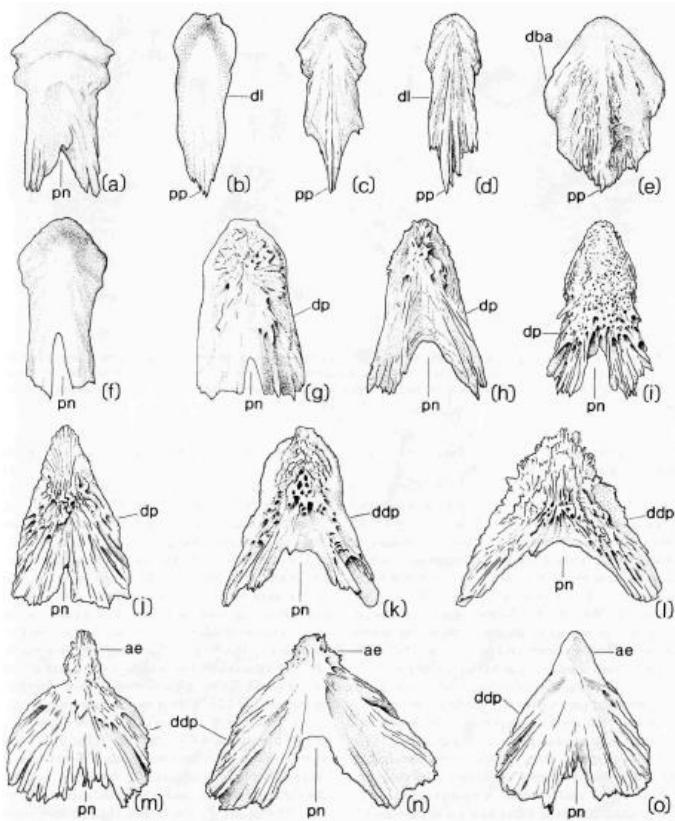


Figure 5. Dermethmoids, dorsal view, anterior up. (a) *Thymallus arcticus*, UMMX (University of Michigan Museum of Zoology); (b) *Brachymystax lenok*, UMMZ; (c) *Hucho perryi*, UMMZ; (d) *Salvelinus namaycush*, UMMZ; (e) *Salmo trutta*, UMMZ; (f) *Oncorhynchus clarki*, UMMZ; (g) *Oncorhynchus mykiss*, UMMZ; (h) *Oncorhynchus mykiss* (redband), UMMZ; (i) *Oncorhynchus rhodurus*, UMMZ; (j) *Oncorhynchus kisutch*, UMMZ; (k) *Oncorhynchus tshawytscha*, UMMZ; (l) *Oncorhynchus tshawytscha*, UMMZ; (m) *Oncorhynchus keta*, UMMZ; (n) *Oncorhynchus nerka*, UMMZ; (o) *Oncorhynchus gorbuscha*, UMMZ. Abbreviations: ae, anterior extension; dba, broad anterior; ddp, strongly divergent posterior wings; dl, long dermethmoid; dp, divergent posterior wings; pn, posterior notched; pp, posterior pointed.

Stearley, RF, & Smith, GR. (1993). "Phylogeny of the Pacific Trouts and Salmons (*Oncorhynchus*) and genera of the Family Salmonidae. *Transactions of the American Fisheries Society*, 122(1), 1-33. Reprinted with permission of American Fisheries Society (<http://www.fisheries.org>).

Also a synapomorphy, *Oncorhynchus* is the only genus in Salmoninae where the intercalary is in direct contact with the prootic (Figure 6, Stearley & Smith, 1993). Further evidence of monophyly includes; a shorter palatine crest; anterior and posterior margins of the quadrate forming an acute angle; premaxillary process of the maxilla not angled strongly dorsal; longer post orbitals and a tubular second infraorbital (Stearley & Smith, 1989; 1993). With the exception of *O. masou* (cherry salmon) and *O. keta* (chum salmon) the caudal region of all Pacific trout and salmon have three epurals (Vladykov, 1963; Stearley & Smith, 1993).

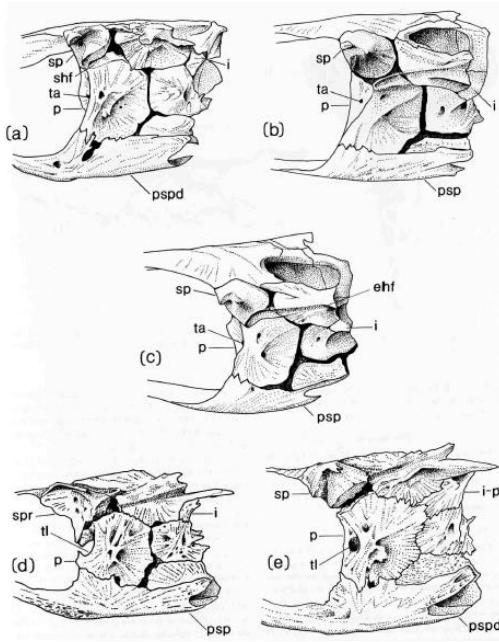


Figure 6. Otic region of neurocranium, left lateral view. (a) *Thymallus arcticus*, UMMZ; (b) *Brachymystax lenok*, UMMZ; (c) *Acantholingua ohridana*, UMMZ; (d) *Salvelinus namaycush*, UMMZ; (e) *Oncorhynchus mykiss*, UMMZ. Abbreviations: ehf, elongate hyomandibular fossa; I, intercalary not contacting prootic; i-p, intercalary contacting prootic; p, prootic; psp, parasphenoid not deep posteriorly; pspd, parasphenoid deep posteriorly; shf, short hyomandibular fossa; sp, ssphenotic without expanded anterior ramus; spr, ssphenotic ramus expanded; ta, trigeminofacial foramen anterior; tl, trigeminofacial foramen lateral and expanded.

Stearley, RF, & Smith, GR. (1993). "Phylogeny of the Pacific Trouts and Salmons (*Oncorhynchus*) and genera of the Family Salmonidae. *Transactions of the American Fisheries Society*, 122(1), 1-33. Reprinted with permission of American Fisheries Society (<http://www.fisheries.org>).

In their most parsimonious relationship, Stearley and Smith (1993) found evidence to suggest that the closest sister group to rainbow trout (*O. mykiss*) are the Pacific salmons and not cutthroat trout (*O. clarki*) as previously thought by Behnke in 1992. Morphologically *O. clarki* have several characteristics that distinguish them from other fishes of the same genus. Unlike *O. chrysogaster* (Mexican golden trout), *O. gilae* (Gila trout), *O. mykiss* and Pacific salmon, cutthroat trout have teeth present on their basibranchial plate in the lower gill arch. Also separate from rainbow trout, cutthroat trout, Mexican golden trout and Gila trout all have frontals that lack an expanded shelf above the orbital (Figure 7), yet possess a more elongate rectangular, anterior ceratohyal in the lower visceral arch (Stearley & Smith, 1993). Such a ceratohyal exhibits a length to depth ration greater than 2.5 (Stearley & Smith, 1993).

Because no morphological synapomorphies linked rainbow trout to cutthroat trout separate from other trout and salmon, Stearley and Smith (1993) felt that cutthroat trout descended from a more basal lineage near the Mexican golden trout (Figure 4).

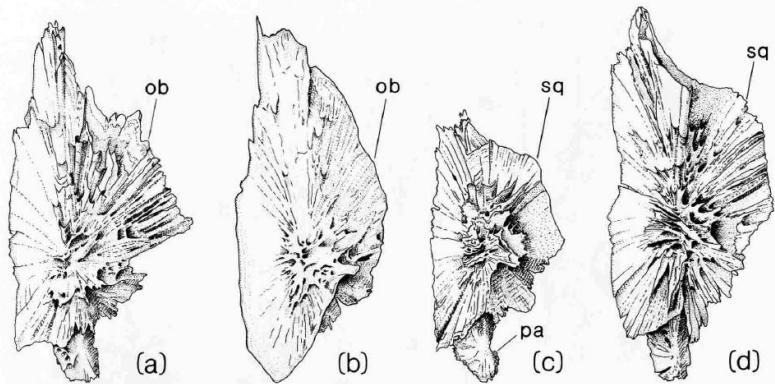


Figure 7. Frontals, right, dorsal view, anterior up (parietals attached except in b). (a) *Salmo trutta*, UMMZ; (b) *Oncorhynchus clarki*, UMMZ; (c) *Oncorhynchus mykiss*, UMMZ; (d) *Oncorhynchus kisutch*, UMMZ. Abbreviations: ob, anterolateral margin oblique; pa, parietal; sq, anterolateral margin squared. Stearley, RF, & Smith, GR. (1993). "Phylogeny of the Pacific Trouts and Salmons (Oncorhynchus) and genera of the Family Salmonidae. *Transactions of the American Fisheries Society*, 122(1), 1-33. Reprinted by permission of American Fisheries Society (<http://www.fisheries.org>).

Morphologically, cutthroat trout are separated from RBT by reduced amounts of spotting on the head and the lack of spots anteriorly below the lateral line (Behnke, 1992). Additionally, WCT possess basibranchial teeth on the lower gill arch (Stearley & Smith, 1993) and can be distinguished externally by the distinctive orange slash below the gill cover (Behnke, 1992). Hybridization with rainbow trout can be detected by the appearance of spots on the top of the head and on the anterior body below the lateral line, as well as by reduced scale counts, increased caecal counts, and loss of basibranchial teeth (Behnke 1992).

Phylogeny based on Genetic Analysis

Prior to Stearley and Smith's morphological examinations, genetic studies to determine the relationship between cutthroat trout, rainbow trout and other Pacific trout and salmon seemed inconclusive. Analyzing phenetic distances of restriction sites for mitochondrial DNA (mtDNA) Thomas *et al.* (1986) found a closer link of rainbow trout to Coho (*O. kisutch*) and Chinook salmon (*O.*

tshawytscha) than to chum, pink (*O. gorbuscha*) or sockeye salmon (*O. nerka*). Unfortunately, they did not include an outgroup such as cutthroat trout or Mexican golden trout (*O. chrysogaster*) which would have established a clear cladistic relationship (Stearley & Smith, 1993). Wilson *et al.* (1985) showed a link between steelhead (anadromous rainbow trout), rainbow trout and cutthroat trout yet all three restriction sites used in the study were shared by all Pacific salmon (Thomas *et al.*, 1986; Stearley & Smith, 1993). Further ambiguity resulted when Gyllensten and Wilson (1987) identified 19 mtDNA fragments, cut by 10 restriction enzymes unique to rainbow and cutthroat trout. Stearley and Smith (1993) compared these fragment lengths with sites mapped by Thomas *et al.* (1986) and claimed that only one of thirteen fragments exhibited derived characters away from the ancestral condition which might support a monophyletic relationship. The authors did recognize that the other six fragments had not been investigated and they await cladistics molecular clarification.

Because the Salmonidae family radiated from a tetraploidization event, (Allendorf & Thorgaard, 1984) the presence of two active growth hormone (GH) genes allowed for duplicate investigation. Using polymerase chain reaction as primers, Oakley and Phillips (1999) examined two growth hormone (GH) introns from 13 species, subspecies and morphotypes within Salmonidae. Growth hormone 2 intron C (GH2C) resulted in a polychotomous node containing *Parahucho*, *Salvelinus*, *Salmo* and *Acantholingga*, and *Oncorhynchus*. For the first intron (GH1C), the single most parsimonious phylogeny displayed a pairing of *Salvelinus* (*S. alpinus* and *S. namaycush*) and not *Salmo* with the Pacific trout and salmon (*Oncorhynchus*). Phylogenetic relationships from both GH introns displayed *O. mykiss* plus *O. clarki* as sister genera with Pacific salmon (Figure 8; Oakley & Phillips, 1999). Likelihood analysis failed to support significant differences between the two phylogenies, yet did reveal that GH1C and GH2C exhibit variable segment lengths (Stearley & Smith, 1999) which can lead to complex patterns of chromosomal evolution (Hartley 1987).

Most recently, investigation into the phylogeny and divergence of Pacific trout focused on the highly fragmented inland cutthroat trout. Assuming that the rate of evolution on each phylogenetic branch (discussed below) was equal, Wilson and Turner (2009) used relaxed molecular clocks and

Bayesian Evolutionary Analysis Sampling Trees (BEAST) to estimate divergence of *Salmo* from *Oncorhynchus + Salvelinus* to occur approximately 18.6 million years ago (MYA). After the separation from *Salvelinus* (16 MYA) the cherry salmon group (*O. masou masou* + *O. m. ishikawai*) were the first division in *Oncorhynchus* at 7.6 MYA. Pacific trout ((*O. mykiss* ssp. + *O. gilae* ssp.) + *O. clarkii* ssp.) diverged from Pacific salmon around 6.3 MYA (Wilson & Turner, 2009). Within the 95% Highest Posterior Density (HPD), cutthroat trout split from the rainbow trout group between 2.3-3.8 MYA. Westslope cutthroat trout are considered to be 1.4 million years old while Rio Grande cutthroat trout are thought to be the youngest subspecies of all Pacific trout, originating between 0.09-0.96 MYA (Wilson & Turner, 2009).

Examining mtDNA and utilizing *Coregonus lavaretus* (common whitefish), *Salmo trutta* (brown trout), *S. salar* (Atlantic salmon) as out-groups, Wilson and Turner (2009) was also able to show a monophyletic genus in *Oncorhynchus* having five distinct clades (Figure 8). They confirmed the findings by Oakley and Phillips that *Oncorhynchus* is the sister group to *Salvelinus* but revealed that without the inclusion of *O. gilae* (*O. g. apache* + *O. g. gilae*) and Mexican golden trout (*O. chrysogaster*) Pacific trout (*O. mykiss* + *O. clarkii* ssp.) is paraphyletic and does not constitute a clade (Wilson & Turner, 2009). Within cutthroat trout, Wilson and Turner (2009) also identified three sub-clades of cutthroat trout. These include coastal cutthroat trout (*O. c. clarki*), westslope and Lahontan cutthroat trout (*O. c. lewisi* + *O. c. henshawi*) and the Yellowstone cutthroat trout group (Yellowstone [*O. c. bouvieri*] + Bonneville [*O. c. utah*] + Colorado River [*O. c. pleuriticus*] + greenback [*O. c. stomias*] + Rio Grande [*O. c. virginalis*]).

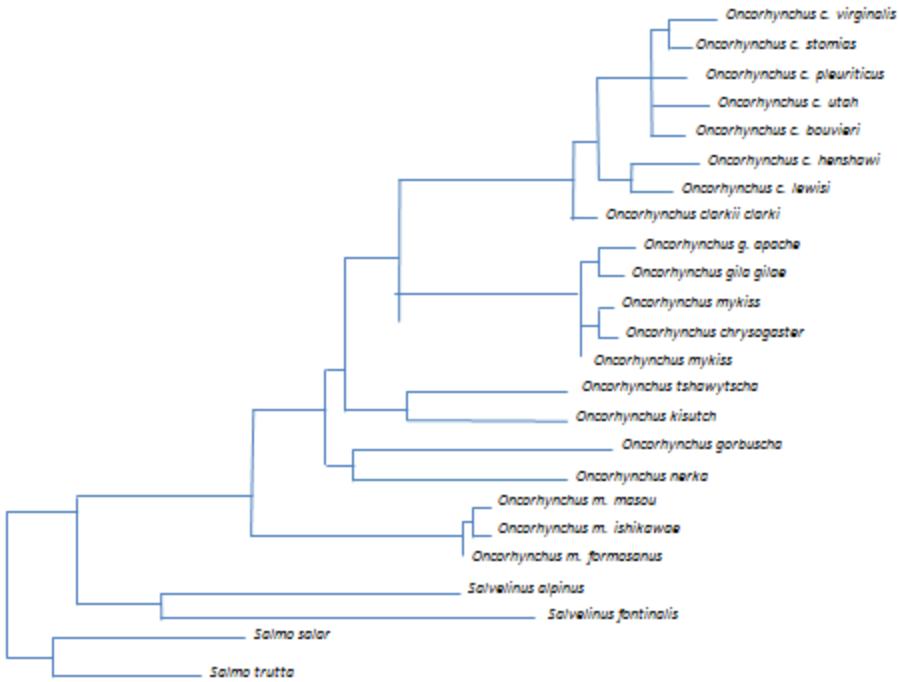


Figure 8. Maximum likelihood phylogenetic tree based on mtDNA for *Oncorhynchus*. Modified from Wilson & Turner, 2009.

Using horizontal starch-gel electrophoresis, Leary *et al.* (1987) examined the genetic variation between seven cutthroat trout subspecies and rainbow trout. They found that very little electrophoretic differentiation existed among greenback, Colorado River and Yellowstone cutthroat trout (YCT), yet there was substantial biochemical genetic differentiation between these fishes and the more basal Lahontan, westslope and coastal cutthroat groups (Leary *et al.*, 1987). Genetic distances were smallest between rainbow trout and coastal cutthroat trout (0.099) increasing to 0.13, 0.246 and 0.247 for WCT, YCT and finespotted Snake River cutthroat trout (*O. clarkii* spp; FSCT), respectively (Table 2). Leary *et al.*'s (1987) results are supported by the genetic work of Wilson and Turner (2009), evidencing the more basal origins of the coastal cutthroat trout, westslope and Lahontan cutthroat trout versus the more derived Yellowstone, Colorado River and greenback cutthroat trout (Figure 8).

Table 2. Nei's genetic distances between rainbow trout and seven subspecies of cutthroat trout. Modified from Leary *et al.*, 1987.

Cutthroat trout subspecies	Rainbow trout	Cutthroat trout subspecies					
		Westslope	Coastal	Lahontan	Yellowstone	Finespotted	Greenback
Westslope	0.130						
Coastal	0.099	0.164					
Lahontan	0.138	0.175	0.077				
Yellowstone	0.246	0.295	0.191	0.164			
Finespotted	0.247	0.297	0.192	0.165	0.006		
Greenback	0.229	0.268	0.194	0.152	0.022	0.025	
Colorado River	0.223	0.280	0.193	0.150	0.012	0.023	0.005

A combined synthesis of morphological and genetic approaches to the phylogeny of Salmoninae can prove challenging. Because of a shared “I” pattern in vomerine teeth, Stearley and Smith’s (1993) morphological data cited *Acantholingga* as the link between Atlantic and Pacific trout and salmon and the more archaic *Brachymystax*. Oakley and Phillips’ (1999) genetic survey clearly showed that *A. ohridana* actually falls into the Atlantic trout and salmon group as *Salmo ohridana* and not a separate more basal genus *Acantholingga*. Refuting the concept of *A. ohridana* as the common ancestor and the fact that *Salvelinus* and not *Salmo* is the sister group of *Oncorhynchus* (Oakley & Phillips, 1999; Wilson & Turner, 2009), data suggests that the “T” shaped vomerine tooth patch evolved independently in both *S. ohridana* and on a raised vomerine crest in *Salvelinus*.

Due to a more elongate rectangular, anterior ceratohyal, *O. chrysogaster* and *O. clarki* were considered the most basal members of their genus by Stearley and Smith (1993). Although Stearley and Smith did not support the idea, later genetic studies thought that cutthroat trout and rainbow trout formed a monophyly (Oakley & Phillips, 1999) but failed to include the Mexican golden trout and Gila trout in their research. Clarification came from recent research when Wilson and Turner (2009) showed that ((*O. mykiss* + *O. chrysogaster*) + *O. gilae* ssp.) + *O. clarkii* ssp) comprise the paraphyletic group of Pacific trout. Taken in conjunction with the grouping by Wilson and Turner (2009), Leary *et al.*’s (1987) findings clearly show that the sub-clade of cutthroat trout are very closely related to the rainbow trout group.

Distribution and Range

Wilson and Turner (2003) felt that geologic events occurring in the Pacific Northwest and the Rocky Mountains gave rise to at least 10 species and 28 subspecies of salmon and trout. As a product of tectonic plate movement, volcanos, and intermittent glacial periods, Montgomery (2000) attributed the adaptive radiation and evolution of pacific salmon to the physiographic change in topography occurring within the Pacific Rim. Similarly, glaciation during the Pleistocene Era gave rise to the divergence of inland cutthroat trout, resulting in at least 14 recognized subspecies (Behnke 1992).

Rainbow Trout

Evolving both sympatrically and independently into multiple subspecies, rainbow trout (*Oncorhynchus mykiss* ssp.) and cutthroat trout (*O. clarki* ssp.) are found throughout western North America. Within the U.S., Canada and Mexico, Behnke (1992) considered rainbow trout to have two major groups with distinct ranges (Figure 9). He grouped the redband (rainbow) trout (*O. m. gairdneri*) of the Columbia River basin (east of the Cascade Mountains and the upper Fraser River basin) together with the redband varieties (*O. m. aquabonita*, California golden trout; *O. m. gilbert*, Kern golden trout; *O. m. stonei*, Sacramento redband trout) from the Sacramento River (Behnke, 1992). Known more commonly as steelhead, anadromous rainbow trout (*O. m. irideus*), are historically distributed along the Pacific coast from Alaska all the way south to Mexico. Behnke (1992) also noted that rainbow trout originating from east Asia are anadromous coastal inhabitants classified as *O. m. mykiss*.

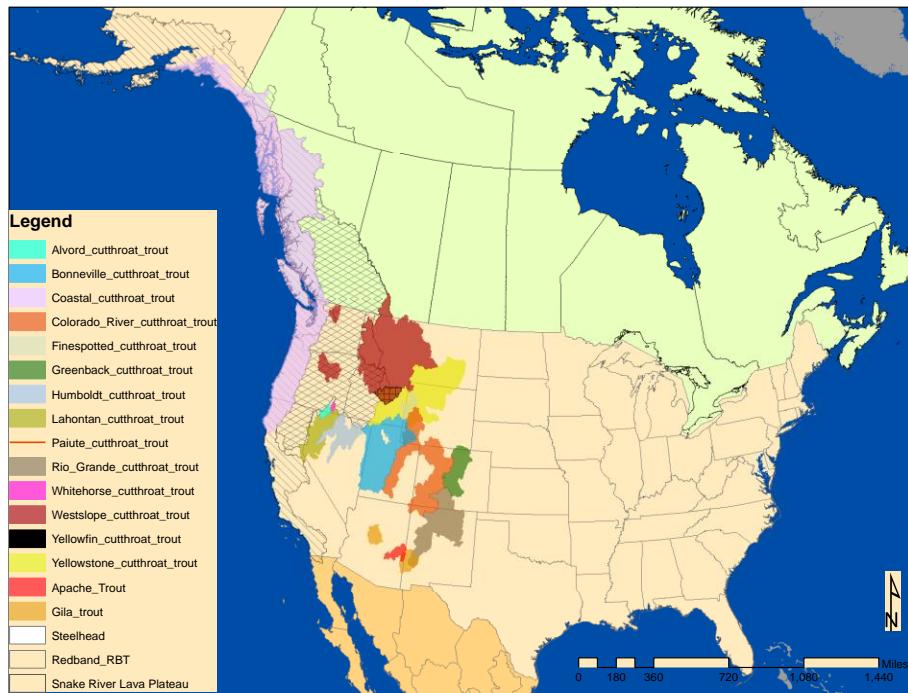


Figure 9. Distribution of Pacific trout in western North America. (Excludes Mexican golden trout, *Oncorhynchus chrysogaster*). Modified from Behnke, 1992.

The first cultivation of rainbow trout for stocking can be traced to the University of California, Berkley in 1870. A precursor for the California Fish Commission, the California Acclimatization Society established the beginnings of the fish culture program by breeding coastal rainbow trout from the San Francisco Bay area (Behnke, 1992). Initial shipments of rainbow trout progeny to New York, Michigan and Japan in 1875-1876 and 1877 respectively, were therefore *O. m. irideus* (steelhead) and not what many considered historically as McCloud River redband trout. Behnke (1992) also outlined that the U.S. Fish Commission's operations on the McCloud River beginning in 1879 harvested both steelhead and resident redband trout eggs. Their brood stock, comprised both of small and large adult trout (presumably redband and steelhead, respectively), were indiscriminately spawned together. Given the size difference Behnke (1992) rationalized that more genetic material was passed on from the steelhead versus the redband trout, which in turn lead to hatchery stocks having more *O. m. irideus* characteristics.

Although it remains unclear which subspecies, or if a hybrid combination of the two, was used for brood stock, between 1880-1888 approximately 2.5 million rainbow trout eggs were shipped from the McCloud River facility to establish federal hatcheries in Wytheville, VA and Northville, Michigan

(Behnke, 1992). Subsequent hatcheries on Redwood Creek, CA and the Willamette, Klamath and Rogue rivers of Oregon, utilized coastal rainbow trout for brood stock. Scott *et al.* (1978) noted that those rainbow trout established in New Zealand in 1883 were steelhead from San Francisco Bay. Consequently, it is safe to assume that, at present, a very large portion of the wide spread distribution of introduced rainbow trout (Figure 10) can be traced to coastal rainbow trout ancestry.

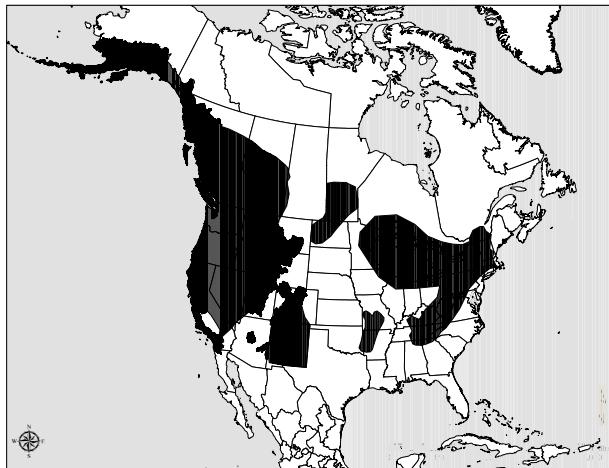


Figure 10. Current North American distribution of rainbow trout (*Oncorhynchus mykiss*) through anthropogenic introduction. Modified from MaCrimmon, 1971.

Cutthroat Trout

As many as 14 sub-species of cutthroat trout have been recognized throughout their range (Behnke, 1992). Coastal cutthroat trout (*Oncorhynchus clarkii clarki*; CCT) occur entirely within the range of steelhead (coastal rainbow trout), stretching along the Pacific coast as far north as Prince William Sound, Alaska and as far south as northern California (Figure 10). Prior to the anthropogenic introduction of rainbow trout, the lack of a waterway connecting the Great basin provided a refuge for Lahontan (LCT), Paiute (*O. c. seleniris*; PCT), Humboldt (*O. c. ssp*; HCT), Alvord (*O. c. alvordensis*, ACT), Whitehorse (*O. c. ssp*; WHCT) and Bonneville (BCT) subspecies of cutthroat trout (Behnke, 1992). The remaining cutthroat trout polytypes inhabit areas of the Rocky Mountains. Westslope, Yellowstone and finespotted Snake River (FSCT) cutthroat trout are found in the upper reaches of the Columbia and Missouri River tributaries, while Colorado River (CRCT), greenback (GBCT) and Rio Grande (RGCT) cutthroat trout are found in the southern Rocky Mountains (Wyoming, Colorado and

New Mexico). Similar to the Alvord cutthroat trout of Nevada, yellowfin cutthroat (*O. c. macdonaldi*; YFCT), which was only found in Twins Lakes, CO, are thought to be extinct (Behnke, 1992).

The historical presence of cutthroat trout can be linked to migration barriers throughout the distribution of the various subspecies. Although redband trout can be found cohabitating with disjunct populations of WCT (e.g. John Day drainage in Oregon), almost all of the contiguous range of WCT west of the continental divide exists upstream from natural barrier falls. This occurrence is most obvious on the Spokane and Kootenai Rivers (Behnke, 1992), where barrier falls prevented colonization of redband trout further upstream. Waterfalls on the Stehekin River within North Cascades National Park, WA, also prevented redband trout from occurring in sympatry with WCT in the Lake Chelan drainage. After examining several specimens, Behnke (1992) concluded that WCT were native to the Methow River just north of the Stehekin and possibly the coldest reaches of the Wenatchee and Entiat Rivers to the south.

Behnke (1992) felt that prior to glacial flooding in the late Pleistocene, YCT occupied much of the Columbia River basin. Due to the flooding, redband trout invaded, initiating a decline of the current range of YCT to above Shoshone Falls on the Snake River (Behnke, 1992). Although not confirmed, the presence of WCT in the Salmon and Clearwater River drainages of Idaho, is thought to be the product of geologic stream capture of WCT from tributaries to the Clark Fork (Behnke, 1992). Behnke (1992) hypothesized that volcanic eruptions in the Pleistocene eliminated all native fishes in the Lost River drainage in Idaho (Snake River Lava Plateau, Figure 9) while simultaneously blocking the river from flowing into the upper Snake River. He concluded that similar stream transfers from the Salmon River drainage served as the origin for the re-colonization of WCT, YCT, redband trout or all three, accounting for the hybrids that he identified from 1934 samples (Behnke, 1992).

Life History & Ecology

Evolving and adapting to cold aquatic environments with relatively sterile waters while in the presence of predators such as bull trout (*Salvelinus confluentus*; BLT) and northern squawfish (*Ptychocheilus oregonensis*) (Behnke, 1979; Marnell *et al.*, 1987), migratory westslope cutthroat trout can exhibit extensive seasonal movements for spawning and overwintering. Evidence has been found that downstream movements of 100km or more (Bjornn & Mallet, 1964; Apperson *et al.*, 1988; Peters, 1988; Muhlfeld *et al.*, 2009b) are an adaptation to higher quality habitat availability (Bjornn, 1971; Peters, 1988). Adult fluvial ecotypes overwinter in rivers of 4th order or greater (McIntyre & Rieman, 1995) while adfluvial fish seek refuge from seasonal extremes in downstream lakes (McIntyre & Rieman, 1995). Adfluvial and fluvial sub-adults reside in streams that are greater than third order (McIntyre & Rieman, 1995). The strategy least observed, lacustrine, fishes spend their entire life, maturing and spawning, within the lake habitat (Carl & Stelfox, 1989). This strategy utilizes the advantages of a lake environment which include more living space, favorable water temperatures with less fluctuation and more abundant forage. However, predation on juveniles by the extremely piscivorous, adfluvial bull trout likely selects against this method.

Resident WCT normally do not move more than 200m from where they emerge and usually don't exceed 300 mm total length (TL; Averett, 1962; Thurow & Bjornn, 1978). Downs (1995) determined that the post-spawning presence of WCT – fish greater than 150 mm fork length (FL) - indicates the presence of a resident population. After fry emergence, all ecotypes can be found cohabitating for one to four years. Migratory juveniles gradually move downstream selecting 2nd-4th order streams (Table 4). Prior to their initial spawning run, sub-adults occupy lakes or rivers (McIntyre & Rieman, 1995) usually returning to their natal streams for spawning. Resident, fluvial and adfluvial life-history forms may occur in the same hydrologic basin (Averett & MacPhee, 1971; Rieman & Apperson, 1989); however there is no clear evidence that the different life history patterns represent a genetic differentiation (Rieman & Apperson, 1989).

Table 3. Summary of life history and habitat use for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Modified from McIntyre & Rieman, 1995.

Life History	Stream Order				Habitat type
	Winter (D-J-F)	Spring (M-A-M)	Summer (J-J-A)	Fall (S-O-N)	
Total Fluvial	Highest densities in 2nd & 3rd order streams				pools
spawners	>3	1-4	1-4	>3	pools with overhead cover
	fry	1.4	1-4	1-4	stream margins, low velocity areas, backwaters & sided channels
	juvenile	2-4	2-4	2-4	main channel pools
	subadult	>3	>3	>3	pools with overhead cover
Adfluvial	spawners	lake	1-4	lake	same as fluvial
	fry	1-4	1-4	1-4	same as fluvial
	juvenile	2-4	2-4	2-4	same as fluvial
	subadult	lake	lake	lake	top of thermocline
Resident	spawners	1-3	1-3	1-3	same as fluvial
	fry	1-3	1-3	1-3	same as fluvial
	juvenile	1-3	1-3	1-3	same as fluvial
	subadult	1-3	1-3	1-3	same as fluvial

Resident WCT are considered isolated headwater populations when smaller low order streams have some form of barrier preventing upstream migration. These barriers include bedrock waterfalls and naturally dry channel segments as well as anthropogenic barriers such as road culverts (Shepard *et al.*, 2005). If no migration barrier exists scale analysis and back growth calculations can also be used to differentiate between adfluvial, fluvial and resident WCT. With the exception of lacustrine fish, fry and juveniles developing in streams exhibit narrowly spaced scale circuli, while adfluvial and fluvial subadult and adults are larger and have widely spaced circuli (Averett, 1962).

Dependent upon local conditions and genetic stock, sexual maturity in WCT usually occurs within 2-6 years (Liknes & Graham, 1988) and can be predicted by total length (Downs *et al.*, 1997). The number of eggs per spawning (fecundity) is also a function of total length (Averett, 1962; Downs *et al.*, 1997; Johnson, 1963; Rieman & Apperson, 1989). Mortality rates for early life stages are very high with

egg-to-fry survival estimated to be 8.5% (Magee *et al.*, 1996). Fertility can be calculated as the product of fecundity, egg-to-fry survival and the probability of being sexually mature (See Appendix A for a Stage Based Population Model on isolated resident WCT).

Unlike Pacific salmon, WCT are not semelparous, but rather iteroparous, with repeat spawners comprising up to 70% of spawning fish (Liknes & Graham, 1988). During spring runoff, the rising arm of the hydrograph initiates movement of migratory fishes (Schmetterling, 2001; Muhlfeld *et al.*, 2009b). Varying over time and distance, spatial and temporal spawning overlap occurs between cohabitating populations of RBT, WCT and their hybrids (Magee *et al.*, 1996; Muhlfeld *et al.*, 2009b). While hybrid WCT backcrosses spawn at intermediate times and intermediate distance (48km) to that of parent WCT and RBT (Muhlfeld *et al.*, 2009b), Muhlfeld *et al.* (2007a) identified that reproductive fitness (the number of offspring per adult) declined with the amount of RBT admixture. Making their migration (20km) upstream from main rivers to lower order tributaries, fluvial rainbow trout and their hybrids take on average 26-28 days to reach their spawning site (Muhlfeld *et al.*, 2009). With spawning lasting from early March through June, water temperatures average around 6°C (Muhlfeld *et al.*, 2009). Although westslope cutthroat trout begin their run about the same time, due to greater migration distances (mean 110km) to lower order tributaries, spawning lasts longer (approximately 52 days) and occurs later (May-late June) in warmer water temperatures (mean 9°C; Muhlfeld *et al.*, 2009). Further contributing to spatial and temporal separation in reproduction, resident populations of WCT in headwater streams spawn later in the season (July; Northcote & Hartman, 1988).

The geographical isolation of inland varieties of cutthroat trout has allowed subspecies such as westslope cutthroats to exploit and utilize similar prey items and microhabitat which supported redband trout further to the west. Although WCT diets occasionally may include zooplankton (McMullin, 1979) and small fish, ultra-oligotrophic environments provide limited forage (Ortmann, 1969; Mauser, 1972) and relegate a majority of their diet to terrestrial invertebrates (Nakano *et al.*, 1992). Forage for RBT includes both adult and larval stages of drifting invertebrates, such as Trichoptera (caddisflies), Ephemeroptera (mayflies) and Diptera (true flies; Angradi & Griffith, 1990).

Microhabitat selection of WCT and stream dwelling RBT have been shown to vary with individual size and season. Baltz *et al.* (1991) observed a positive correlation between RBT total length and pool depth during summer months in Rock Creek, CA. Furthermore, their results indicated that individual RBT select microhabitat pools of slower velocity and greater water depth in relation to a decline in photoperiod and water temperature (Baltz *et al.*, 1991). In a like manner, during the winter months, Bonneau & Scarneccchia (1998) observed aggregations of adult and juvenile cutthroat trout in large pools which were closely associated with cover. Also acting as drift foragers, WCT occupy mid-water focal points beneath surface currents near the center of pools while smaller fish stay closer to the margins (Table 4; Nakano *et al.*, 1992; McIntyre & Rieman, 1995, Bonneau & Scarneccchia, 1998).

Prey availability and optimum foraging position is limiting in these stream environments leading to competitive foraging behaviors (Chapman, 1962; Keeley & Grant, 1995; Seiler & Keeley, 2007a). Although no known literature documents a distinction between observed aggressive behavior in cohabitating WCT and RBT, sympatrically occurring RBT and RBT x cutthroat hybrids have marginally faster growth rates (Seiler & Keeley, 2009; Bear *et al.*, 2007) and monopolize the central feeding position (Seiler & Keeley, 2007a). Possibly utilizing a visually assessed competitive advantage based on thicker bodies, larger paired (pectoral and pelvic) fins and a longer caudal peduncle (Hawkins & Quinn, 1996; Seiler & Keeley, 2007a; 2007b), RBT and their hybrids capture more prey than cutthroat trout during simultaneous foraging (Seiler & Keeley, 2007a). Consistent with these morphology differences rainbow trout and their hybrids have a higher critical swimming velocity than cutthroat trout (Hawkins & Quinn, 1996; Seiler & Keeley, 2009).

Bear *et al.* (2007) compared growth rates and upper lethal water temperatures for WCT to RBT using a 60 day acclimated chronic exposure (ACE) thermal test (Selong *et al.*, 2001). Peak growth rates for both species were not significantly different (RBT 13.1°C; WCT 13.6°C). Rainbow trout had a higher tolerance for warmer water. Between water temperatures of 8-18°C, juvenile RBT and WCT showed similar survival rates (82-100%; Bear *et al.* 2007). Westslope cutthroat trout began to exhibit statistically significant mortality beginning at 20°C (64.3%) with survival decreasing with treatment water

temperatures (12.5% at 22°C and 0 at 24°C; Bear *et al.*, 2007). Given these results, Bear *et al.* (2007) estimated the 60-day ultimate upper incipient lethal temperature (UUILT) for rainbow trout to be 24.3°C (95% CI = 24.0-24.7°C), while the 7-day test was 1.7°C higher (26.0°C). The estimated UUILT for WCT after 7 days was 24.1°C but only 19.6°C (95% CI = 19.1-19.9°C) after 60-day exposure (Bear *et al.*, 2007).

Current status of Westslope Cutthroat Trout

Shepard *et al.* (2005) did a comprehensive analysis on the status of WCT in the northwestern U.S. They surmised that WCT occupy 33,500 miles of their historical range (56,500 miles; Shepard *et al.*, 2005). The reduction of approximately 41% is almost solely due to anthropogenic activities. Compounding factors such as over fishing (Behnke, 1979; MacPhee, 1966; Thurow & Bjornn, 1978), habitat degradation and reduction (Rieman & Apperson, 1989) and the introduction of non-native species (Liknes & Graham, 1988) are the biggest contributors. Available genetic testing suggests that WCT, with no genetic introgression, only comprise 3,400 miles (10%) of their occupied range (Shepard *et al.*, 2005). Relative to Behnke's (1992) historical distribution, that accounts for only 6% of the fish's original habitat (Shepard *et al.*, 2005).

Spanning the continental divide and providing headwaters to three different oceans (Figure 11), Glacier National Park serves as a portion of the headwaters for the North Fork and Middle Fork of the Flathead Rivers, as well as the Missouri River and the South Saskatchewan River. The park is one of the few areas where abundant, genetically pure, WCT populations can still be found. As part of an ongoing fisheries monitoring program, Downs *et al.* (2011; 2013) established baseline abundance and condition data for age-1 and older WCT ($TL \geq 45\text{mm}$) within Glacier National Park (GNP).

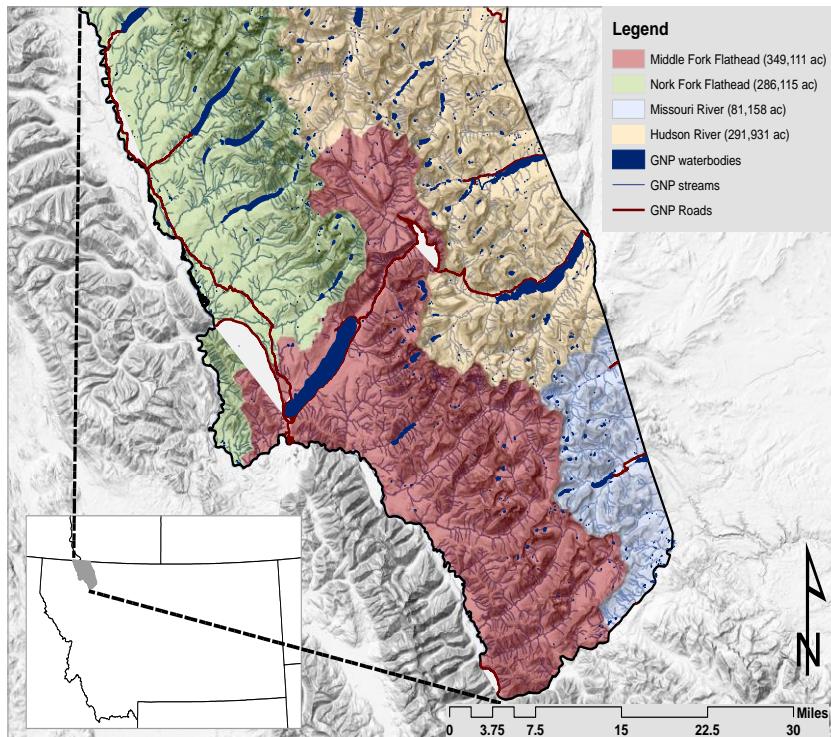


Figure 11. Watersheds of Glacier National Park. Modified from Downs *et al.*, 2013.

GNP Tributaries of the North Fork of the Flathead River

Comprising the largest portion of the western boundary of GNP, five representative tributaries of the North Fork were selected for sampling. A third order stream originating in GNP, Akokala Creek, has been documented as having RBT x WCT hybrids (Muhlfeld *et al.*, 2009). Downs *et al.* (2011) estimated the density of age-1 and older WCT ($TL \geq 45\text{mm}$) in Akokala Creek to be $0.79 \text{ fish}/100\text{m}^2$ in 2009, while Downs *et al.* (2013) observed a density of $0.38 \text{ fish}/100\text{m}^2$ in 2010 (Table 4). McGhee Creek, another stream thought to contain a population of hybridized WCT, also exhibited a decline in density of age-1 and older fish from 2009 (Downs *et al.*, 2011) to 2010 and again in 2012 (Downs *et al.*, 2013). It should be noted that the sampling reach for McGhee Creek was longer in 2012 than in 2009 or 2010; however, densities were calculated using estimated fish abundance normalized by reach distance, which should allow for comparison of the different sample results.

Table 4. Density and hybridization status of westslope cutthroat trout sampled in tributaries of the North Fork of the Flathead River, Glacier National Park, MT. Modified from Downs *et al.*, 2011; 2013.

Watershed	Waterbody	Stream Order	Migratory/ Resident or Isolated Population	Hybridized (Yes/ No or Unknown)	Density (WCT/100m ²) by Sample Year			
					2009	2010	2011	2012
North Fork	Spruce	3	MR	Unknown	3.1	1.89	-	-
North Fork	Ford	3	MR	No	4.8	2.9	8.0	7.7
North Fork	Akokala	3	M	Yes	0.79	0.38	-	-
North Fork	McGhee	3	MR	Yes	5.3	-	3.7	0.98
North Fork	No Name	2	RI	No+	-	-	12.5	11.5

At the northern edge of GNP (flowing out of Canada), Spruce Creek was sampled in 2009 and again in 2010. Although the genetic status for WCT in Spruce Creek has not yet been assessed, between 2009 and 2010 there was a reduction in fish density from 3.1 to 1.89 WCT/100m² (Downs *et al.*, 2011; 2013). Identified by Muhlfeld *et al.* (2009) as not having hybrids, Ford Creek is a third order tributary between Spruce Creek and Akokala Creek. Ford Creek had a density of 4.8 and 2.9 WCT/100m² in 2009 and 2010 but 8.0 and 7.7 WCT/100m² in 2011 and 2012 (Downs *et al.*, 2011; 2013). As with McGhee Creek, different and slightly longer stream reaches were sampled on Ford Creek in 2011 and 2012 versus 2009 and 2010, yet normalized fish density shows that there was an increase in abundance for the stream.

Of the five representative stream tributaries selected for sampling on the North Fork, No Name Creek is the only one thought to support an isolated resident population of WCT (Downs *et al.*, 2013). Previously unsampled, a small, second order stream, originating in the Apgar Mountains just east of the intersection of the North Fork and the Camas Road, No-Name Creek noted in 2011 as qualifying for good WCT habitat. After exploratory observations revealed a robust population, sampling was initiated on what was termed No-Name Creek (Downs *et al.*, 2013). The initial depletion survey conducted in 2011 revealed an estimated population of 39 with a density of 12.5 WCT/100m² (Downs *et al.*, 2013). Due to the length frequency distribution of WCT (Figure 12) and the likelihood that the road culvert running under the Camas Road prevented upstream migration, the population was designated by Downs *et al.* (2013) as isolated residents. Subsequent sampling in 2012 confirmed the population to be doing well

with an estimated density of 11.5 WCT/100m² and a first pass catch per unit effort (CPUE₁) of 69.1 fish/hour (Downs *et al.*, 2013).

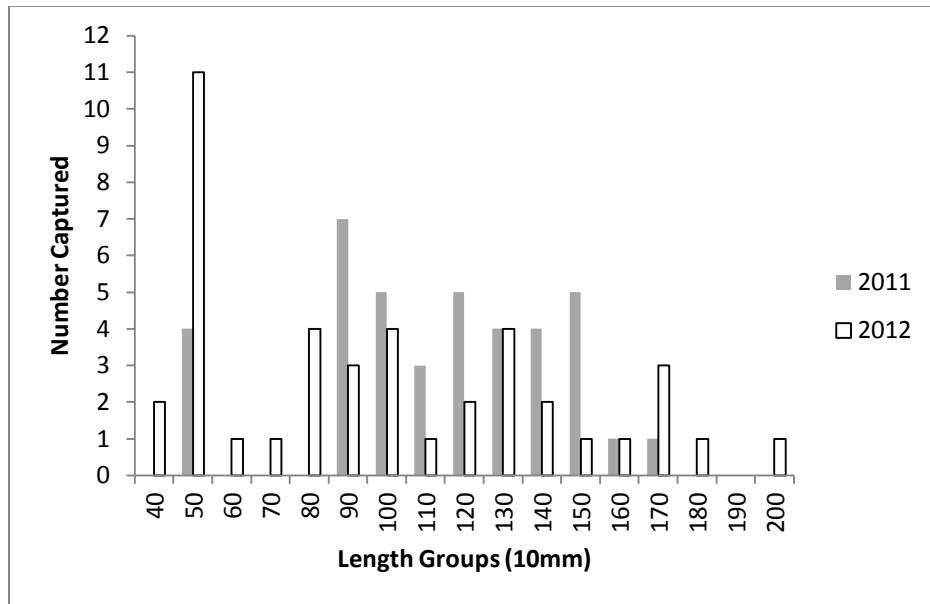


Figure 12. Length-frequency histogram for WCT captured on No-Name Creek, GNP, 2011-2012. Reproduced with permission from Downs *et al.*, 2013.

GNP Tributaries of the Middle Fork of the Flathead River

With the main stem river originating in the Great Bear and Bob Marshal Wilderness of the Flathead National Forest, the Middle Fork of the Flathead has several major tributaries flowing out of GNP. Providing essential spawning and rearing habitat for the endangered BLT, many of the GNP streams flowing into the Middle Fork are closed to fishing for their entire length (Ole, Park, Muir, Coal, Nyack and Fish Creeks). The National Park Service continues to monitor fish populations in Autumn, Muir, Fern and Fish Creeks.

Near Lake McDonald, Fern Creek is a small, second order stream flowing out of the Apgar Mountains into Fish Creek. Although no genetic assessment has been made of WCT in the stream, Downs *et al.* (2011) identified a perched road culvert under the Camas Creek Road as being a possible migration barrier and the existing population may be considered as isolated residents. Although WCT density was lowest in 2011(3.8 WCT/100m²), general densities increased and the population estimates from 2009-2012 almost doubled (28 in 2012; 95%CI: 18-38) from the original estimate of 15 (95%CI:

13-17) in 2009 (Downs *et al.*, 2013). Unlike Fern Creek, Fish Creek has no known fish passage barriers yet, the genetic integrity of WCT has not been tested within the water body. Westslope cutthroat trout density was greatest in 2009 (12.2 WCT/100m²) for Fish Creek and has declined marginally since (Table 5).

Table 5. Density and hybridization status of westslope cutthroat trout sampled in tributaries of the Middle Fork of the Flathead River, Glacier National Park, MT. Modified from Downs *et al.*, 2011; 2013.

Watershed	Waterbody	Stream Order	Migratory/ Resident or Isolated Population	Hybridized (Yes/ No or Unknown)	Density (WCT/100m ²) by Sample Year			
					2009	2010	2011	2012
Middle Fork	Autumn	3	RI	No ⁺	1.4	2.4	8.4	12.2
Middle Fork	Muir	3	MR	Unknown	7.6	13.6	7.4	-
Middle Fork	Fern	2	RI+	Unknown	4.3	5.3	3.8	8.2
Middle Fork	Fish	3	MR	Unknown	12.2	5.3	7.6	7.2

Isolated by both bedrock waterfalls and a drainage culvert running under the Burlington Northern Railroad, Autumn Creek supports an isolated resident population of WCT (Downs *et al.*, 2011). Although genetic samples have been taken from captured individuals, results have yet to be determined. However due to the complexity of migration barriers, it is very unlikely that anthropogenic introgression has occurred within Autumn Creek. Both densities and the estimated populations (6-2009; 10-2010; 47-2011; 55-2012) have increased for Autumn Creek since sampling began in 2009. Due to its proximity to U.S. Highway 2, the Bear Creek – Middle Fork public access point and the Autumn Creek Trail, Autumn Creek undoubtedly has been submitted to heavy fishing pressure. This positive increase in both fish density and estimated population may likely be a result of park wide catch-and-release regulations imposed for WCT in 2010.

GNP Tributaries of the St Mary's River and South Saskatchewan River

East of the continental divide two major drainages flow out of GNP: the Missouri River and the South Saskatchewan River. Wild, Boulder and Lee Creeks are all tributaries to the St. Mary River, which empties into the South Saskatchewan River in Alberta, Canada. Supporting migratory runs of BLT, both Boulder Creek and Lee Creek have been documented as having hybrid RBT x WCT (Mogen & Kaeding,

2004). Likely selecting against a large WCT/hybrid population, Boulder Creek has a robust population of BLT trout with an estimated population of 102 in 2009 and 82 in 2011(Downs *et al.*, 2013). Lee Creek also supports more BLT than WCT with densities of 7.0, 4.5 and 4.9 BLT/100m² in 2009, 2011 & 2012, respectively (Table 6).

Table 6. Density and hybridization status of westslope cutthroat trout sampled in tributaries of the St Mary's River and South Saskatchewan River, Glacier National Park, MT. Modified from Downs *et al.*, 2011; 2013.

Watershed	Waterbody	Stream Order	Migratory/ Resident or Isolated Population	Hybridized (Yes/ No or Unknown)	Density (WCT/100m ²) by Sample Year			
					2009	2010	2011	2012
St. Mary	Wild	3	RI	No	11.1	-	7.4	21.4
St. Mary	Boulder	3	MR	Yes	1.6	-	1.9	-
St. Mary	Lee	2	MR	Yes	5.8		2.6	4.6

A somewhat isolated 2nd order stream flowing southeast into St. Mary's River, Downs *et al.* (2013) proposed that the lower reaches of Wild Creek are intermittent during dry summer months. Although it is purported that Wild Creek has a genetically pure WCT population, the presence of a juvenile BLT collected in 2011 (Downs *et al.*, 2013) raises some question as to whether the stream remains isolated. Regardless, the population of WCT within Wild Creek seems to be doing very well as it has the highest density (21.4 WCT/100m²) of all streams sampled within GNP (Downs *et al.*, 2013).

Introgressive Hybridization

Considering the geographic overlap of both native and invasive rainbow trout to historic cutthroat trout range, similar habitat utilization and ecology, and their close genetic, morphological and physiological relationship, it is not surprising that hybridization has occurred. Both scientists and fisheries managers alike have struggled to categorize hybrid zones and identify the mechanisms supporting introgression (Allendorf *et al.*, 2001). Before awareness of biological introductions surfaced as a major concern, most scientific investigations into RBT - cutthroat trout interactions neglected to consider if cohabitating populations were historically sympatric or originally allopatric. More recent work has focused on how coevolving sympatric populations of steelhead RBT and coastal cutthroat trout

(Hartman & Gill, 1968; Campton & Utter, 1985; Docker *et al.*, 2003) and redband RBT and westslope cutthroat trout (Kozfkay *et al.*, 2007) remain stable while occupying similar habitats and utilize similar resources. Various other studies have addressed the hybridization of invasive RBT with native YCT (Gunnel *et al.*, 2008), GBCT and CRCT (Metcalf *et al.*, 2008), as well as WCT (Rubidge *et al.*, 2001; Osterg & Rodriguez, 2002; Hitt *et al.*, 2003; Weigel *et al.*, 2003; Boyer *et al.*, 2008; Muhlfeld *et al.*, 2009a; 2009b). Until these interactions and the mechanisms driving them are fully understood, no sound management practices can hope to combat the negative anthropogenic effects inadvertently set into motion.

Sympatric Populations & Interspecific Reproductive Barriers

When found sympatrically, both anadromous and resident populations of *O. c. clarki* and RBT are thought to maintain a spatial and temporal separation in spawning (Hartman & Gill, 1968). Using horizontal starch-gel electrophoresis, Campton and Utter (1985) identified hybridization of stocks of RBT and coastal cutthroat trout among several Puget Sound streams. The authors found a disproportional amount of young-of-the-year (YOY) hybrids but showed that hybrids were infrequent in the adult populations. They hypothesized that postzygotic isolating mechanisms resulting from differing numbers of chromosomes may have led to reduced fertility, high juvenile mortality, and migratory disorientation of first generation (F_1) hybrids (Campton & Utter, 1985).

Some have proposed that negative interactions including microhabitat displacement occur when hatchery fish are stocked into wild populations. Conducting a review of such effects Weber and Fausch (2003) noted that most studies reported more aggressive behavior of hatchery-reared salmonids and their offspring to that of wild populations (Fenderson *et al.*, 1968; Steward & Bjornn, 1990; Bachman, 1984). This could be a result of farmed fishes not having established the social hierarchies observed in wild stocks (Steward & Bjornn, 1990). While Fleming *et al.* (2002) noted that faster growing fishes are selected for in hatcheries, it has been shown that higher levels of growth hormones can increase aggressive behavior in salmonids (Johnsson & Bjornsson, 1994).

Docker *et al.* (2003) investigated further into the erosion of interspecific reproductive barriers between hatchery bred and native reproducing sympatric populations of RBT and CCT. The authors felt that through selective breeding and domestication of hatchery reared fishes, the genetic makeup of farmed RBT would be altered enough to erode the natural selective barriers to hybridization. This hybridization could lead to gamete wasting or outbreeding depression of parental populations (Allendorf *et al.*, 2001), which could eventually lead to extinction of the native species (Rhymer & Simberloff, 1996).

Testing the hypothesis that introgressive hybridization occurs more in hatchery supplemented populations, Docker *et al.* (2003) found evidence that the frequency of hybridization between sympatric CCT and RBT was higher where native RBT populations had been supplemented with hatchery fish. Unlike Campton and Utter, their research focused on juveniles and they did not sample adults; therefore the level of hybridization among adults remained undetermined. Also the issue of juvenile mortality, reproductive fitness and homing disorientation of spawning hybrids was not addressed. They did, however, conclude that the stocking of non-native hatchery strains of RBT would have significant impact on native coastal cutthroat trout. Furthermore, their results suggest that the negative effects of anthropogenic introgressive hybridization (e.g. outbreeding depression) could be magnified by the degeneration of postmating reproductive isolating mechanisms due to the introduction of hatchery reared fishes (Docker *et al.*, 2003).

As discussed above, westslope cutthroat trout range historically overlapped redband RBT's native range. With the objective of documenting a natural hybrid zone with sympatric populations of WCT and RBT, Kozfkay *et al.* (2007), conducted hook and line sampling on tributaries of Middle Fork of the Salmon River, ID. Examining stocking records, they found that five of the eleven tributaries sampled had headwater lakes which had been previously stocked with WCT, YCT and RBT, yet the main Middle Fork Salmon River had never been supplemented with hatchery fishes (Kozfkay *et al.*, 2007). Tissue samples in the form of fin clippings were analyzed over four co-dominant nuclear loci to differentiate between RBT, WCT and possible hybrids. To be able to infer the directionality of mating, Kozfkay *et al.*

(2007) used methods outlined by Amussen *et al.* (1987) to calculate allelic cytonuclear disequilibrium (cD) parameters (equations 1-4):

$$cD_1 = \text{freq} (R/r) - [\text{freq} (R) * \text{freq} (r)], \quad (1)$$

$$cD_2 = \text{freq} (H/r) - [\text{freq} (H) * \text{freq} (r)], \quad (2)$$

$$cD_3 = \text{freq} (W/r) - [\text{freq} (W) * \text{freq} (r)], \quad (3)$$

and

$$cD = cD_1 + 0.5cD_2, \quad (4)$$

where freq = allelic frequency, R= RBT nuclear genotype, r = RBT mtDNA haplotype, H = the hybrid nuclear genotype, and W = the WCT nuclear genotype. When cD_1 was positive, it indicated that maternally derived mtDNA for RBT was associated with RBT nuclear alleles, whereas a positive cD_2 value showed maternal RBT association with hybrid nuclear alleles. Conversely, a negative cD_2 value indicated female WCT mtDNA association with the nuclear heterozygotes of hybrids more often than expected, while a negative cD_3 indicated that WCT nuclear alleles were associated more with maternal WCT mtDNA (Amussen *et al.*, 1987). Additionally, using both a Hardy-Weinberg and linkage equilibrium analysis, the authors tested the individual cD data for each sample site to determine the occurrence of random mating or if possibly assortative mating or sex-based directionality of breeding were factors.

Of the stream reaches sampled, Kozfkay *et al.* (2007) found only three that were exclusively inhabited by WCT (upper Indian Creek, Little Indian Creek, and Garden Creek). Two of the lowest streams in the drainage (Ship Island Creek and Papoose Ck., Figure 13) had the highest percentage of RBT introgression, 48% (CI 24-55%) and 10% (CI 3-25%), respectively (Kozfkay *et al.*, 2007). Ship Island Creek which had 23 RBT, 2 WCT and 29 backcross hybrids (F_n ; the most of any stream) displayed a cD_2 result of 0.04, indicating that female RBT were backcrossing with hybrids; yet Papoose Creek having only 2 F_n hybrids (52 RBT; 7WCT) had a negative cD_2 value (-0.03) suggesting that female WCT were spawning with F_n hybrids (Kozfkay *et al.*, 2007). Of the remaining twelve sampling sections containing hybrids, only the middle section of Indian Creek had other female RBT breeding with F_n hybrids. Conversely, one of the seventeen sampling locations (Wilson Creek), which had been historically

stocked with RBT at its headwater lake, had both RBT and WCT, yet displayed no interbreeding. Consequently, Kozfkay *et al.* (2007) noted that for Ship Island Creek, a complete breakdown of reproductive isolating mechanisms had occurred.

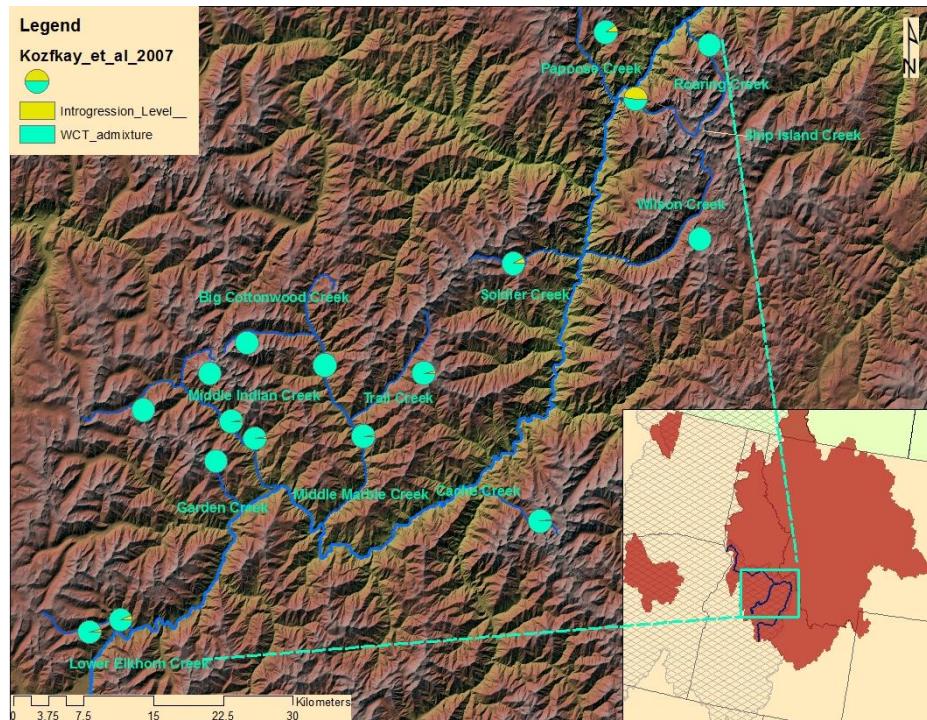


Figure 13. Introgressive hybridization among sympatric westslope cutthroat trout and rainbow trout populations submitted to low density stocking for tributaries of the Middle Fork Salmon River, ID. Modified from Kozfkay *et al.* 2007.

The cytonuclear associations showed evidence that there was a strong tendency for assortative mating between RBT, WCT and hybrids within the sympatric population (Kozfkay *et al.*, 2007). Although a difference in spatial and temporal spawning is thought to limit hybridization in sympatric salmonids (Hartman & Gill, 1968), research has shown that the overlap between WCT and RBT spawning can increase hybridization (Henderson *et al.*, 2000; Muhlfeld *et al.*, 2009b). First generation hybrids (F_1) were more often the product of female WCT and male RBT parentage, with strong asymmetrical F_n backcrossing with cutthroat trout. This could be the product of female WCT arriving later to the spawning sites after most female RBT have spawned, leaving male RBT to mate with female cutthroat trout.

Of the tributaries of the Middle Fork Salmon River which had prior stocking of their headwater lakes, only Ship Island Creek had a population with more than 20% introgression by RBT and none of the unstocked sites had more than 10% introgression (Kozfkay *et al.*, 2007). Although low levels of hybridization were present in most of the streams, Kozfkay *et al.* (2007) stated that the severity of introgression seemed to be independent of the sample population's proximity to stocking locations. Moyle and Light (1996) evidenced that the consequences of anthropogenic introgressive hybridization are a function of the magnitude, timing and frequency of introductions. Due to the remoteness of the watershed the last known stocking of RBT in the Middle Fork Salmon River drainage occurred at Heart Lake on Wilson Creek in 1983. This is interesting because of the streams that had both RBT and WCT present, Wilson Creek was the only one not to exhibit hybridization (Kozfkay *et al.*, 2007).

The authors concluded that, with the exception of Ship Island Creek, hybridization is not causing a genomic extinction for WCT in the selected tributaries of the Middle Fork Salmon River. They also felt that diagnostic genetic markers are needed in order to determine the nature of spawning dynamics of sympatric populations of WCT and RBT submitted to supplemental stocking. It seems logical to conclude that for the Middle Fork Salmon River, an area historically containing sympatric RBT and WCT, that low intensity subsidies to native fishes from hatchery sources has not had a significantly negative impact on fish assemblages.

Allopatric Populations & Anthropogenic Hybridization

Ostberg and Rodriguez investigated hybridization of introduced RBT with allopatric WCT at the western terminus of their historic range. Although the stocking history within the Lake Chelan, WA drainage has been long and convoluted, it is clear that recreational fishing was augmented annually with RBT stockings beginning in the early 1900's and continued until 2003 (Ostberg & Rodriguez, 2006). The remainder of hatchery supplementation took place on the headwaters of the Stehekin River from 1917-1998 (Ostberg & Rodriguez, 2006). The authors also noted that several streams and lakes that were historically void of fish above barrier falls, were stocked with both RBT (North Fork of Bridge Creek and McAlester Lake) and WCT (McAlester Lake).

Given the introduction of RBT into the barren North Fork of Bridge Creek, Ostberg and Rodriguez (2006) found the most genetically pure RBT in proximity to the mouth of that stream (Figure 14). In contrast to the sympatric population on the Middle Fork Salmon River (Kozfkay *et al.*, 2007), the majority of F₁ hybrids resulted in crosses between female RBT and male WCT (Ostberg & Rodriguez, 2006). Cytonuclear disequilibrium results further supported that RBT introgression not occurring in the immediate vicinity of the source population decreased with increased elevation (Ostberg & Rodriguez, 2006). Both genetically pure female WCT and female F_n hybrids selected fishes of RBT parentage to mate with in lower elevation sites and nearer the mouth of the source stream (Ostberg & Rodriguez, 2006).

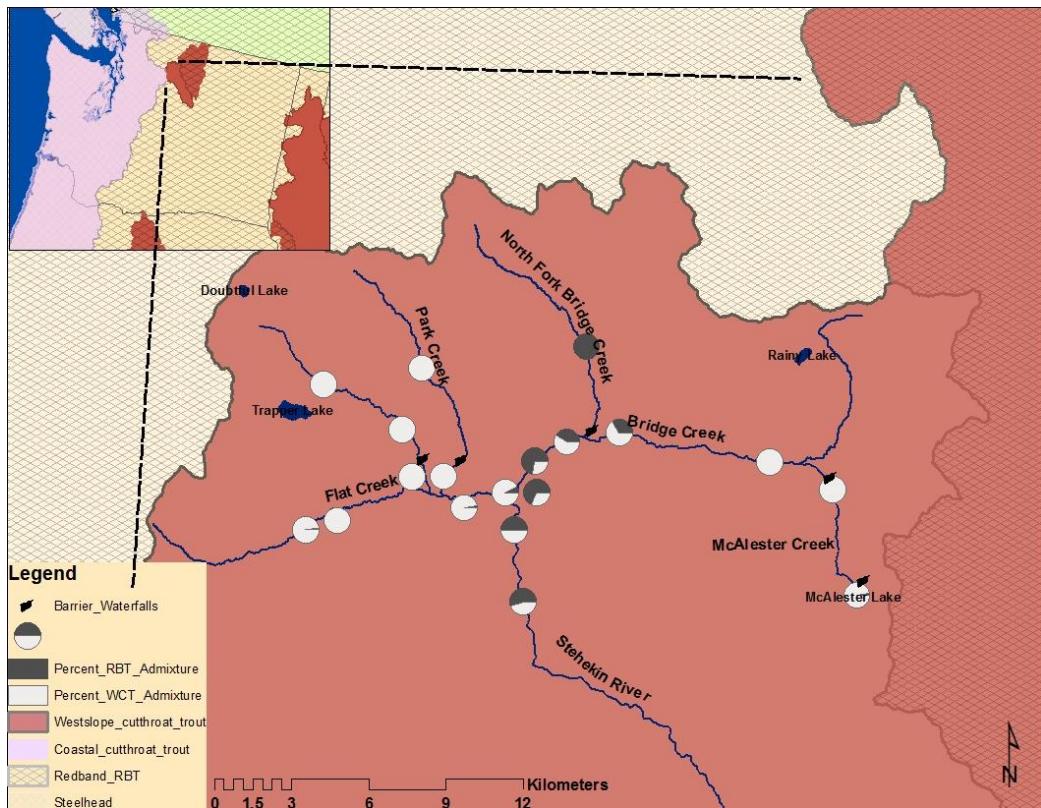


Figure 14. Anthropogenic hybridization of allopatric westslope cutthroat trout with introduced rainbow trout in tributaries of the Stehekin River, WA. Modified from Ostberg & Rodriguez, 2006.

Only above drainages with barrier waterfalls which were not submitted to RBT stocking, did they find pure populations of WCT (Ostberg & Rodriguez, 2006). Discussing possible explanations for their

results, Ostberg and Rodriguez (2006) proposed that decreased water temperatures coinciding with higher elevations might be disadvantageous to introduced RBT gene complexes, thereby creating a “semipermeable thermal barrier.” They also proposed that the introduced population of rainbow trout on the North Fork of Bridge Creek and the annual stockings of Lake Chelan acted as a source population (Osterberg & Rodriguez, 2006) for stepping stone invasion of RBT in the Skehekin River Drainage.

Originally considered a stronghold for allopatric westslope cutthroat trout (Liknes & Graham, 1988), Hitt *et al.* (2003) conducted sampling to characterize the spatial and temporal patterns of hybridization within the Middle and North Forks of the Flathead River, MT (hereafter referred to as Middle Fork and North Fork, respectively). Stocking records from Montana Fish, Wildlife and Parks, showed that approximately 20 million *O. mykiss* had been stocked into the basin above the dam on Flathead Lake beginning in the late 1800’s continuing until 1969 (M. Deleray, Montana Fish, Wildlife & Parks [MFWP], 490 North Meridian Road, Kalispell, MT 59901, unpublished data). Hitt *et al.* (2003) hoped to determine how the water temperature regime, channel geomorphology and watershed condition affected the extent of hybridization within the Upper Flathead drainage.

Forty-two sample sites were tested and 57% (24) of the populations showed evidence of hybridization (Hitt *et al.*, 2003). Excluding Whitefish River, Abbot Creek had the highest percentage of hybridization (97.5%), and all hybrids >10% introgression were within 25km of the confluence of the North Fork and the Middle Fork (Hitt *et al.*, 2003). Unbeknownst to the authors at the time of publication, in 1997 an unintentional introduction of approximately 70,000 RBT (Muylfeld *et al.*, 2009b) of *O. m. irideus* genetic parentage (steelhead; R. Leary, University of Montana Conservation Genetics Laboratory, Missoula, MT 59812, unpublished data) occurred from a private hatchery at Sekokini Springs (Figure 15). Located downstream from the junction of the North Fork and the Middle Fork Rivers, these introduced hatchery fish were likely the source of the hybrid swarm Hitt *et al.* (2003) identified in Abbot Creek. Although not statistically significant, Hitt *et al.* (2003) observed that higher elevation areas (above 1450 m) with the steepest slope and the smallest hydrologic catchments, had lower numbers of hybrid fishes. Considering the downstream proportions of introgression, Hitt *et al.* (2003) concluded that the

spatial distribution of hybridization was correlated with the distance to and extent of introgression in neighboring sample sites and the source population (Abbot Creek).

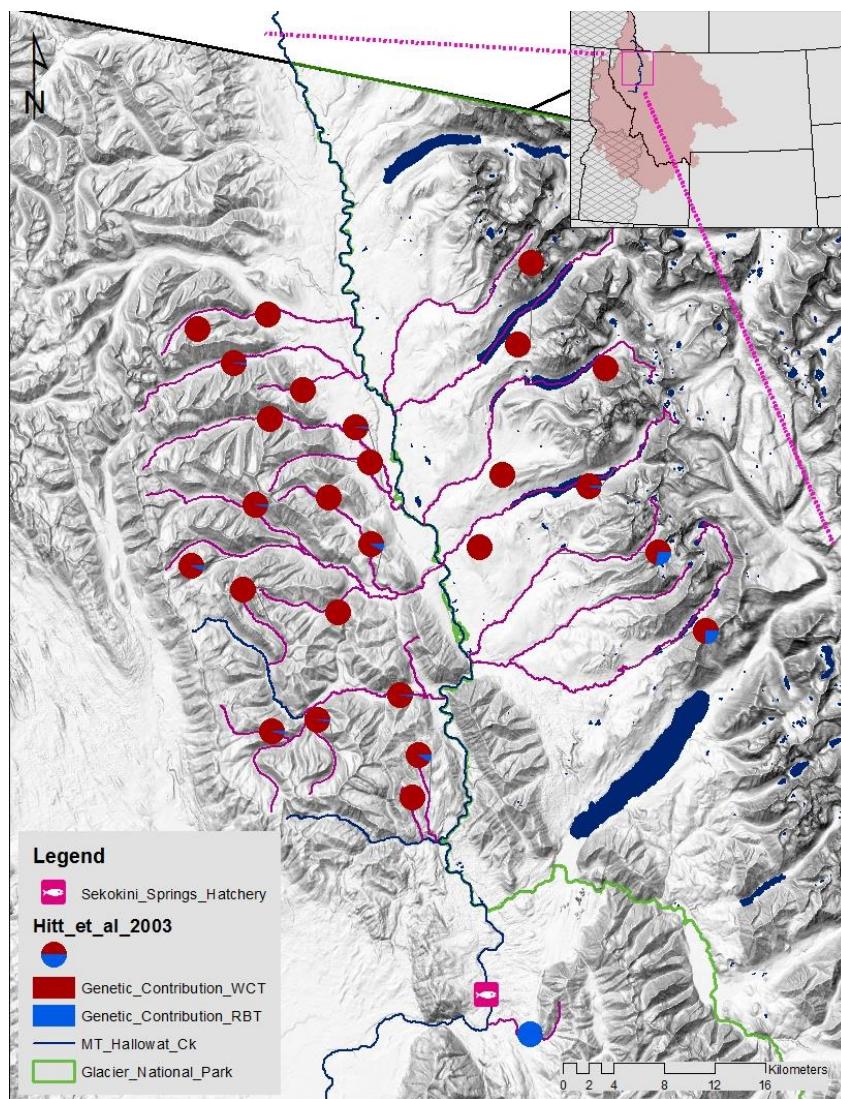


Figure 15. Anthropogenic hybridization of allopatric westslope cutthroat trout and introduced rainbow trout in tributaries of the North Fork Flathead River, MT. Modified from Hitt *et al.* 2003.

Further investigations of the same area supported the idea that RBT initially colonized Abbot Creek prior to upstream expansion. Within their study of the North Fork, Boyer *et al.* (2008) found that 85% of RBT alleles identified were also present in samples taken from Abbot Creek. Similar to earlier research regarding allopatric populations of WCT, (Hitt *et al.*, 2003 - upper Flathead River; Weigel *et al.*, 2003 - Clearwater River, ID; Osterberg & Rodriguez, 2006 - Stehekin River, WA), the amount of

invasive *O. mykiss* admixture decreased as fluvial distance increased from the source (Figure 16; Boyer *et al.*, 2008). Also suggesting simultaneous long distance dispersal, first generation hybrids (WCT X RBT) were found approximately 32km upstream in Cyclone and Anaconda Creeks (Boyer *et al.*, 2008). Boyer *et al.* (2008) therefore determined that the rainbow trout invasion of the upper Flathead River Basin was spreading via both through stepping stone and continental-island patterns of invasion.

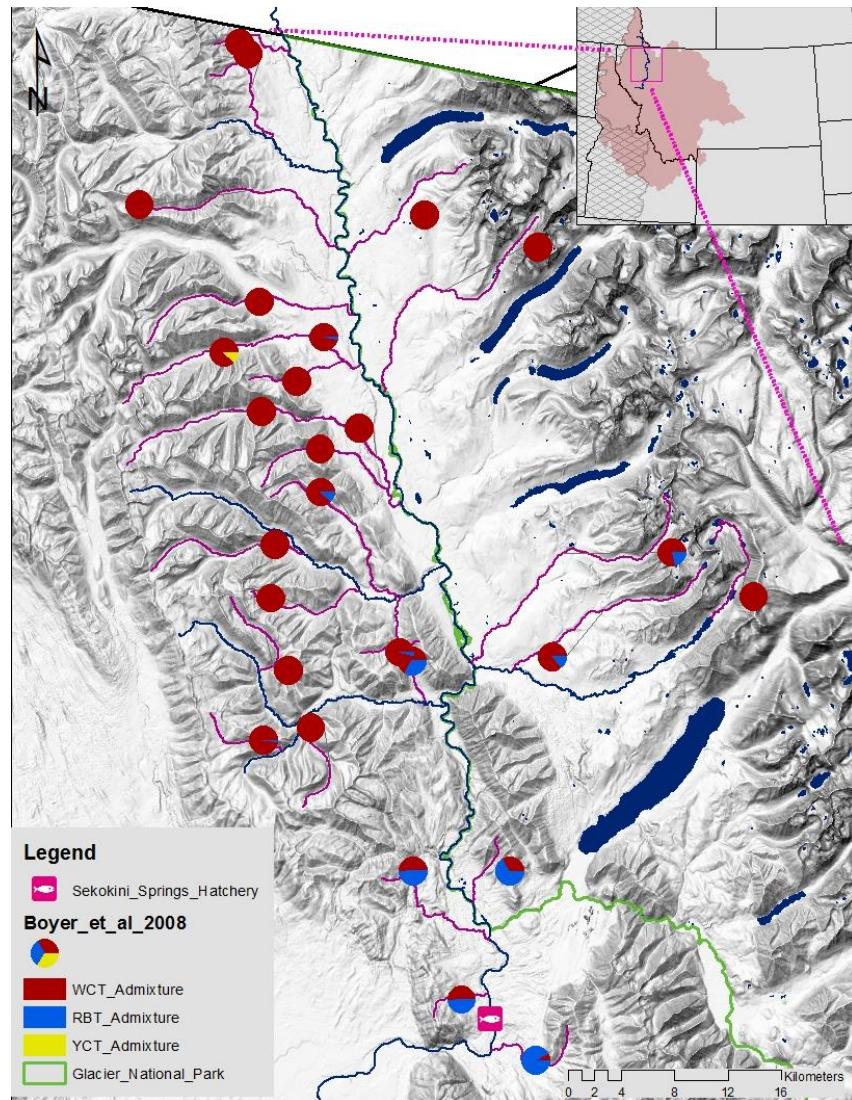


Figure 16. Continued anthropogenic hybridization of allopatric westslope cutthroat trout and introduced rainbow trout in tributaries of the North Fork Flathead River, MT. Modified from Boyer *et al.* 2008.

Extending the sampling design upstream and into Canadian headwaters, Muhlfeld *et al.* (2009b, 2009c) continued the research on the upper Flathead River Basin by examining the local habitat features,

watershed variables and spawning dynamics associated with the occurrence and amount of hybridization. Determining the mechanism behind the continental-island hybrid invasion, Muhlfeld *et al.* (2009b) identified overlapping spatial and temporal spawning patterns between WCT, RBT and their hybrids within the North Fork. Although they did not find significant effect of road density on increased hybridization, they did corroborate Hitt *et al.* (2003) finding's that hybridization was more pronounced where road-stream intersections (considered land disturbance) were more frequent (Muhlfeld *et al.*, 2009b). Additionally, microhabitats of sampling sites with introgressive hybrids were on average narrower (mean wetted width 3.9m) and at lower elevations (mean 1137m) than sample sites where no hybrids were found (mean wetted width 5.4m, mean elevation 1304m; Muhlfeld *et al.*, 2009b).

Because RBT had the longest spawning period (11 March – 20 June), almost completely encompassing the WCT run (9 May – 25 June), the only pre-zygotic reproductive isolating mechanism prohibiting hybridization was likely assortative mating. Considering that Ostberg and Rodriguez (2006) correlated the breakdown of assortative mating with proximity to increasing densities of anthropogenic introduced RBT, it seems evident that interspecific reproductive barriers adapted by allopatric cutthroat trout are completely overwhelmed with increasingly greater densities of invasive RBT. Since previous research already supports that anthropogenic hybridization increases in streams with warmer water temperatures (Muhlfeld, 2007) and high land use disturbance (Hitt *et al.*, 2003) it becomes even more concerning that none of these local-habitat features, landscape characteristics, or biotic factors seem to limit hybridization (Boyer *et al.*, 2008). Given the body of the available research Muhlfeld (2007) concluded that without the reduction or elimination of the spread of introgressive hybrids, westslope cutthroat trout as a distinct subspecies, is in great peril of extinction.

Conservation Considerations & Management Alternatives

Intuitively, over exploitation through fishing was thought to be the initial reason for WCT decline. MacPhee (1966) described WCT that were caught twice as easily as invasive brook trout (*Salvelinus fontinalis*) while Behnke (1979) projected that 124 hours of fishing per hectare would result in overexploitation of stream dwelling WCT. Total mortality (fishing mortality plus natural mortality) for

WCT has approached 75% for areas such as the St. Joe River and Kelly Creek in Idaho (Thurow & Bjornn, 1978). Increases in abundance of WCT within GNP for non-hybridized (Downs *et al.*, 2011; 2013) streams could be a result of decreased in exploitation. In 2010, special fishing regulations were imposed within the park requiring the catch-and-release of all native members of Salmoninae (*Salvelinus confluentus* and *O. c. lewisi*) (C. Downs, Fisheries Biologist, Glacier National Park, personal communication, 2013).

Even though populations of WCT may take years to reach dynamic equilibrium (asymptotic dynamics; Figure A, Appendix A) by removing fishing induced mortality, the population growth rate (λ) of resident isolated populations can be estimated at 1.54 (Appendix A). Thurow and Bjornn (1978) concluded that if habitat is not limiting, then populations of WCT can positively respond to the implementation of special fishing regulations in as little as three years. Several isolated streams (Autumn Creek and Wild Creek) exhibited increases in density of WCT coinciding with implementation of catch-and-release regulation. Taken together with other isolated streams (No-Name Creek) these waters provide what are thought to be genetically pure sources of WCT and therefore deserve special conservation considerations.

Since hybridization reduces fitness (Muhlfeld *et al.*, 2009a), those streams that were sampled within GNP documented as having hybrids (Akokala, Boulder, Lee and McGhee Creeks) likely would exhibit lower densities. Both Akokala Creek and McGhee Creek exhibited reductions of fish densities by at least 50% over sampling years. Furthermore, since fishing induced mortality should be close to zero, streams that are not undergoing introgression should be growing. Of the streams that have no known hybrids (Autumn, Ford, No-Name and Wild Creeks) all showed increases in WCT densities. Fish Creek and Spruce Creek both exhibited declines in WCT suggesting that hybridization may be occurring. It must be understood and stated that sampling methods used by Downs *et al.* (2011; 2013) were not designed to test this hypotheses, however these observations suggest that future monitoring and study is warranted.

Reduction of the historical range for WCT can be attributed in part to isolation or elimination of habitat due to anthropogenic barriers to migration. These include but are not limited to the construction of dams, irrigation diversions and culverts (Rieman & Apperson, 1989). Compromising long term persistence, gene flow can be reduced in isolated populations (McIntyre & Rieman, 1995; Kruse & Hubert, 2001; Wofford *et al.*, 2005) accounting for significantly fewer alleles and lower expected heterozygosity (Talyor *et al.*, 2003). Small isolated populations are also susceptible to extinction caused by environmental and demographic stochasticity (Dunham *et al.*, 1997; Hilderbrand, 2003). Consequently, Hilderbrand and Kershner (2000) estimated that 8km of stream habitat was needed for the persistence of high WCT population densities (≥ 0.3 fish/m) and that low abundance streams (≤ 0.1 fish/m) would need a total of 25km of habitat for sustainment. Of the four isolated streams sampled (Autumn, Fern, No-Name and Wild Creeks) by Downs *et al.* (2011; 2013) only Wild Creek completely meets the requirements for persistence of a high density population, with approximately 10 km of stream habitat (total fluvial distance of 1-3rd order stream sections calculated from USGS Hydrologic Dataset using ArcGIS Spatial Analysis Tool). Both Autumn and No-Name Creeks have about 7.7 km of stream habitat, which when considering average fish abundance over sampling years (0.28 & 0.48 fish/m, respectively), is likely enough to maintain future genetically pure populations of WCT.

Isolated hydrologic basins providing a combination of lake and stream habitats free of anthropogenic hybridization has proven to be the best possible scenario for the persistence of WCT. Fraley and Shepard (2005) determined that the WCT population above the Hungry Horse Dam (on the South Fork of Flathead River) is among the largest in average size (total length) and longest-lived populations in Montana. Having all life history strategies, this population would likely exhibit a large amount of intra-specific gene flow with increased heterozygosity. Cases where isolation eliminates hybridization may give insight into pre-anthropogenic conditions.

Several models have been established to try to predict the negative impacts of global climate change on native members of Salmoninae. Williams *et al.* (2009) suggested that due to the increased occurrence of wildfire attributed to global climate change, 37% of the current range of WCT is at high

risk of extinction. Wenger *et al.* (2011) forecasted that due to increasing water temperatures and biotic interactions associated with global climate change and introduction of invasive rainbow trout, respectively, the available habitat for WCT will be reduced by an additional 58% by 2080. The authors concluded that nonnative species account for 33% of WCT habitat loss currently, and predicted that invasive species would continue to depress cutthroat trout abundance by 26% in the future (Wenger *et al.*, 2011). Wenger *et al.* (2011) did note that induced by warmer temperatures, winter flooding should limit the spread of fall spawning invasive species such as brook trout and brown trout (*Salmo trutta*).

Discussion

Submitted to low intensity stocking, populations of cutthroat trout and rainbow trout also undergo limited anthropogenic hybridization. Whether anthropogenic in nature or not, interspecific reproductive barriers seem to limit introgression with natural selective processes through differences in spatial and temporal spawning (Hanson, 1977; Henderson *et al.*, 2000; Muhlfeld *et al.*, 2009b) and assortative mating (Campton & Utter, 1985; Ostberg *et al.*, 2004; Kozfkay *et al.*, 2007). In these populations when hybridization does occur, reduced fitness (Henderson *et al.*, 2000; Muhlfeld *et al.*, 2009a), high juvenile mortality due to environmental factors (Fausch *et al.*, 2001) and migratory disorientation of hybrids (Compton & Utter, 1985; Moore *et al.*, 2010) may serve as further postzygotic selection mechanisms.

Conducting a review of the available research, it is apparent that the single most important factor when considering the spread of anthropogenic introgressive hybridization is the concentration of and proximity to the source population of introgression. For allopatric populations of WCT, the level of introduction of invasive rainbow trout governs the extent and characterization of the source hybrid swarm. After a hybrid swarm develops, introgressive hybridization and invasion initially exhibits a stepping stone pattern (Hitt *et al.*, 2003; Ostberg & Rodriguez, 2006; Boyer *et al.*, 2008). Additionally, due to the migratory spawning nature of both rainbow trout and cutthroat trout, island patches of hybridization occur large distances away from the swarm. This continental-island pattern of invading hybrids further amplifies the stepping stone pattern moving the introgression upstream at an alarming rate (Muhlfeld *et al.*, 2009b).

Given the similar aquatic thermal regimes and optimal growth temperatures of rainbow trout and westslope cutthroat trout it is unlikely that lower water temperatures is or will be a limiting factor for anthropogenic hybridization. Peak growth rates for RBT actually occur at slightly low water temperatures (13.1°C) versus that of WCT (13.6°C), whereas the 60 day UUILT for WCT is 19.6°C versus 24.3°C for RBT (Bear *et al.*, 2007). Lending to the fact that cutthroat trout subspecies are highly adaptable and a phenotypically variable species (Leary *et. al.*, 1987; Allendorf & Leary, 1988), Behnke (1992) observed that Humboldt cutthroat trout thrive in streams with temperatures as high as 26°C and noted that he had caught HCT in small streams with no flowing water where spring floods had lodged debris in trees 2m above the dry streambed.

Although previous research has found an inverse relationship between elevation and hybridization (Ostberg & Rodriguez, 2006; Muhlfeld *et al.*, 2009b), it has also been shown that a negative correlation of elevation on water temperatures exists (Lanka *et al.*, 1987; Muhlfeld *et al.*, 2009b) thereby reducing abundance (Lanka *et al.*, 1987; Coleman & Fausch, 2007) and growth of cutthroat trout (McGrath *et al.*, 2008). Dwyer and Kramer (1975) found that metabolic rates of cutthroat trout decrease as water temperatures drop below 15°C, while growth is significantly reduced below 7°C (Hubert & Gern, 1995). Therefore, it is more likely that for WCT the Elevation Refuge Hypothesis is a factor, not of water temperature, but rather the fish's ability to adapt to extreme flow conditions.

Culminating in mid-summer, discharge for glacially governed flow regimes gradually rise during spring as temperature induced snow melt and subsequent glacier melt peaks (Milner & Petts, 1994). Connell (1978) predicted that habitats exposed to high levels of disturbance would have lower species diversity, yet those species present would be highly tolerant or able to rapidly recolonize after perturbation (Intermediate Disturbance Hypothesis). In areas of low disturbance, highly competitive species should monopolize resources also producing areas of low species diversity (Connell, 1978). As a result, species diversity would be greatest in intermediate areas of disturbance because a variety of taxa could tolerate the moderated conditions. Stating that flow is major determinant of physical habitat, Bunn and Arthington (2002) suggested a positive correlation of flow on biotic composition. Water temperature

and channel stability has been shown to be the two most limiting factors influencing invertebrate community structure in glacial streams (Milner & Petts, 1994; Milner *et al.*, 2001). Bunn and Arthington (2002) also suggested that aquatic species evolved specific life history strategies as a direct response to natural flow regimes.

Salmoninae spawning patterns for mountain drainages are thought to be an adaptation at least in part to timing and depth of channel bed mobility (Montgomery *et al.*, 1999). The Bed Scour Hypothesis predicts that survival to emergence is a function of either burying eggs below the annual scour depth or avoiding spawning during times of likely bed mobility (Montgomery *et al.*, 1999). Subsequently, Montgomery *et al.* (1999) found salmonid spawning distributions supporting this concept. Considering the extensive seasonal reproductive migration of fluvial and adfluvial WCT to headwater tributaries and the delayed timing of spawning, it is easy to postulate how westslope cutthroat trout have evolved unique ecological and life history traits that allow them to occupy geographic distributions governed by glacially fed, hydrologic regimes.

Certain investigations have examined the influence of flow regimes on hybridization (Hitt *et al.*, 2003; Muhlfeld *et al.*, 2007). Although Fausch *et al.* (2001) found evidence that spring and summer flooding impeded rainbow trout recruitment, Hitt *et al.* (2003) proposed that it was unlikely that flow regime and other environmental factors would affect introgression once a source population had been established. Furthermore, they predicted that environmental and ecological factors should not be expected to prevent the spread of hybridization (Hitt *et al.*, 2003). Evident in subsequent research (Boyer *et al.*, 2008; Muhlfeld *et al.*, 2009b), this assumption holds true for such areas as the upper Flathead Basin where anthropogenic hybridization is likely a product of a single point source of hybrid swarm establishment. In areas of sympatry (Kozfkay *et al.*, 2007) or low density stocking of invasive RBT (Ostberg & Rodriguez, 2006), interspecific reproductive barriers appear to limit introgressive hybridization. Where introductions are more established, migrations barriers preventing upstream movement may be the only viable management strategy ensuring persistence of pure stocks of westslope cutthroat trout (Ostberg & Rodriguez, 2006; Cook *et al.*, 2010).

Conclusions

Due to the genetic and morphological similarities between RBT and WCT future management of the resources will be challenging. Further stocking of rainbow trout to sympatric populations of RBT and WCT without regard to frequency or density will breakdown interspecific reproductive barriers and lead to extensive anthropogenic hybridization. If allopatric populations of WCT are continually stocked the retreat of genetically pure westslope cutthroat trout will continue up into headwater reaches until anthropogenic introgressive hybridization leads to genomic extinction.

Although artificial migration barriers will limit genetic drift and reduce the likelihood of persistence due to demographic and environmental stochasticity, no other effective management alternatives have been proposed. Future research should focus on the influences of individual watershed hydrologic flow regimes (timing, frequency and magnitude) on the level and extent of anthropogenic introgressive hybridization between RBT and WCT.

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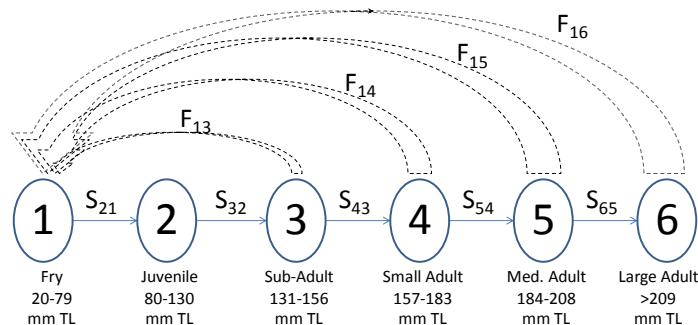
Appendix A

Stage Based Matrix Population Model

Life cycle graph

Since resident westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; WCT) rarely exceed 300 mm total length (TL; Averett, 1962; McIntyre & Rieman, 1995; Thurow & Bjornn, 1978) stage classification was adapted from Downs and White (1997). The authors found that from nineteen isolated headwater streams female resident WCT less than 149mm fork length (FL) were generally immature. Mean fecundities were reported for sexually mature females within three size classes: small adults (150-174mm FL), medium adults (175-199mm FL) and large adults (>200mm FL) (Downs *et al.*, 1997). Using Carlander's (1969) conversion equation for fork length to total length: $TL=1.05*FL$ application of these stage classes coincided with length-at-age observed by Downs (1995) (Figure A3).

Figure A3. Life Cycle Graph for Resident WCT



Population Parameters

Because Downs *et al.* (1997) showed that the probability of being sexually mature was a function of fork length average stage TL was adapted to their model to predict the probability of being sexually mature within each stage (Equation A1). Even though they found that almost all females less than 157mm TL were sexually immature, their regression equation for sexually maturity resulted in 3% of the

population of Sub-Adults being capable to reproduce. Conversely, for small adults the probability of being sexually mature increased to 44%, 95% for medium adults and 100% for large adults.

$$M = \frac{\exp(-20.28+0.13\left(\frac{TL}{1.05}\right))}{1+\exp(-20.28+0.13\left(\frac{TL}{1.05}\right))} \quad (\text{A1})$$

Fecundity has also been shown to be a function of total length (Averett, 1962; Downs *et al.*, 1997; Johnson, 1963; Rieman & Apperson, 1989). Downs *et al.* (1997) combined the results of their investigation of isolated headwater westslope cutthroat trout with that of Averett (1962) and Johnson (1963) resulting in a fecundity best fit model (Equation A3).

$$E = -790.7 + 6.2\left(\frac{TL}{1.05}\right) \quad (\text{A2})$$

As might be expected, finding estimates of westslope cutthroat trout egg-to-fry survival proved very challenging. Mortality rates for early life stages are very high and sometimes estimates are made based on what is thought to happen (Bjornn *et al.*, 1977). Egg-to-fry survival was estimated to be 8.5% based on research conducted by Magee *et al.* (1996). This value was derived from observations made on two headwater streams of the Missouri River. One of these streams, Cache Creek, was also used in observations conducted by Downs *et al.* (1997) for fecundity and sexual maturity at size estimates. Resulting fertility parameters (Equation A3) were calculated using the product of fecundity (E), egg-to-fry survival and the probability of being sexually mature (M) (Equation 3).

$$F = E * 8.5\% * M \quad (\text{A3})$$

Natural mortality is also a difficult parameter to determine. Almost all studies attempting to estimate mortality include populations susceptible to fishing. Reiman and Apperson (1989) reviewed existing estimates of total mortality and noted that populations under fishing pressure can exhibit mortality between 57-72%. Bjornn *et al.* (1977) conducted a study of angling mortality versus natural mortality on the St. Joe River in northern Idaho. Natural mortality was estimated to be 47% following the implementation of special fishing regulations (Bjornn *et al.* 1977). Although no estimates of natural mortality was found for resident WCT, Reiman and Apperson (1989) concluded that natural mortality of fluvial and adfluvial WCT to be between 30-50%. Assuming that the population in question is not being

exploited or catch-and-release regulations are in effect, natural mortality would be higher for smaller fish due to such factors as predation and competition; therefore survival of fry to juvenile and juveniles to sub adult is set at 50%, while survival of sub-adults and adults stages are estimated to be 60% and 70% respectively.

Method of Analysis

Given these population parameters a matrix population model was designed in Matlab (Appendix B). The asymptotic population growth rate (λ) is defined analytically as the dominant Eigen value for the population matrix (\mathbf{W}). Numerically, λ is equal to the exponential of the slope of log densities for a specific stage after reaching asymptotic dynamics. The stable stage distribution (\mathbf{w}) is the proportion of the total population occupied by each stage after the population reaches asymptotic dynamics. It is numerically calculated as the population abundance of a specific stage divided by the summation of all stage densities at the same time. Analytically it is the right Eigen vector for the matrix population model (Equation A4). For each Eigen value λ a left and right Eigen vector exist, where the left Eigen vector is

$$\mathbf{W} * \mathbf{w} = \lambda * \mathbf{w} \quad (\text{A4})$$

$$\mathbf{v} * \mathbf{WCT} = \mathbf{v} * \lambda \quad (\text{A5})$$

associated with the reproductive values (\mathbf{v}) (Equation A5). Under asymptotic dynamics the reproductive values measure the relative contribution of individuals in each stage to the overall population density.

To determine how sensitive λ is to changes in the population parameters (\mathbf{W}) a sensitivity matrix can be calculated using the stable stage distribution (\mathbf{w}) and the reproductive values (\mathbf{v}) (Equation A6).

$$\text{sensitivity} = \frac{\mathbf{v} * \mathbf{w}^T}{\mathbf{v}^T * \mathbf{w}} \quad (\text{A6})$$

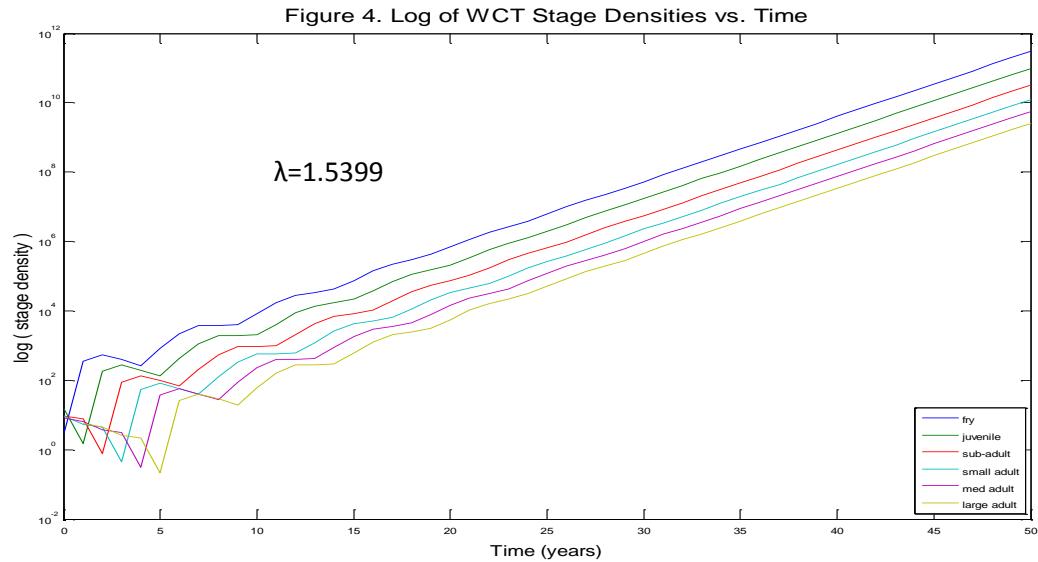
$$\text{elasticity} = \frac{\mathbf{w}_{ij}}{\lambda} * \frac{\partial \lambda}{\partial \mathbf{w}_{ij}} \quad (\text{A7})$$

Elasticity, or the amount in which λ is affected by proportional changes in transition rates, was calculated (Equation A7). Since the focus of this discussion is resident WCT the initial population

abundance (N_w) is based on a sample conducted for an isolated headwater stream of the Middle Fork of Flathead River, Montana (Autumn Creek; Downs *et al.*, 2013).

Results & Discussion

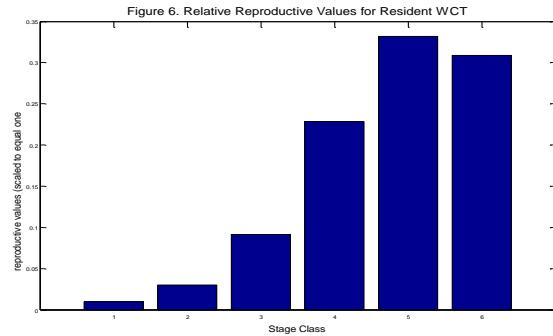
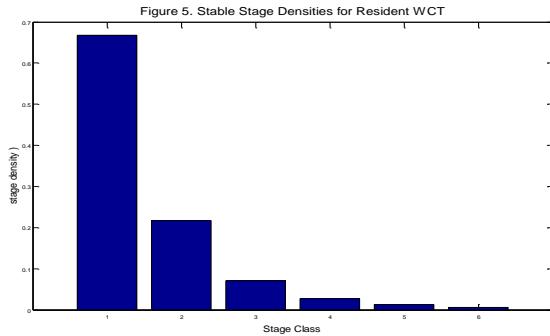
The population projection undergoes transient dynamics for approximately twenty years after which it exhibits an asymptotic growth rate of $\lambda=1.54$ (Figure A4). It is apparent that given the available population parameters, the population density will increases over an extremely long time period (50 years). Extended transient dynamics may be attributed to slow growth and low fertility. Considering fertility terms are a function of total length and associated growth is slow for resident WCT the initial population (3 fry; 15 juveniles; 9 subadults; 9 small adults; 8 med adults; 0 large adults) takes a long time to reach the stable stage distribution (Figure A5).



Similar growth rates were projected by Reiman and Apperson (1989) when they conducted simulations for an age-structured population model subjected to very little fishing pressure. Although their model was based on fluvial and adfluvial WCT they found that populations having high growth rates and low natural mortality would produce populations three times larger than ones with low growth or high mortality. Some may argue this comparison is not valid because adfluvial and fluvial fish are thought to grow faster than resident WCT (Reiman & Apperson, 1989) but Downs (1995) made

observations to the contrary. He observed that Age 2 resident fish length (Stage 3 - subadult fish in this model) was similar to fluvial and adfluvial populations and growth rates were even slightly higher in Age 1 (Stage 2-juvenile) resident WCT (Downs, 1995). By Age 3 adfluvial growth rates were higher than resident fish (Stage 4 – small adults) and by Age 4 fluvial cutthroat trout also outgrew resident fish (Downs, 1995).

Analysis of the stable stage distribution (Figure 5) reveals a distribution where majorities of the population are fry (Stage 1). Relative reproductive values for resident WCT was highest for Stage 5 (184-208 mm TL) indicating that intermediate adults have the greatest potential to contribute to future stocks (Figure 6).



The population growth rate showed the same sensitivity (0.63) to changes in transition parameters from fry to juveniles as it did from juveniles to sub-adults (Figure 7). These findings are supported by Reiman and Apperson (1989) who found that changes in recruitment to juvenile stocks of WCT produced the highest sensitivity of λ . Sexually maturity, transition from sub-adult to small adult, showed the second highest sensitivity (0.51) while sensitivity of λ to changes in fertility rates was relatively small. Sensitivity of lambda to proportional changes in transition parameters, or elasticity, was largest (0.20) for fry to juveniles and juveniles to sub-adults. There is however a significant effect of proportional changes in fertility rates on λ , elasticity of 0.0675 small adult-to-fry, 0.0759, medium adult-to-fry and 0.0555 large adult-to-fry (Figure 8).

Figure 7. Sensitivity of Lambda to Changes in Resident WCT Population Parameters

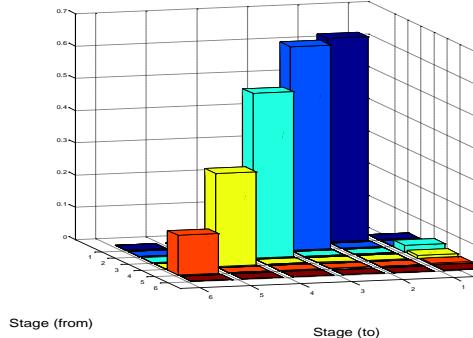
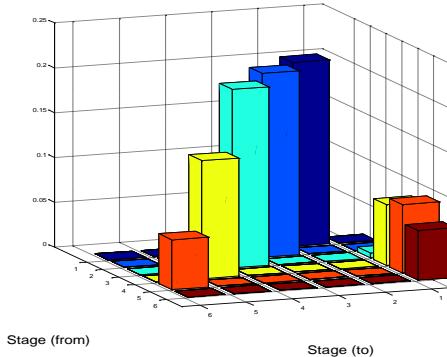


Figure 8. Elasticity of Lambda to Proportional Changes in Resident WCT Population Parameters



Conclusions

Westslope cutthroat trout are highly susceptible to fishing. Although analysis of population parameters estimated by Downs *et al.* (1997) show a positive asymptotic growth rate and a low sensitivity of λ to changes in recruitment of Age-0 fish it takes a long time for the population to reach asymptotic dynamics. Furthermore these estimates do not consider exploitation due to fishing. Thurow and Bjornn (1978) reported greater densities of cutthroat trout fry in stream reaches closed to fishing and concluded that fishing may have limited fry recruitment in other unregulated reaches. The duration of the transient dynamics only confirms that should populations of isolated headwater WCT be subjected to unregulated fishing pressure (where larger resident fish are removed) the population dynamic would be drastically altered. This is also evident when considering the sensitivity of λ to changes in survival rates. Based on Thurow and Bjornns (1978) if total mortality is adjusted for fishing pressure, survival rates of 30%, the asymptotic annual population growth rate (λ) goes from 1.54 down to 0.93 and does not reach asymptotic dynamics for approximately twenty-five years. Therefore it is recommended that isolated headwater populations be managed under special catch and release regulations to prevent population decline.

Transition parameters used in this projection reflect estimates of sexual maturity at length, fecundity and egg-to-fry survival of isolated headwater WCT. Conversely, mortality rates were estimates based on fluvial and adfluvial populations. Although these values may be similar, no research is available to confirm this assumption. In order to more accurately project what may happen in future

populations of isolated headwater WCT it is recommend that specific research be conducted to identify both natural mortality rates and fishing induced mortality rates within resident WCT.

Furthermore because isolated headwater populations represent genetically pure fish these populations should be monitored to insure no invasive species are introduced. Considering WCT conservation as whole, alternate conservation strategies may include the installation of fish migration barriers to systems where all life history forms occur. Although this genetically isolates local populations it may be the only way to sustain WCT as a distinct species. Regardless because isolated headwater WCT represent genetically pure fish and introgressed hybrids comprise so much of the current range, isolated populations remain of the utmost importance.

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