Growth, movement, survival and spawning habitat of coastal cutthroat trout

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This is to certify that I have examined this copy of a master's thesis by

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and have found that it is complete and satisfactory in all respects,
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General Introduction

Ecological communities are structured by a combination of abiotic conditions including physical habitat, and biotic interactions between the species in an ecosystem. This structuring occurs in two stages. The extent of habitat and resources used by a species is first defined by the threshold abiotic conditions a species may tolerate—the fundamental niche, and then is further limited by interspecific interactions to habitats and resources a species is well-adapted to use relative to other members of the community—the realized niche. For stream-rearing salmonids, a group of closely-related fishes with a circumpolar native distribution in freshwater habitats of the northern hemisphere, structuring of ecological communities is typically determined by the available regional species pool and the habitat requirements of individual species. Species then employ niche partitioning mechanisms which may reduce negative ecological interactions such as competition and interspecific hybridization.

In coastal areas of the Pacific Northwest from northern California to southeast Alaska, coho salmon (*Oncorhynchus kisutch*), coastal cutthroat trout (*O. clarkii clarkii*), and steelhead (anadromous rainbow trout—*O. mykiss*) are the most common group of native, stream-rearing salmonids. Similarities between species result in substantial overlap in physical habitat and biotic resource use. The extent of habitat and resource partitioning between species is likely to affect competition, which may occur between all three species, and interspecific hybridization, which occurs between coastal cutthroat and steelhead, although these processes are not well understood.

This thesis consists of two chapters which examine how abiotic and biotic factors affect the ecology of coastal cutthroat trout and their interactions with steelhead and coho

salmon. The first chapter examined the extent of spawning habitat segregation between cutthroat trout and steelhead, and its potential for limiting hybridization between the two species. This project used spatially explicit and continuous sampling of trout populations throughout a watershed in conjunction with molecular genetics to improve upon previous research, much of which has been limited by spatial scale or inability to accurately differentiate between steelhead, cutthroat and hybrids. Results of this project increase knowledge of the mechanisms allowing for continued species integrity in coastal cutthroat and steelhead, despite the viability of hybrids. The second chapter employed mark-recapture techniques to study cutthroat trout ecology during rapid colonization and population growth of sympatric coho salmon, re-colonizing part of their native range after a century of exclusion. The influence of physical habitat quality, temporal environmental variation, and coho salmon density were tested as potential factors explaining variability in cutthroat trout growth, movement and survival. The results of this chapter improve understanding of the relative importance of density-dependent and density-independent factors in regulating trout populations. Results are of use for resource managers contemplating the effects of migration barrier removal and restoration of native salmon populations on extant resident species.

Chapter 1:
Habitat-based spatial segregation in spawning sites of coastal cutthroat trout and steelhead and implications for hybridization

Abstract

Introgressive hybridization between native and closely related introduced species is a conservation concern for many fishes. However, hybridization may also occur as a natural process between sympatric native species where its prevalence is determined by the effectiveness of natural reproductive isolating mechanisms. Understanding the mechanisms that limit or promote hybridization between native species may offer important lessons for conservation in areas of anthropogenically-induced hybridization. In coastal watersheds of the Pacific Northwest native coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and steelhead (anadromous coastal rainbow trout—*O. mykiss irideus*) hybridize, yet maintain species integrity. One explanation for the lack of complete introgression is spatial segregation of spawning areas between species, but this process is poorly understood. To determine the degree of spatial reproductive segregation between coastal cutthroat trout and steelhead we sampled juvenile trout with the assumption that the distribution of recently emerged fry was representative of parental spawning areas. We used genetic markers to classify individuals as hybrids or pure parent species, and assigned individuals to age classes based on length. In conjunction with fish sampling, we collected physical stream habitat measurements in a spatially continuous framework of 35 reaches from tidewaters to headwaters in a small (20 km^2) coastal watershed in Washington State. Cutthroat trout, steelhead and hybrid trout comprised 35%, 42%, and 23% of fish collected, respectively. Spatial structure in species occurrence was apparent, resulting in varying proportions of each species depending upon location within the watershed. Our results showed strong segregation of spawning areas between coastal cutthroat trout and steelhead. Contributing watershed drainage area at a site was the best predictor of species occurrence. Drainage area was correlated positively with steelhead occurrence and negatively with cutthroat trout occurrence. Hybrid fry were found in areas occupied by both parental species but were more prevalent in transitional areas. A similar pattern was observed in older juveniles of both species but there was more overlap, suggesting substantial movement of trout post-emergence. Our results offer strong support for spatial reproductive segregation as a factor limiting hybridization between steelhead and coastal cutthroat trout.

Introduction

Introgressive interspecific hybridization as a result of non-native species introductions or habitat alteration is a conservation threat to many species worldwide (Rhymer and Simberloff 1996). The mechanisms regulating the frequency of occurrence and spatial distribution of hybridization are thus crucial to evaluating the conservation threats posed. Hybridization typically occurs in narrow clinal or patchy mosaic hybrid zones, and the degree to which hybrids proliferate beyond these zones is determined by a balance between dispersal of hybrids and natural selection against them (Barton and Hewitt 1985, 1989). Ultimately, the fitness of hybrids relative to parental species determines the occurrence and spread of hybridization (Arnold and Hodges 1995). Understanding the factors controlling hybridization is particularly important for freshwater fishes because it is especially common in this group (Allendorf and Waples 1996, Scribner et al. 2000).

In the Western United States, introgressive hybridization with anthropogenically-introduced rainbow trout (*Oncorhynchus mykiss*) has caused the decline of many subspecies of cutthroat trout (*O. clarkii* sp.), and has contributed to their listing under the Endangered Species Act (Allendorf and Leary 1988, Allendorf et al. 2001). Where non-native rainbow trout have been introduced, there is sufficient spatial and temporal overlap in reproduction to allow hybridization with native cutthroat subspecies (Henderson et al. 2000, Muhlfeld et al. 2009b), with resulting fitness declines for hybridized populations (Muhlfeld et al. 2009a). However, hybridization may also occur as a natural process between native sympatric trout species, where conservation implications are less clear.

Natural hybridization occurs between coastal cutthroat (*O. clarkii clarkii*) and coastal rainbow trout (*O. mykiss irideus*) in areas of the Pacific Northwest where the species evolved in sympatry. Some combination of natural reproductive isolating mechanisms such as spatial and temporal segregation of spawning, assortative mating, or low hybrid fitness, was thought to preserve species integrity (Campton and Utter 1985, Trotter 1989). Although the two species share similar juvenile life histories, commonly rearing in streams for several years after emergence, their life histories diverge at this point. Coastal cutthroat trout display a variety of migratory patterns including both potamodromous and anadromous forms, but rarely migrate to the open ocean beyond the coastal shelf, and usually spend less than a year at a time in marine waters (Trotter 1989). Their populations often have substantial resident non-migratory components including both males and females. In contrast, coastal rainbow trout populations are typically dominated by the anadromous form, known as steelhead (all coastal rainbow trout referred to as steelhead hereafter), for which anadromy involves long-distance, multi-year pelagic ocean migrations, and their populations frequently contain only small non-migratory components which are predominantly males (McMillan et al. 2007, Quinn 2005). These differences in life history lead to differences in adult body size between the species, which could facilitate behavioral assortative mating and spatial segregation of spawning areas, since the characteristics of selected spawning sites is influenced by body size in salmonids (Quinn 2005). In addition, differences in life history during migratory stages could result in lower fitness of hybrids if they adopt intermediate and potentially maladaptive migratory behaviors (Baker et al. 2002, Hawkins 1997, Ostberg et al. 2004, Young et al. 2001), which limited observations suggest they may (Moore et al. 2010).

Despite differences in life history, and potential reproductive isolating mechanisms, natural hybridization between coastal cutthroat and steelhead (Campton and Utter 1985) has been observed throughout the range of sympatry from northern California (Baumsteiger et al. 2005) to Alaska (Williams et al. 2007). Although natural hybridization between the two species has been identified as a conservation concern (e.g. Baker et al. 2002, Bettles et al. 2005, Heath et al. 2010), hybridization between the two species may also be viewed as a natural evolutionary process, which occurs between many closely related sympatric taxa (Barton and Hewitt 1985, Ostberg et al. 2004). Supporting this view, introgressive hybridization and its attendant hybrid swarms comprised of entirely hybrid individuals are rarely observed in populations of coastal cutthroat and steelhead. To date, the only documented hybrid swarms are found in resident populations above migration barriers, where both species are present only as stream residents, or in populations with a history of hatchery introductions (Bettles et al. 2005, Docker et al. 2003, Johnson et al. 1999).

There is a need to better understand the mechanisms determining the occurrence and frequency of hybridization in space and time. It is generally thought that within sympatric populations of steelhead and coastal cutthroat trout, spatial or temporal reproductive isolation may limit hybridization, resulting from cutthroat trout spawning earlier in the season and in smaller streams located higher in watersheds, consistent with their body size (Campton and Utter 1985, Hartman and Gill 1968, Trotter 1989). It is doubtful that temporal segregation is a primary reproductive isolating mechanism because the timing of spawning between coastal cutthroat trout and steelhead overlaps substantially in Washington, where cutthroat trout may initiate spawning as early as mid-December and spawning often continues through at least May (Trotter 1989), while steelhead initiate spawning as early as the beginning of January and can continue through June and into July (McMillan et al. 2007).

Spatial segregation is a more likely reproductive isolating mechanism but has not been thoroughly investigated. Early studies (e.g. Hartman and Gill 1968, Trotter 1989) suggested greater use of upstream areas and smaller streams by cutthroat relative to steelhead. However, these studies relied on visual identification of trout species, which is now known to have a high rate of error (Baumsteiger et al. 2005, Kennedy et al. 2009). Subsequently, Ostberg et al. (2004), using genetics to indentify trout, documented a similar pattern of increasing cutthroat prevalence in upstream areas and steelhead in downstream areas with hybrids intermediate, suggesting a clinal hybrid zone is present, in which coastal cutthroat and steelhead maintain separate niches along habitat gradients, with hybridization occurring in transitional areas where niche overlap occurs (Hagen and Taylor 2001). However, Ostberg et al. (2004) did not quantify habitat characteristics, noting that further research was needed to describe the relationship between physical habitat characteristics and the occurrence of hybridization. Others have found relationships between watershed-scale habitat attributes and the proportion of hybrids at a single or small number of sites within a watershed, but have not determined if the occurrence of parent species and hybrids varied at a sub-watershed scale (Heath et al. 2010). In addition, studies often have not addressed the potential interaction between fish age or time of year, and their spatial distribution, which can only be expected to mirror that of their parents (thus revealing the spatial distribution of hybrid spawning events) before they have moved substantially from the natal area (Einum et al. 2008, Teichert et al. 2011). Extensive movement is common among sub-yearling trout soon after emergence during their first summer, and even more frequently by age one or two (Hoffman and Dunham 2007, Kahler et al. 2001). A study design that accounts for fish age and time of year, and includes spatially continuous sampling across habitat gradients within a watershed (Fausch et al. 2002, Torgersen et al. 2006), is needed to improve understanding of habitat-based spatial segregation of spawning between coastal cutthroat and steelhead.

We used molecular genetics to assess the extent of spatial segregation in spawning habitat between coastal cutthroat and steelhead in relation to physical habitat gradients. Our specific objectives were: 1) to characterize the spatial distribution of juvenile coastal cutthroat trout, steelhead, and hybrids along a stream continuum within a small watershed; 2) to correlate observed longitudinal distribution patterns with potential explanatory habitat variables; 3) to determine whether differences exist between distribution patterns observed for young of year versus older age classes of juvenile trout; 4) to determine whether hybridization is bi-directional or asymmetric between both sexes of coastal cutthroat and steelhead, and whether potential directionality has a spatial component (are hybrids spatially assorted by maternal genotype?).

Methods

Study Site

The Ellsworth Creek basin is a 20 km^2 watershed in Pacific County, Washington (Figure 1.1), tributary to tidal portions of the Naselle River and Willapa Bay. It is situated in coastal hills underlain by primarily tertiary marine sedimentary sand and siltstones, with crescent formation basalts in upper areas of the watershed (Walsh et al. 1987). Elevations range from sea level to 500 m and the basin is characterized by a stream network featuring narrow incised valleys, steep slopes, and locally high topographic relief as a result of its fluvial land-forming processes. The watershed is entirely forested, and is currently owned and managed as a preserve by The Nature Conservancy (TNC). Despite the effects of past silviculture, Ellsworth Creek contains robust populations of chum salmon (*Oncorhynchus keta*), coho salmon (*O. kisutch*) and multiple life history forms of coastal cutthroat trout, and steelhead, as well native sculpins (*Cottus* sp.) and lampreys (*Lampetra* sp.).

Fish and Habitat Data Collection

We used single-pass electrofishing in an upstream direction to collect trout in June 2008. Sampling occurred in discrete 100 m reaches separated by equal or greater distances of non-sampled channel. We sampled 20 reaches in mainstem Ellsworth Creek from the end of tidal influence upstream for approximately 4.5 km and 15 reaches in three tributaries from their confluences with the mainstem upstream 0.5-1.5 km. In each reach, we attempted to capture at least two age 0+ trout fry and two older trout. A key assumption of our study was that the distribution of age 0+ trout would closely approximate the distribution of their parental spawning sites because at the time of the study (late June), trout fry would have recently emerged from the interstices and had limited time and physical capability to disperse far from natal sites (e.g. atlantic salmon, Einum et al. 2008, Teichert et al. 2011). Accordingly, sampling in each reach ended once the numeric goals were obtained to avoid potential excessive sampling of siblings, which could bias the relationship between genotypes and habitat. We anesthetized each fish with tricaine methane-sulfonate (MS-222) in buckets containing stream water in order to obtain a caudal fin clip, scales, and fork-length measurements. Fin tissues were air-dried onto waterproof paper in the field and then stored at -40°C until DNA extraction. We also collected habitat data for each study reach, including latitude and longitude using hand-held GPS units, channel gradient (% slope) using clinometers, and bank-full channel width, which was measured as a perpendicular channel cross section extending between the stream banks from point at which scour stopped and perennial non-aquatic riparian vegetation began.

DNA Extraction and Analysis

Our molecular methods generally followed Ostberg and Rodriguez (2004) with some modifications. We obtained 2 mm diameter hole-punches of each fin tissue from dried samples and placed them in individual tubes containing T1 lysis buffer and Proteinase K. DNA extractions were performed with a DNeasy Blood and Tissue 96-Well plate kit (Qiagen). We used four PCR primer pairs known to amplify species-specific co-dominant nuclear DNA markers (Ostberg and Rodriguez 2002, Ostberg and Rodriguez 2004) (Table 1.1). The PCR amplifications used 20-µl reaction volumes with 10-50 ng of genomic DNA, 10 mM Tris-HCl (pH 9.0), 50 mM KCl, 2.0 mM MG_2CL, 0.2% Triton X-100, dNTPs at 200 µM each, 1.0 U of Taq Biolase DNA Polymerase (Bioline), and 0.125 µM primers. The PCRs were amplified for 35 temperature cycles as follows: initial 94°C dwell for 2 min. (4 min. for OCC 16), followed by 94°C denaturing for 30 sec., followed by the primer-specific annealing temperature for 1.5 min (Table 1), followed by 72°C extension for 1.5 min., followed by 72°C dwell for 3 min. PCR products were visualized on 2% agarose gels stained with ethidium bromide. Band sizes were estimated using a HyperLadderIV 100-bp ladder size standard (Bioline).

In addition to the four nuclear DNA markers used for species identification, we used a mitochondrial DNA marker to identify the species for all hybrids. We amplified the ND2 region of the mitochondrial genome and then used the restriction enzyme *Csp*6I to digest it, yielding products which easily distinguish between coastal cutthroat and steelhead (Ostberg and Rodriguez 2006, Young et al. 2001).

Species Assignments

Species and hybrid assignments followed Ostberg et al. (2004). Individuals displaying homozygous steelhead products at all four loci (8 markers), were called steelhead and individuals displaying homozygous cutthroat trout products for all four loci (8 markers), were called cutthroat trout. Individuals with heterozygous products for all loci (4 cutthroat and 4 steelhead markers), were called F1 hybrids, and all other individuals with mixed marker compositions were called, collectively, Post-F1 hybrids, indicating a mixture of backcross and later generation (e.g. F2, F3) hybrid genotypes. The use of four markers allowed us to confidently classify pure parent species and F1 hybrids, but classifying hybrids and backcrosses beyond the F1 generation would have required many more markers (Boecklen and Howard 1997).

Age Assignments

Following species assignments, length frequency histograms were constructed to characterize ages of fish from the distribution of lengths for each species (Figure 1.2). The length frequency distribution including all individuals revealed a tri-modal distribution with sufficiently large (~20 mm) gaps between modes (Figure 1.2a) to allow the assignment of ages to individuals based on their length. Individuals between 27 and 59 mm fork length were designated age 0+, individuals between 82 and 155 mm were designated age 1+, and individuals between 180 and 196 mm were designated age 2+.

Statistical Analysis

To relate habitat characteristics to species distribution data, we used generalized linear models to test for relationships between the proportion of fish of a given genotype (steelhead, cutthroat trout, hybrid) in each reach and the habitat characteristics in that reach. Because trout can move substantial distances from where they emerge during their first year of life (Hoffman and Dunham 2007), analyses were conducted separately for each species-age combination. We combined ages 1+ and 2+ because of the small number of age 2 individuals and because there was no reason to separate them since both age classes would have had opportunities to move substantially from their emergence site. The proportion of fish of each genotype at each site (rather than each fish) was treated as the independent unit of observation. The model was then weighted by the number of fish of that age class collected at the site. A logit-link function was used, which tests for linear correlation between predictor variables and the response on a logit scale with a binomial error distribution. The predictor variables tested included stream gradient; bank-full width (bfw) of the channel; and drainage area contributing to each sample reach, which was estimated using ArcInfo 9.3

(ESRI, Inc., 380 New York St., Redlands CA 92373-8100). Separate models were constructed for each species-age class combination (e.g., age 0+ steelhead). Akaike's Information Criterion for small sample sizes (AICc) was calculated to compare and rank the various models. The lowest AICc value denoted the best model and models with ΔAICc < 2 were considered very plausible as well (Burnham and Anderson 2002). All statistical analyses were performed in R (R Developement Core Team 2011) unless otherwise noted.

Results

Fish Samples and Habitat Characteristics

Stream reaches sampled spanned a wide range of habitat conditions, from low gradient unconfined alluvial depositional channels just above the Ellsworth Creek estuary, to high gradient confined hillslope-process dominated transport channels in the headwaters. The watershed basin area contributing to stream reaches sampled spanned two orders of magnitude (16.67-1660.38 ha), the range of bankfull widths spanned just under one order of magnitude (1.83-13.72 m), and gradients ranged from 1.5 to 7% slope (Table 1.2). We collected tissue from 130 trout, which ranged in size from 27 to 196 mm fork length, with modes around 40 mm, 120 mm, and 190 mm (Figure 1.2a). Between 0-5 age 0+ (mean = 1.77), and 0-10 age 1 and 2+ trout (mean = 1.86) were sampled in each reach (Table 1.3).

Genetic Results

Of the 130 samples collected, DNA was successfully extracted from 127 and PCR amplification of all four nuclear loci was successful for 121. For the remaining 6 fish the three successfully amplified markers were used to assign species according to Ostberg et al.

(2004). A bimodal distribution was apparent in the number of individuals with each number of cutthroat and steelhead markers (Figure 1.3). The bimodality of the distribution and the presence of individuals with every possible marker count suggested that trout in Ellsworth Creek basin were not part of one hybrid swarm, but rather comprised populations of steelhead (42%), cutthroat (35%), and hybrid trout (23%) including various post-F1 hybrid and backcross classes.

Among 1+ age individuals, steelhead, cutthroat trout, and hybrids were present, although no F1 hybrids were present among 0+ age individuals and all age 2+ individuals were cutthroat trout (Table 1.3). The largest proportion of age 0+ fish were steelhead (63.1%), while the largest proportion of age 1+ trout were cutthroat trout (53.4%). Hybrids were a smaller proportion of both age 0+ fish (12.3%) and 1+ age fish (36.2%), with F1 hybrids comprising 7% of the 1+ age trout (Table 1.3). Statistical analyses to compare proportions of genotypes between age classes were not calculated due to the spatially disparate structure of sample collections and the differing life histories of parental species, both of which could confound interpretation of such analyses.

Amplification of a mitochondrial DNA marker, which we had intended for all fish classified by nuclear markers to be hybrids (n = 29), was markedly less successful. Mitochondrial DNA was successfully genotyped for a total of six individuals (Table 1.4), including a single age 0+ post-F1 hybrid, and multiple age 1+ F1 and post-F1 hybrids. All individuals contained steelhead mtDNA, suggesting asymmetric hybridization between cutthroat and steelhead, although the scope of inference is limited by the small sample size.

Distribution of Steelhead, Cutthroat Trout, and Hybrids

The distribution of cutthroat trout, steelhead and hybrids in Ellsworth Creek showed apparent spatial partitioning between species for both age 0+ (Figure 1.4) and age 1 and 2+ fish (Figures 1.5). Age 0+ steelhead were found in lower areas of the watershed typified by larger contributing basin areas, lower gradients and greater bankfull widths (Table 1.5), and were only found in the mainstem of Ellsworth Creek and in a few cases the lowermost reaches of tributaries. In contrast age 0+ coastal cutthroat were only found in the smaller tributaries and the upper reaches of large tributaries with generally smaller contributing basin areas, higher gradients and smaller channel bankfull widths (Table 1.5). Only 8 age 0+ trout were identified as hybrids (all post-F1 hybrids), limiting inferences about their distribution. All were found in four study reaches; three at the upper limit of steelhead distribution and the lower end of cutthroat trout distribution, and one in a tributary within the cutthroat distribution (Figure 1.4). Habitat characteristics where age 0+ hybrids occurred were intermediate to but overlapping with those of parent species (Table 1.5). As expected given the likelihood of their movement over time, spatial partitioning among age 1+ and 2+ cutthroat trout, steelhead, and hybrids was not as apparent. While the general pattern for age 1+ and 2+ was similar to that seen in age 0+ trout for steelhead, with most being found in the mainstem of Ellsworth Creek, the pattern was markedly different for cutthroat trout, which were more widely distributed the watershed (Table 1.5; Figure 1.5).

There were strong correlations between predictor variables (basin area and bankfull width, 0.49; basin area and channel gradient, -0.65; channel gradient and bankfull width, -0.83) so models were constructed using each variable independently, as well as multiple variable models, which included the best variable from the single variable models.

Contributing basin area was the best single variable model explaining the distribution of age 0+ steelhead and cutthroat trout distribution, and was the best overall model when considering all variables for age 0+ cutthroat trout (Table 1.6; Figure 1.6). Models including basin area explained between 64.8-82.5% of the variability in age 0+ steelhead distribution and 65.7-70.4% of the variability in age 0+ cutthroat trout distribution (Table 1.6). Although bankfull width and gradient explained a considerable amount of the variability in single variable models, they were highly correlated with basin area and thus added little predictive power to models already containing basin area (Table 1.6).

Age 0+ steelhead and cutthroat trout occurrence were correlated with habitat variables in opposing directions (Table 1.7). Age 0+ steelhead occurrence was positively correlated with basin area, while age 0+ cutthroat occurrence was negatively correlated with basin area in all models (Table 1.7; Figure 1.6). Age 0+ steelhead occurrence was negatively correlated with gradient, while age 0+ cutthroat occurrence was positively correlated with gradient in all models (Table 1.7). Age 0+ cutthroat occurrence was consistently negatively correlated with bankfull width, whereas the relationship between age 0+ steelhead occurrence and bankfull width was inconsistent (Table 1.7).

Models developed to correlate the distribution of age 1+ and 2+ trout with habitat characteristics generally revealed basin area to be an important variable, with considerably less support for models not containing basin area (Table 1.8; Figure 1.6) but the best models only explained 28.5% of the variability in steelhead and 36.1% in cutthroat trout occurrence (Table 1.8), about half of the variability explained in age 0+ models. The best fit model for age 1+ and 2+ cutthroat trout also included bankfull width, although this variable in the absence of basin area was not a good predictor of age 1+ cutthroat distribution.

Discussion

Species and age composition

Genetic analysis of juvenile trout revealed that pure coastal cutthroat trout, steelhead, and hybrids were present in Ellsworth Creek, and that hybridization had progressed beyond the first (F1) generation. The presence of multiple age classes for all of these genetic groups with the exception of F1 hybrids, and the presence of post F1 hybrids suggest that hybrid survival and fitness is greater than zero. The lack of age 0+ F1 hybrids in this study and the greater relative abundance of post F1 hybrids among age 1+ fish suggests that initial hybridization events between pure cutthroat and steelhead may not occur every year, consistent with previous studies (Baumsteiger et al. 2005, Ostberg et al. 2004). Some studies in which hybrids were only found within the 0+ age class have suggested that the first winter may be a critical period of low survival for hybrids, allowing for seemingly limited gene flow between coastal cutthroat and steelhead populations and the maintenance of the two as distinct species (Campton and Utter 1985, Hawkins 1997). However, the presence of 1+ hybrids in this study and others (e.g. Ostberg et al. 2004) suggests that other mechanisms, such as lower survival of hybrids than the parental species later in life, may allow the species to remain functionally distinct despite occasional but ongoing production of hybrid offspring. The similarity of freshwater life histories of cutthroat and steelhead has led to speculation that the fitness of hybrids is more likely to differ from the parental species later, during migratory (anadromous) life stages where their life histories differ (Baker et al. 2002, Baker 2001, Campton and Utter 1985, Young et al. 2001). Indeed, Moore et al. (2010) observed that marine migration patterns were very divergent between coastal cutthroat, which remained in the vicinity of their natal stream, and steelhead, which quickly migrated toward open ocean waters, with hybrids displaying an intermediate pattern with unknown consequences on their growth potential or predation risk.

Distribution of Cutthroat Trout, Steelhead and Hybrids

The collection of longitudinally continuous fish distribution, age, and habitat data allows for improved characterization of species distributions and their habitat associations along continuous riverine habitat gradients or "riverscapes" (Fausch et al. 2002, Torgersen et al. 2006). Applied to hybridization, this study design allows for the distinction between clinal and patchy hybrid zones (e.g. Barton and Hewitt 1985), and for a description of habitat characteristics which may have given rise to, or regulate hybridization between two species.

Our objective was to characterize the spatial distribution of coastal cutthroat trout, steelhead, and hybrids and determine whether segregation of spawning areas was apparent and if it was associated with habitat characteristics at a sub-watershed scale. Our finding of strong spatial segregation between spawning areas of the species, with the occurrence of coastal cutthroat and steelhead exhibiting relationships of opposing directions (steelhead positive, cutthroat negative) with contributing basin area to a stream reach, suggests that spatial segregation has the potential to limit gene flow between coastal cutthroat and steelhead. Similar segregation is known to occur between other pairs of closely related salmonids including bull trout (*Salvelinus confluentus*) and introduced brook trout (*S. fontinalis*) (DeHaan et al. 2009), and bull trout and Dolly Varden (*S. malma*) (Hagen and Taylor 2001), and likely results from slight differences in habitat preferences between species. Such segregation may be adaptive for coastal cutthroat and steelhead given the low fitness of interspecific hybrids between the other subspecies of cutthroat and introduced rainbow trout (Muhlfeld et al. 2009a). It is likely that the long period of co-evolution experienced by coastal cutthroat and steelhead has allowed them to develop more complete spatial segregation of reproduction relative to anthropogenically-induced co-occurring cutthroat and rainbow trout subspecies, where substantial spatial reproductive overlap, introgressive hybridization, and displacement of native cutthroat has occured (Muhlfeld et al. 2009b, Weigel et al. 2003). Some evidence for this hypothesis is seen in cases where other cutthroat and rainbow trout subspecies naturally occur. In the Clearwater River, Idaho, steelhead and westslope cutthroat (*O. c. lewisii*) naturally co-occur and strong spatial segregation of cutthroat and rainbow trout has been observed (Kozfkay et al. 2007).

In contrast to the spatial distributions of age 0+ trout, which were strongly segregated, we observed more spatial overlap in older trout indicative of movement from natal areas. The models correlating occurrence with habitat characteristics explained approximately half of the variability that the same models did for age 0+ fish and age 1+ and 2+ cutthroat trout and hybrids were widely distributed throughout the watershed. Although it is possible that the difference in distribution between the two age classes in this study represents inter-annual differences in parental spawning distributions, it is more likely the result of downstream movement by older fish, which is a common ontogenetic habitat shift observed in diadromous and migratory fish species (Jonsson and Jonsson 1993). Additionally, supporting this view, we did not find age 1+ or 2+ age fish in any of the three reaches with the least contributing basin area, suggesting that although these areas may be used for spawning by cutthroat, they are not suitable rearing habitat for older fish; likely a function of their lack of depth, cover, and flow.

The lack of spatial segregation seen in older trout relative to recently emerged age 0+ fish observed in this study may be responsible for an absence of strong spatial segregation observed in other studies. Many previous studies have either relied upon field identification (e.g. Hartman and Gill 1968, Trotter 1989), which necessitates using older fish and is still wrought with error related to misidentification of cutthroat, steelhead and hybrids (Baumsteiger et al. 2005). In addition, by sampling trout throughout an entire watershed and by matching the spatial scale of our explanatory habitat variables with our fish sampling (reach-specific), we observed greater segregation than studies which sampled fish in few locations. Ostberg et al. (2004) also found a general pattern of numerical dominance by steelhead in lower reaches of streams and coastal cutthroat trout dominance in upper reaches, with hybrids more common in the middle reaches. However, spatially discontinuous sampling precluded characterizing the distribution of each species along continuous longitudinal physical habitat gradients, and the timing of juvenile sampling limited their ability to identify species-specific spawning areas due to dispersal from natal spawning sites. Heath et al. (2010) correlated watershed-scale environmental characteristics with the proportions of hybrids and coastal cutthroat and steelhead in a number of coastal streams in British Columbia, finding positive associations between measures of habitat destruction and hatchery stocking with the proportion of hybrids. Higher proportions of hybrids were also found in smaller watersheds in their study. They did not, however, link specific habitat characteristics with the occurrence of hybridization, and their study design precluded determining whether the occurrence of parent species and hybrids varied at a sub-watershed scale, which other studies (e.g. Ostberg et al. 2004) have established to occur. It is not unreasonable to expect that without the use of molecular methods to positively identify the species of juveniles, the incorporation of age in our analysis, and likely, the timing of sampling to coincide with fry emergence our results might have failed to indentify such strong spatial segregation.

In addition to identifying spatial segregation of spawning areas between parent species, a goal of this study was to determine the directionality of hybridization and whether it varied in relation to habitat characteristics. Our scope of inference is limited due to small sample size, but all hybrids contained maternal steelhead mtDNA, suggesting unidirectional hybridization with only cutthroat male x steelhead female crosses occurring. Previous studies have found bidirectional hybridization between coastal cutthroat and steelhead (Bettles et al. 2005), as well as unidirectional hybridization in both directions in certain cases; female cutthroat x male rainbow only (Williams et al. 2007) and male cutthroat x female steelhead only (Ostberg et al. 2004). Notably, in both cases where unidirectional hybridization was observed, the life history of the male species' population was predominately resident, while the female species' population was migratory. This has led to the suggestion that interspecific 'sneak spawning' by resident males of either species may be a source of hybridization events between coastal cutthroat and steelhead (McMillan et al. 2007, Ostberg et al. 2004). The absence of any steelhead older than age 1+ in our study may offer an additional reason for our observation of unidirectional hybridization because there the vast majority, if not all steelhead may leave the watershed prior to maturing as residents.

In the context of previous studies, the strong spatial segregation we observed suggests the potential for sex-based roles in the occurrence of hybridization. Several studies have found cytonuclear associations (eg. nonrandom associations of mtDNA and nuclear DNA; see Arnold 1993) in cutthroat trout and steelhead populations containing hybrids (Bettles et al. 2005, Ostberg and Rodriguez 2006, Young et al. 2001). In these studies there was a strong positive association between the maternal species of an individual and the proportion of nuclear DNA assigned that species. In fact Young et al. (2001) found that the mtDNA of backcrossed individuals was always same as the parental species with which the backcross occurred. Taken together with the strong spatial segregation of parental species observed in this study, the prevalence of cytonuclear association in hybridizing populations of coastal cutthroat and steelhead leads us to speculate that the spatial structure of parent species' spawning areas and the directionality of hybridization may be facilitated by female choice (of conspecific mates or allospecific spawning sites), and/or sex-biased dispersal of individuals from areas of allopatry (increased movement of reproductive males into spawning areas of other species) (e.g. Wirtz 1999). We identify the need for future work to increase understanding of sex-based roles in occurrence of hybridization.

Conclusions

Our results suggest that spatial segregation of spawning sites between coastal cutthroat and steelhead may be more complete than previously recognized. Partial spatial reproductive isolation may thus serve to limit introgression between sympatric populations of these species in their native range. Our results highlight the efficacy of combining molecular techniques with spatially continuous field study designs that are scaled to the spatial extent of expected variability in response variables.

Chapter 2:
Effects of abiotic and biotic factors including coho salmon density on growth, movement and survival of coastal cutthroat trout

Abstract

Growth, movement and survival of stream rearing salmonids are influenced by a combination of abiotic and biotic factors. Common influential biotic factors may include attributes of individual fish such as size and condition, and community ecology including inter- and intra-specific competition, and common abiotic factors include stream discharge, temperature, and habitat quality. Construction of fish passage facilities at Landsburg Dam, WA in 2003 provided access to upstream habitats in the Cedar River and Rock Creek, enabling colonization by formerly extirpated native coho *(Oncorhynchus kisutch)* and Chinook (*O. tshawytscha*) salmon populations. Rapid spatial and numerical expansion of stream rearing coho salmon populations in areas occupied by populations of coastal cutthroat trout (*O. clarkii clarkii*) provided an opportunity to examine the relative importance of abiotic and biotic factors including interspecific density effects on cutthroat growth, movement and survival. We PIT tagged 1851 cutthroat trout in Rock Creek from 2005 to 2009 in 14 seasonal events, and simultaneously collected habitat data and enumerated fish populations. We recaptured 394 individuals during subsequent tagging events and detected 34 % of the tagged cutthroat trout leaving the creek using a PIT antenna array. We used GLMs to describe variability in growth and Cormack-Jolly-Seber (CJS) models to analyze variability in survival of cutthroat trout. The most rapid growth occurred during spring and early summer, and most movement and emigration from Rock Creek occurred in late fall and winter, corresponding to periods of higher discharge. Summer growth of cutthroat trout parr was positively correlated with stream discharge and negatively correlated with density of conspecifics and initial size, while summer growth of trout fry was negatively correlated with initial size and declined across years. There no evidence of spatial structure and weak evidence for temporal structure in survival, and no abiotic or biotic covariates increased model strength. We observed no effects of coho salmon densities on cutthroat trout growth or survival despite almost an order of magnitude increase in salmon density over the course of the study. Our results suggest that abiotic conditions including seasonality and discharge, and intra- rather than inter-specific density influenced cutthroat trout populations.

Introduction

Populations of stream dwelling salmonids can be affected by inter- and intra-specific density-dependent processes that regulate abundance through competition for limited resources, and by density-independent processes that determine abundance by affecting survival (Hearn 1987, Milner et al. 2003). Density-independent environmental factors such as stream size (Berger and Gresswell 2009, Ebersole et al. 2009), discharge (Berger and Gresswell 2009, Harvey et al. 2006, Harvey et al. 2005, Teichert et al. 2010), habitat quality (Boss and Richardson 2002), and temporal variation (Berger and Gresswell 2009, Carlson et al. 2008) all affect the growth, movement and survival of stream salmonids. Density-dependent effects on growth, movement, and survival due to intra-specific (Gowan and Fausch 2002, Harvey et al. 2005, Imre et al. 2005, Imre et al. 2004, Keeley 2001, Rosenfeld et al. 2005), and interspecific (Glova 1986, Harvey and Nakamoto 1996, Sabo and Pauley 1997) interactions are frequently observed as well. Furthermore, habitat type (e.g. pools vs. riffles), food availability, and size of individuals can interact with fish density to influence growth and survival (Rosenfeld and Boss 2001, Rosenfeld et al. 2005).

Intra-specific competition is more frequently documented in salmonid populations than interspecific competition, suggesting differences in ecology and life history attributes between salmonid species can influence the strength of competitive interactions (Milner et al. 2003). In low elevation coastal areas of the Pacific Northwest, salmonid species that rear in streams include coastal cutthroat (*Oncorhynchus clarkii clarkii*) and rainbow trout (*O. mykiss*), as well as coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon (Quinn 2005). Chinook and coho salmon are fall-spawning species that produce large numbers of offspring which emerge earlier and at a larger size than those of spring–spawning cutthroat and rainbow trout (Quinn 2005). Competition between juvenile Chinook salmon and trout may be minimized, however, due to the predominance of ocean-type Chinook, which spend only a few weeks to a few months rearing in rivers before migrating to marine areas (Myers et al. 1998).

The potential for competition between coho salmon and trout species is much greater. Coho salmon typically spend 18 months in streams prior to seaward migration (Quinn 2005), using stream habitats occupied by juvenile cutthroat trout (Bisson et al. 1988). Given their numerical and size advantages, coho salmon may competitively displace, or contribute to reduced growth and survival of juvenile cutthroat (Glova 1984, 1986, Sabo and Pauley 1997, Trotter 1989, Young 2004). At the habitat unit scale, competition with coho salmon forces trout to use higher velocity habitats (e.g. riffles) where they are competitively superior to salmon (Glova 1986) but experience reduced growth rates relative to low velocity habitats (e.g. pools) (Rosenfeld and Boss 2001). Moreover, trout appear to prefer pools in the absence of salmon (Glova 1986). At the reach scale (Frissell et al. 1986), coho may be the dominant salmonid species in terms of abundance and biomass in low gradient areas and lower in watersheds (Glova 1984, Rosenfeld et al. 2000).

Most studies on competitive interactions between coho salmon and trout have involved populations in areas of co-occurrence but competitive dynamics may differ where species have experienced a period of isolation. For example, in cases where resident trout are naturally or anthropogenically-separated from anadromous salmon by dams or other migration barriers, resource use by cutthroat may expand from the realized toward the fundamental niche (Hutchinson 1957), which has been observed in experimental manipulations with these two species when coho were removed (Glova 1986) . The removal of migration barriers is used to restore anadromous salmon populations, but it has the additional consequence of altering competitive dynamics in stream salmonid communities (Kiffney et al. 2008, Pess et al. In press). Understanding the impacts of salmon recolonization and the effects of associated increases in salmonid densities on extant resident species in stream rearing areas is important for resource managers weighing the benefits of restoring extirpated native species against the potential for impacts on extant native resident species (Brenkman et al. 2008, McMichael and Pearsons 1998, Pearsons and Temple 2007).

For over 100 years the Landsburg Diversion Dam blocked access to upstream habitats for migrating fish on the Cedar River, WA. Native Chinook and coho salmon were extirpated from over 20 km of mainstem and 13 km of tributary habitat in Rock Creek. Moreover, rainbow and coastal cutthroat trout populations, which had previously existed in a variety of potamodromous and anadromous forms, were restricted to obligatory residency above the dam. The Cedar River Habitat Conservation Plan called for the completion of fish passage facilities by 2003 at Landsburg Dam (HCP 2000) and studies were initiated to document salmon re-colonization and the ecosystem effects of fish migration-barrier removal (Anderson et al. 2008, Anderson and Quinn 2007, Kiffney et al. 2008, Pess et al. In press). Recolonization of the upper Cedar River by salmon began in the first year following construction of the fish ladder when coho and Chinook salmon colonists spawned above the dam (Anderson and Quinn 2007). Populations and spatial distributions of adults and juveniles of both species continued to increase each year following barrier removal, increasing the opportunity for interactions with resident species (Kiffney et al. 2008). Although restoring habitat connectivity appears to have benefited coho and Chinook salmon populations, the effects on resident species are unknown. Similarities in habitat use and behavior between cutthroat trout and coho salmon suggest that salmon colonization in the Cedar River and its sole accessible tributary, Rock Creek, could have significant impacts on trout populations. If there is a large amount of overlap in habitat and resource use between salmon and trout (Bisson et al. 1988, Glova 1984, 1986, Rosenfeld et al. 2000), the addition of large numbers of juvenile salmon to the upper Cedar River and tributaries could lead to increased interspecific competition. However, if there is little resource overlap, salmon recolonization would have little effect on competition.

The process of salmon colonization in the upper Cedar River and Rock Creek offered a unique opportunity to measure the influence of competition on the dynamics of resident fish populations. The objective of this study was to determine the relative importance of abiotic and biotic factors affecting growth, movement, and survival of cutthroat trout populations during a period of rapidly increasing coho salmon abundance. We used mark-recapture techniques in conjunction with collection of habitat and environmental data to evaluate the factors affecting growth, movement and survival of coastal cutthroat in Rock Creek over a four year period from 2005 to 2009.

Methods

Study Site

The Cedar River is a 487 km^2 watershed originating at the crest of the Cascade Mountains in Washington State and draining westward into Lake Washington. The upper Cedar River flows west from its headwaters in the Cascade Mountains over a series of impassible waterfalls before continuing through 53 km of historic anadromous fish habitat to Lake Washington, which drains directly to marine waters in Puget Sound. The upper 20 km of the anadromous reach was inaccessible to migrating fish species from 1901 until 2003 when a fish ladder was constructed to allow fish passage above Landsburg Diversion Dam, a low head dam used for municipal water diversion.

Rock Creek is a 15 km^2 tributary with approximately ~13 km of habitat accessible to anadromous fish that enters the Cedar River 2 km above Landsburg Dam. Rock Creek has a rain-dominated hydrograph with peak flows in winter months and low flows in summer. Rock Creek is fed primarily by rainfall runoff and groundwater from its headwaters in low-lying foothills, which flows through a section of forested wetlands before entering a more confined section in its lower 3 km to its confluence with the Cedar River. Although past timber harvest has resulted in reductions in large woody debris in streams in some areas, habitat conditions are largely intact within the upper Cedar River watershed, owing to protection from development as a result of its function as the source of drinking water for the city of Seattle.

Fish Collection and Habitat Surveys

Fish and habitat sampling occurred in 14 tag and recapture events during three seasons (end of winter, mid-summer, and fall) each year from 2005 through 2009 (Table 2.1). Sampling considered reach and habitat unit scales to account for ecological processes which might vary between scales (Frissell et al. 1986). Tag and recapture events occurred in 26-52 discrete pools and pool-like habitat units within three 200-500 m reaches numbered 1-3 in ascending order moving upstream from the mouth of Rock Creek to rkm 2.5 (Figure 2.1). Only pools and pool-like habitat units were sampled for this study because pools act as congregation points for several fish species during summer low flow periods (Glova 1986). Fish were collected using three-pass electrofishing depletion (Carle and Strub 1978); captured individuals were held in buckets, anesthetized with MS-222 (80 mg/L), measured (fork length to the nearest mm) and weighed to the nearest 0.1 g. Individuals greater than 60 mm and 2 g, which were large enough to manage the impacts of tagging on survival and growth (Peterson et al. 1994), were identified to species and implanted with a 12 mm Passive Integrated Transponder (PIT) tag into their body cavity using a syringe sterilized in 70% ethanol. After processing, all fish were released in the habitat unit in which they were captured.

PIT Tags contain a unique code that can be read on subsequent capture occasions, including electrofishing and remote antenna arrays. These features of mark-recapture allowed us to quantify growth, movement and survival of tagged individuals (Prentice et al. 1990). In addition to capturing and tagging fish, three rows of stream-spanning stationary PIT tag antenna arrays at the mouth of Rock Creek were continuously operated starting in September 2005 allowing the detection of fish immigrating to and emigrating from Rock Creek. These antennae also allowed us to quantify detection efficiency and determine the direction of movement for most fish (Connolly et al. 2008).

Tagging efforts occurred in distinct seasonal events in which all reaches and habitat units were sampled over a period of three to seven days. Tagging events occurred once in late winter-early spring, mid-summer, and early fall from 2005-2009. A variable number of habitat units were sampled during each event due to the omission of reaches during some tagging events, and the elimination and creation of habitat units resulting from changes in channel morphology during high flow events. With the exception of reaches that were not sampled during an event, an effort was made to sample a consistent number of habitat units within each reach.

Prior to or following each tagging event, physical habitat surveys were completed on all habitat units to quantify maximum and tail-out (depth at cross-section acting as control of water elevation for pools) depths and surface areas, water velocity, and to characterize substrate composition and available cover types. Water temperature data were collected by a series of continuously deployed data loggers. Stream discharge data were not available for Rock Creek, so we used discharge data from the Raging River (USGS 12145500) near Fall City, WA, which is representative of the temporal pattern of discharge in Rock Creek and has similar hydrological characteristics but approximately three times the drainage area. Because we wished to distinguish potential effects of stream flow, which varies predictably at a seasonal timescale, from seasonal effects, we used a measure of flow anomalies which related the flow on given date to the long-term mean daily flow for that date (mean percent of mean daily flow). These anomalies were then averaged across each between-sampling interval for use as a covariate in growth and survival analysis.

Growth, Movement and Survival Analysis

Growth of individual fish over seasonal intervals was calculated by comparing initial weights with recapture weights and was measured as specific growth rate [ln (final weight - initial weight) / number of days between capture events]. A series of candidate generalized linear models (GLMs) including various combinations of environmental and biological covariates, as well as directional temporal effects (fixed year effect) were constructed to explain observed variability in summer to fall growth rates for all years of the study. Insufficient statistical power due to small sample sizes precluded adequate model construction for other seasonal growth intervals and for analysis of patterns in annual growth. Initial weight was included in growth models to account for allometric scaling of growth with size; however, it is possible that some of the variability in growth ascribed to length was the result of other factors such as decreasing suitability habitat in Rock Creek with increasing body size, which could be a result of ontogenetic changes in habitat needs (Jonsson and Jonsson 1993). We used forward stepwise selection to construct models of the relationship between growth and each covariate of interest, and only models that were at least marginally significant ($p < 0.1$) were carried on for inclusion in multiple variable models (Kutner et al. 2004). Akaike's Information Criterion for small sample sizes (AICc) was calculated to compare and rank the various models containing multiple covariates. The lowest AICc value denoted the best model and models with ΔAICc < 2 were considered very plausible as well (Burnham and Anderson 2002). All statistical analyses were performed in R (R Developement Core Team 2011) unless otherwise noted.

Two methods were used to assess trout movements including comparing the locations of recaptured fish with their original tagging locations as well as using remote detections of individuals at PIT antenna arrays located at the mouth of Rock Creek. In addition to describing the frequency and temporal structure of trout movements, movement indices were also included in growth models as continuous (movement distance) and categorical (moved v. did not move) covariates. Linear regression was used to relate fish length at tagging with log-normalized time before first emigration from Rock Creek.

Cutthroat trout survival and covariates affecting it were modeled using Cormack-Jolly-Seber (CJS) open population models (Cormack 1964, Jolly 1965, Lebreton et al. 1992, Seber 1965) using program RMARK (Laake and Rexstad 2008), an R package which prepares data input files for program MARK (White and Burnham 1999) and extracts the results for interpretation within the R interface. Survival modeling followed the stepwise process recommended by Lebreton et al. (1992), where 1) the fully time-dependent model was assessed for goodness of fit (described later), 2) the best model of capture probabilities was established while holding survival constant, and 3) the best model of survival was established while using the best model of capture probabilities. Akaike's Information Criterion for small sample sizes (AICc) was calculated to compare and rank the various models that included temporal or spatial structure. The lowest AICc value denoted the best model, and this model was used for abiotic and biotic covariate analyses. Models with ΔAICc < 2 were considered very plausible as well (Burnham and Anderson 2002).

CJS models incorporate a binary capture history for each fish (observed/not observed) and the length of this history corresponds to the number of capture occasions in a study. The model structure simultaneously estimates the probability of apparent survival (the proportion of animals remaining alive and within the study area) between occasions and the probability that surviving individuals are encountered on each occasion. Apparent survival is appropriate for open populations where individuals can leave the study area and it is not possible to differentiate between fish that died and fish that emigrated. The CJS model assumes 1) all marked animals present at time *i* have an identical probability of being captured, p_i, during that period and of surviving, Φ_i, between time *i* and the following sampling event $i+1$; 2) that tags (marks) are not lost or undetected in captured individuals; 3) sampling occasions are instantaneous; 4) emigration of tagged individuals is permanent; 5) the probability of capture and survival is independent among individuals (Williams et al. 2002). Our study reasonably satisfied assumptions 3-5: The length of time of sampling events relative to the time between events was very small (3), we excluded known emigrants from our analyses (4; see below), and there was no *a priori* reason to suspect a lack of independence between sampling of individuals (5). Tag retention and detection rates (2) have been high in comparable studies of cutthroat trout (Berger and Gresswell 2009), although some tags were undoubtedly lost or not detected and we have not corrected for this minor negative bias. Identical capture probability for all animals in each period (1) was the most difficult assumption to satisfy since fish may move within the study area and certain locations may be more or less conducive to their capture. Efforts were made to meet assumption 1 through accounting for sampling intensity by constructing separate models for data subsets that included the same sampling frequency and intensity.

Because CJS models estimate apparent survival of animals alive and remaining in the study reach, estimates of apparent survival will increasingly diverge from "true" survival with increasing emigration. To improve the precision of our estimates of apparent survival (referred to hereafter simply as survival) and capture probabilities, we applied the methods of Horton and Letcher (2008) in which the capture history of individuals known to have emigrated (i.e., detected at the mouth of Rock Creek) was modified to include a 1 for the most recent sampling event (because the animal was alive and subsequently emigrated) and the frequency associated with that capture history was changed to -1, which results in the individual's capture history being excluded from the model likelihood following its last capture. Although some fish undoubtedly emigrated without detection, consistently high antenna detection efficiency (~92 %) over time, likely minimized this problem (Pess et al. In press).

Additional modifications to survival modeling, in which separate models were constructed for reach-time period subsets of encounter histories, were necessitated by inconsistent surveying of study reaches. Reaches 2 and 3 were not sampled during all events, which would have violated CJS assumptions (#1 above—identical capture probabilities) had those data been included with reach 1 data from all periods, so two separate datasets were used to model cutthroat trout survival. One survival analysis included data only from reach 1 and spanned sampling events 2-14 corresponding to fall 2005 through fall 2009, for which downstream antenna detection data were available to censor capture histories of known emigrants. The second survival analysis included pooled data from reaches 1 and 3 for sampling events 7-14 corresponding to summer 2007 through fall 2009. For both analyses, time intervals were set to the number of decimal months between sampling events to account for varying amounts of elapsed time between events.

Program RELEASE within MARK was used to assess the goodness of fit of full models (separate estimate of survival (Φ) for each time period) for both datasets and to generate estimates of the variance inflation factor (c-hat), a measure of over-dispersion. Goodness of fit tests suggested no significant overall lack of fit for either dataset; however, for the reach 1 dataset, c-hat was equal to 1.33, and this value was thus used to adjust model selection criteria (QAICc), standard errors and confidence intervals, resulting in somewhat reduced statistical power. A value of c-hat = 1.0 was used for the reach 1 and 3 dataset since the estimate generated by release was < 1.

A series of covariate survival models using various combinations of environmental and biological variables were constructed to explain variability in survival. Due to the long duration of the study and the attendant difficulty of interpreting the effect of initial conditions on subsequent survival far in the future, as well as the unavailability of covariate data for each individual within all tagging periods, quantifying the effect of covariates was restricted to the survival interval immediately following tagging for all individuals. We used 95% confidence intervals around the coefficient (slope) to assess the importance of individual covariates. A CI not overlapping zero was thought to signify a biologically meaningful relationship.

Results

Fish Tagging and Habitat Characteristics

Between summer 2005 and fall 2009 we tagged 1851 cutthroat trout (mean length = 113 mm, range 60-280 mm) in Rock Creek and recaptured 394 unique individuals with a total of 483 recaptures including individuals recaptured multiple times (Table 2.2). Coho salmon and sculpins (*Cottus* sp.) comprised the majority of the remaining fish population in Rock Creek. Rainbow trout, *O. mykiss*, were < 10% of the trout population in the creek, and their capture histories, movements and growth rates were excluded from analyses of cutthroat growth and survival but were included in trout densities modeled as covariates. It is difficult to distinguish between the two trout species in small individuals but these fish were assumed to be cutthroat trout based on preponderance of that species in Rock Creek. Abiotic and biotic conditions in Rock Creek hypothesized to potentially affect cutthroat growth and survival did not show a directional change over time, with the exception of coho density, but are reported for reference (Table 2.3). Coho salmon density, which started at 0.04 fish/m^2, below that of trout (mean = 0.20 fish/m^2), increased significantly ($p< 0.001$) over time to 0.32 fish/m^2, surpassing trout density (Figure 2.2). Trout density did not show a significant linear trend across years ($p= 0.803$).

Fish Movements

We used both physical recaptures of tagged cutthroat trout and detections at stationary antennas to assess movement patterns. The two methods yielded contrasting results. Seventy percent of cutthroat trout that were physically recaptured at any point following tagging were recaptured in the original habitat unit where they were encountered. Of the fish that did move between captures, the mean distance was 110 m (54 m excluding five fish that moved between reaches). Although it is unknown whether individuals moved within Rock Creek between sampling events, less than 1% (15 fish) of all cutthroat and trout fry tagged were recaptured by electrofishing after having been detected emigrating from Rock Creek.

In contrast to the general lack of movement observed among direct recaptures through electrofishing, antenna detections suggested many of cutthroat trout moved between Rock Creek and the Cedar River, and the proportion moving was relatively stable over time. A substantial proportion of fish tagged in each reach (range 8-23%, reach 3; 42-53%, reach 1) were detected at the mouth of Rock Creek (Table 2.2). The minimum distance fish traveled from reaches 3 and 2 was 2223 and 1672 m, respectively, with fish traveling 0-430 m from habitats in reach 1. These distances were generally greater (0 to 20-fold greater) than the mean distance of 110 m observed for the small proportion of fish that moved between capture events. The proportions were also relatively constant among years within each reach.

Antenna detections showed consistent seasonality which appeared correspond to changes in stream flows. Initial emigration (as opposed to downstream movements of previously detected individuals) from Rock Creek increased and peaked in fall and early winter months, corresponding to increased stream discharge (Figure 2.3). Although mean monthly stream flows remain high from November through January before dropping slowly through the spring and summer, emigration peaked in November and the declined before flows declined. Emigration during late winter and spring months was slightly greater than during mid-summer, the yearly low point. The monthly timing of downstream directional movements for individuals previously detected emigrating was similar to the timing of first-time emigrants, whereas upstream movements increased somewhat earlier in the summer with their yearly low in late spring (Figure 2.3). There was also evidence of length-dependent emigration from Rock Creek: for those fish that were detected emigrating ($n = 523$), there was a significant negative correlation between initial fish length and the amount of time before first emigrating from Rock Creek ($p < 0.001$; Figure 2.4.)

Seasonal Growth

Seasonal growth rates were calculated for fish that were captured in consecutive tagging events. Fewer trout were tagged or recaptured during spring than during summer and fall, resulting in limited sample sizes for fall to spring (winter) and spring to summer (spring) growth rates relative to summer to fall (summer) growth. Variance was unequal between seasons (Levene's test, $p= 0.02$), so a Generalized Least Squares ANOVA with unequal variance was used to test for an effect of season on growth. Growth rates varied seasonally ($p < 0.001$) (Figure 2.5), and was greater in spring (mean = 0.0053± 0.0004) than in summer (mean = 0.0020 ± 0.0002), ($p < 0.001$), or fall (mean = 0.0011± 0.0002), ($p < 0.001$), but fall and summer growth rates were not significantly different ($p = 0.335$).

Summer Growth

The frequency distribution of trout lengths during the summer allowed us to distinguish fry (age 0+ fish, < 90 mm) from parr (age 1+ and older fish, > 90 mm fork length). Separate models were constructed for these age groups to describe the effects of biological and environmental variables on specific growth rates (Table 2.4). The best model of summer parr growth included a positive relationships with flow and negative relationships with initial body weight and trout density, but explained a small proportion of the variability in growth (model $R^2= 0.08$). The second best model, which was only slightly less plausible ($\Delta AICc= 1.13$) than the top-ranked model, included a negative relationship with temperature in addition to the other variables from the best model. The best model of cutthroat fry summer growth included negative relationships with initial body weight and year (fit as a continuous fixed effect) meaning that summer growth declined over the course of the study (model $R^2=0.34$). The second most plausible model ($\Delta AICc= 2.30$) also included a positive relationship with flow. Habitat characteristics including distance upstream from the mouth of Rock Creek, stream reach, maximum and residual habitat depth, habitat unit surface area were not significantly correlated with growth for both age classes and were not included in the best models. Biological variables including biomass density and numerical density of coho salmon and total salmonids, as well the individual attributes including condition factor, and whether fish moved or not, were not correlated with summer growth of cutthroat trout parr or fry.

Survival and Capture Probabilities of Cutthroat

There was some evidence of both spatial and temporal dependence on capture probabilities of cutthroat trout. The best model predicting capture probabilities for the reach 1 analysis of fall 2005-fall 2009 data included a negative correlation with the time-since-marking (TSM) plus an additive effect of time-dependence—adjustment of survival estimates for each capture event (model: p~ TSM + time), although there was only slightly less support ($\Delta QAIC_c$= 2.20) for the solely time-dependent model (p~ time) (Table 2.5). The best model of capture probabilities for the combined reaches 1 and 3 dataset from summer 2007- fall 2009 data was a model including an interaction between reach and time dependence (model: p~ reach : time), although coefficients for reach 3 capture probability were lower in all but one period (Table 2.5). Season was not included in the best model for either dataset; however, support for more fully parameterized models which included full time-dependence suggest that survival was temporally variable but not consistently so among seasons.

There was weak evidence that survival decreased with time since marking (reach 1, reaches 1 and 3 datasets) and varied with time (reaches 1 and 3 dataset only), while survival did not vary among reaches. The best models of survival probabilities for the reach 1 dataset were the null model of constant survival over time and a model including a negative correlation with TSM, which together accounted for 87% of the model weight (Table 2.6). Season was not included in the best models of survival for the reach 1 dataset. The best models of survival for the reaches 1 and 3 dataset included a negative correlation with TSM and either an additive or multiplicative (interaction) effect of time dependence meaning that monthly survival generally declined with increasing time since marking for all individuals and there was also significant time-dependence (independent survival within each time period) (Table 2.6). Models for the reaches 1 and 3 dataset were not well differentiated by model selection criteria, however, and the null model of constant survival (ΔAICc= 2.21) was almost as plausible as models including temporal structure. Reach and season were not included in the best model for the reaches 1 and 3 dataset.

For both datasets, the null model of constant survival was a better fit than models incorporating individual abiotic and biotic covariates (Table 2.7). All individual abiotic and biotic covariates had 95% confidence intervals that overlapped zero, indicating that they did not affect survival.

Discussion

Movement

Electrofishing recaptures and remote detections of tagged cutthroat trout at the mouth of Rock Creek provided contrasting characterizations of movement. Most cutthroat trout recaptured by electofishing were in the same habitat unit where they were tagged, and the distance moved by these fish was equivalent to the length of a few adjacent habitat units within a reach (~ 100 m). This indication of limited movement is partially an artifact of our methods, however. The same habitat units and reaches were repeatedly sampled so only individuals remaining in sampled habitat units and study reaches or moving to other sampled reaches or habitat units would be susceptible to recapture, thus reducing our ability to detect movements to areas outside of sample reaches (Gowan et al. 1994). Moreover, most recaptures occurred at the end of the summer, and antenna detections indicated that this was the season when movement was least common.

In contrast to limited cutthroat movement as inferred by physical recaptures and antenna detections before the first recapture, long-term antenna detections suggested many trout moved relatively considerable distances. More than a third of the tagged trout were detected at downstream antennas, and < 1% of these fish were subsequently detected in Rock Creek, indicating that the population is characterized by a mix of local site fidelity and long-range movement. Evidence of length-dependent emigration in our study suggests that fish may eventually move downstream out of study reaches as part of an ontogenetic niche shift as they continue to grow and their resource needs can no longer be met in small tributary habitat like Rock Creek (Jonsson and Jonsson 1993). In fact there appeared to be a threshold of ~150 mm length at tagging, over which size all individuals that were detected emigrating did so within the first year after tagging. This size corresponds to the typical size of typical smolts in cutthroat populations and was also the size at which piscivory became more common in cutthroat in the Cedar River basin (P. Kiffney, unpublished data). The seasonal increase in detections during fall and early winter coincided with increasing stream discharge, which is often associated with movement in coastal cutthroat trout (Bryant et al. 2009) and other salmonids (Peterson 1982). Additionally higher flows could enable movement by reducing the predation risk associated with movement through increased depth as a form of cover (Lonzarich and Quinn 1995).

Growth

We found the highest growth rates from spring to midsummer and lower growth rates from midsummer through fall and fall through winter periods. Spring has been associated with higher growth rates in Atlantic salmon (Bacon et al. 2005), and may provide an optimal balance of temperature, food availability, and stream discharge. Warmer temperatures in Rock Creek during spring reduce physiological constraints that may limit growth during winter without exceeding thresholds that often result in lower growth during summer months (e.g. Davidson et al. 2010, McCarthy et al. 2009). Discharge in Rock Creek remains relatively high in the spring, and this can enhance growth (Teichert et al. 2010), perhaps related to increased invertebrate drift or usable habitat area. Models of summer growth supported the important role of stream discharge, with strong support for models including a positive correlation between flow and growth for both cutthroat parr and fry, as has been observed in other studies of stream salmonids (Harvey et al. 2006). Reduced growth during late summer and early fall, when low flows concentrate fish in remaining areas with suitable depth (Glova 1986), may be due to food limitation and increased energetic demands from elevated temperatures.

The negative correlation between cutthroat trout parr growth and trout density suggests that intraspecific competition affects growth. Conspecific density dependence has long been recognized to regulate stream salmonid populations (Milner et al. 2003), and may manifest in reduced growth (Harvey et al. 2005, Keeley 2001, Teichert et al. 2010). Trout density was not included in the best model of cutthroat fry growth, which could result from spatial separation of different age-groups of trout in the stream (Rosenfeld and Boss 2001).

In contrast, there was no evidence that interspecific competition affected resident cutthroat. Specifically, coho salmon density was not included in the best models of cutthroat trout growth despite almost an order of magnitude increase in mean coho density from 2005 through 2009. In addition there was a great deal of variation in coho density between habitat units in each year, allowing for within-year effects of coho density to be observed, had they occurred. The role of interspecific competition on stream salmonids is not well resolved; one hypothesis suggests that evolved niche segregation minimizes interactions between co-occurring species, whereas an alternate hypothesis suggests that realized niches of co-occurring species represent a reduction from the resources that species might use in isolation (Hutchinson 1957, Milner et al. 2003). Harvey et al. (1996) found a negative effect of steelhead density on coho salmon growth. Conversely, two studies failed to detect effects of increasing stream-rearing spring Chinook salmon densities on growth and abundance of rainbow trout in the Yakima River, WA. The lack of negative impacts in our study may be a result of habitat partitioning; coho salmon prefer slower, deeper areas and are primarily surface feeders, whereas cutthroat trout have less association with depth and prefer microhabitats with good conditions for foraging on invertebrate drift (Bisson et al. 1988). It is possible, however, that coho populations have simply not reached a threshold density where they begin to affect cutthroat growth, or that potential effects will not manifest in a relationship with density at the habitat unit scale. Interestingly, trout fry summer growth declined across years of the study, and though the reason is unknown, the only factor known to have undergone directional change over the course of the study was the abundance and density of coho salmon.

Survival

Surprisingly, seasonal and spatial variation, and individual covariates were not included in the best models of coastal cutthroat trout survival. It was expected that environmental conditions such as discharge, temperature, and food availability, which are seasonally variable in streams, and influence important aspects of cutthroat ecology including growth rates and various life history transitions (Milner et al. 2003, Thorpe et al. 1998), would result in seasonal survival patterns. Indeed, survival of coastal cutthroat in small Oregon streams was lower during late summer-fall periods, coinciding with the period of lowest discharge (Berger and Gresswell 2009). Interactions between season and age class or size on survival of stream salmonids, observed in brown trout (Carlson et al. 2008), may have limited our ability to detect an effect of seasonality since exact fish ages were not available. Additionally, survival bottlenecks related to density may operate over relatively short intervals of time (Milner et al. 2003) with fish moving to mitigate competitive interactions (Gowan and Fausch 2002, Keeley 2001). This competition-mediated movement may have alleviated any density effects on individuals through more efficient use of variable resources over a spatial scale greater than the habitat unit. However, the lack of an observable effect of coho salmon density on cutthroat trout survival, despite substantial increases in salmon density, suggests that other factors may be more important in explaining variation in cutthroat survival in Rock Creek.

Considerations for futures survival studies involving resident salmonids

We observed marked variation in capture probabilities among reaches and as function of time, underscoring important considerations for study design. Capture efficiency varied throughout the study, but other than detections of emigrants at antennas during fall and winter months, capture probabilities were low during the end of winter sampling events. This was likely a function of elevated discharge and low temperatures relative to mid-summer and end of summer periods which reduced the effectiveness of electrofishing, especially in habitat units that were deep and swift, or had abundant wood debris or other cover. Including information about emigration in order to censor capture histories improved precision of estimates of capture probabilities and survival for winter months, when most fish emigrated. However, the use of mobile underwater PIT tag detectors, which read PIT tags without requiring fish to be captured, have demonstrated higher tag detection efficiency for coastal cutthroat than electrofishing (Berger and Gresswell 2009) and may improve survival and capture estimates, particularly where electrofishing efficiency is reduced. It should be noted that lower capture efficiencies during the spring may have also been a result of fish spreading out within or beyond study reaches relative to summer and fall due to greater usable area at higher flows, resulting in a lower proportion of fish occupying deeper habitat units where sampling was focused.

The use of PIT tags is increasingly used to monitor survival of stream salmonids. Methodological limitations encountered during data collection and analysis for this study generated several recommendations for future studies employing similar methods:

1. *Life history of study species*—PIT tags are frequently used to monitor survival and movement stream salmonids. For obligate migrant species such as Pacific salmon (as opposed to resident and facultative migrant species), simplifying assumptions about emigration may be made. All surviving individuals must emigrate (smolting) and may be considered dead if not detected emigrating, allowing survival for individuals

to be known rather than estimated with computationally-intensive models. This may reduce the considerable uncertainty inherent in survival models, which are dependent upon (often variable) capture efficiency in streams.

2. *Need to incorporate emigration*—A substantial proportion of trout emigrated from study reaches, which without censoring capture histories, would have increased the divergence of apparent survival estimates from true survival, and potentially, reduced our ability to determine factors affecting it. This problem may also bias the temporal structure of survival estimates due to seasonality in the timing of emigration.
3. *Importance of sampling consistency and intensity*—In order to satisfy model assumptions to estimate survival of resident fish, the spatial extent of sampling should be consistent among events. Skipping habitat units or reaches during certain intervals will cause violations of model assumptions which may preclude spatial or temporal analyses of interest. Sampling a large proportion (not just pools) of habitat within reaches may result in higher capture probabilities and thus more robust estimates of survival and covariates of interest.

Conclusions

Our results suggest that abiotic factors and intraspecific competition may have stronger influence on resident trout populations than interspecific competition. Seasonal and within-season variation in stream discharge affected growth and movement of trout, and intraspecific density dependence affected growth of larger trout. Despite almost a tenfold increase in juvenile coho salmon density over four years, we observed no adverse impacts on cutthroat trout populations. It is possible that impacts will emerge in the future as coho salmon populations continue to expand in spatial distribution and abundance. However, juvenile coho salmon densities are already comparable to those found in similar streams in the Pacific Northwest, and the lack of impacts thus far may be explained by resource partitioning between the species resulting from a legacy of co-evolutionary history. Our results suggest that restoration of native anadromous salmon populations is not likely to adversely impact resident salmonid species relative to natural variability.

General Summary

Habitat degradation, which can alter abiotic conditions, and introduction of non-native species, which can alter interspecies interactions, are two anthropogenic perturbations that may result in changes to community structure and have negative impacts on salmonids. Habitat fragmentation, including the construction of impassible dams on rivers, has resulted in the extirpation of migratory stream rearing salmonids, thus altering the potential for interspecies competition. Widespread introductions of non-native rainbow trout have resulted in displacement of, and hybridization with, native cutthroat trout (*O. clarkiii*) subspecies throughout the western United States. Understanding how abiotic and biotic factors influence stream salmonid communities is thus important for their management and conservation due to the frequent occurrence of anthropogenic disturbances in their ecosystems.

This project addressed knowledge gaps regarding the effects of abiotic and biotic factors on the ecology of coastal cutthroat and their interactions with steelhead and coho salmon. The first chapter showed that coastal cutthroat trout and steelhead segregated their spawning habitat spatially within a watershed. Cutthroat used smaller streams with less contributing basin area than did steelhead, and there was little overlap between species, suggesting spatial segregation may limit the potential for interspecific hybridization and thus facilitate the maintenance of coastal cutthroat and steelhead stocks despite the viability of hybrids. The second chapter showed that coastal cutthroat growth and movements were affected by abiotic factors including seasonality and stream flows, with greater growth in the spring and greater movement in the fall than other periods of the year, and summer growth negatively correlated with stream flow. Biotic factors such as individual fish size and density of conspecific density also affected growth and movement. However, despite a tenfold increase in coho salmon densities during the 4 year study there was no relationship between coho density and trout density, growth, movement, or survival, suggesting the two species currently partition their resource use to the extent that factors other than competition with coho salmon may have more influence on cutthroat populations. It is possible that if coho salmon populations increase further in this system competition may occur as there is overlap in habitat use by these species.

Strong partitioning of resource use between coastal cutthroat trout and other native salmonids was evident in both chapters. Segregation of spawning habitat between cutthroat and steelhead likely results in a reduced rate of interspecific hybridization and segregation of resource use between cutthroat trout and coho salmon likely results in weak interspecific competition. Partitioning of resources between species in this native stream rearing salmonid community appear to minimize some of the negative impacts associated with interspecies interactions that are apparent where nonnative species have been introduced. Our results suggest that effective resource partitioning mechanisms may arise in native species which have undergone long periods of co-evolution thus minimizing the strength of negative interspecies interactions and their attendant ecological impacts.

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Tables

Table 1.1. Bi-parental PCR primer sets, primer products, and annealing temperatures for markers used to distinguish coastal cutthroat trout (CT) from steelhead (STH).

Bi-parental Primer set	Primer Source	Marker Size (bp)	Speciess	Annealing Temp (°C)
OM-47	(Ostberg and Rodriguez 2004)	275 300	CT STH	66
OM-55	(Ostberg and Rodriguez 2004)	180 200	CT STH	66
OCC-36	(Ostberg and Rodriguez 2004)	275-285 325	STH CT	66
OCC-16	(Ostberg and Rodriguez 2002)	280 380	STH CT	50

Table 1.2. Summary statistics for habitat characteristics and fish sampling by reach in the Ellsworth Creek, WA.

Parameter	Mean	Min.	Max.	St. Dev.
Basin Area (ha)	573	17	1660	480
Gradient (% slope)	2.80	1.50	7.00	1.30
Bankfull Width (m)	7.30	1.80	13.70	2.80
Age 0+ Sampled	1.77	0	5	1.37
Age 1 and 2+ Sampled	1.86	0	10	1.93
Total Fish Sampled	3.63	1	11	2.06

Table 1.3. Species assignments based on genetic analysis and length frequency histograms for Ellsworth Creek trout by age.

Species	Age 0+	%	Age 1+	%	Age 2+	%	All Ages	%
Cutthroat	13	21.0	27	44.3	4	100.0	44	34.6
Steelhead	41	66.1	13	21.3	0	0.0	54	42.5
F1 hybrid	0	0.0	7	11.5	0	0.0	7	5.5
Post F1 hybrid	8	12.9	14	23.0	0	0.0	22	17.3
All hybrids	8	12.9	21	34.4	0	0.0	29	22.8
Totals	62	100.0	61	100.0	4	100.0	127	100.0

Table 1.4. Mitochondrial marker types by age class and hybrid class.

Age	Hybrid Type	MtDNA[2]	Count
0	F1	STH	NA[1]
0	F1	CT	NA[1]
0	Post-F1/Backcross	STH	1
0	Post-F1/Backcross	CT	0
1+	F1	STH	3
1+	F1	CT	0
1+	Post-F1/Backcross	STH	2
1+	Post-F1/Backcross	CT	0

[1] No age 0 trout were classified as F1 hybrids (see Table 3).

[2] STH = steelhead; CT = coastal cutthroat trout

Table 1.5. Habitat characteristics of reaches where young of year and older juvenile coastal cutthroat (CT), steelhead (STH) and hybrids occurred in Ellsworth Creek, WA.

		Basin Area (ha)				Gradient (% slope)				Bankfull Width (m)			
Species	Age	mean	st. dev	min	max	mean	st. dev	min	max	mean	st. dev	min	max
STH	0	850.6	450.4	163.5	1660.4	2.4	1.0	1.5	4.0	8.7	2.6	4.5	13.7
CT	0	141.8	108.9	16.7	323.8	3.7	1.2	2.0	6.0	4.4	1.8	1.8	7.0
Hybrid	0	574.5	499.4	39.8	1388.2	3.1	1.2	1.5	4.0	8.7	4.7	3.1	13.7
STH	1	832.2	398.2	242.7	1373.0	2.2	0.8	1.5	4.0	9.1	2.3	6.4	13.7
CT	1	340.3	247.2	86.5	988.4	3.1	1.4	1.5	7.0	6.9	2.3	4.3	13.7
Hybrid	1	565.2	525.8	163.5	1660.4	2.9	1.0	1.5	4.0	7.2	2.6	4.3	13.3
All reaches		573.0	479.7	16.7	1660.4	2.8	1.3	1.5	7.0	7.3	2.8	1.8	13.7

Table 1.6. Model selection results for habitat variables affecting the proportion of age 0+ steelhead and cutthroat trout in Ellsworth Creek and tributaries. Models are listed from most plausible (ΔAIC*c*=0) to least plausible. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i). All single variable and multiple variable models, which include the most important single variable, are shown. Models were not fit for age 0+ hybrids because age 0+ hybrids were collected in only 4 reaches.

Species	Model[1]	AIC*c*	ΔAIC*c*	Relative likelihood	Akaike weight (w_i)	R^2	w_I/w_i
Steelhead	BA, G	26.7	0.00	1.00	0.67	0.81	1.00
	BA, G, BFW	28.4	1.75	0.42	0.28	0.82	2.40
	BA	33.3	6.64	0.04	0.02	0.65	27.71
	BA, BFW	33.5	6.84	0.03	0.02	0.68	30.61
	G	44.7	17.98	0.00	0.00	0.45	8031.04
	G	53.6	26.90	0.00	0.00	0.30	693182.80
Cutthroat	BA	26.9	0.00	1.00	0.32	0.66	1.00
	BFW	27.4	0.50	0.78	0.25	0.65	1.28
	BA, G	27.8	0.88	0.64	0.21	0.69	1.56
	BA ,BFW	28.5	1.58	0.45	0.15	0.68	2.21
	BA, BFW, G	30.0	3.06	0.22	0.07	0.70	4.61
	G	48.0	21.06	0.00	0.00	0.24	37434.57

[1] BA = log (contributing basin area), G = channel gradient, BFW = bankfull channel width

Table 1.7. Maximum likelihood estimates of intercepts and slopes for models correlating age 0+ species distributions with habitat variables[1] in the Ellsworth Creek, WA. Models are listed for each species in order of fit starting with the best model.

Species	Model	Intercept	BA	G	BFW
Steelhead	BA, G	32.8	2.567	-1.689	
	BA, G, BFW	-42.454	3.32	-1.679	-0.223
	BA	-39.178	2.618		
	BA, BFW	-51.148	3.567		-0.316
	G	4.798		-1.42	
	G	-3.029			0.513
Cutthroat	BA	35.427	-2.461		
	BFW	5.639	-1.095		
	BA, G	30.798	-2.332	0.795	
	BA ,BFW	23.077	-1.428		-0.475
	BA, BFW, G	21.431	-1.524	0.682	-0.347
	G	-4.25		0.96	

[1] BA = log (contributing basin area), G = channel gradient, BFW = bankfull channel width

Table 1.8. Model selection results for habitat variables affecting the proportion of age 1+ and 2+ steelhead and cutthroat trout in Ellsworth Creek and tributaries. Models are listed from most plausible (ΔAIC*c*=0) to least plausible. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i). All single variable and multiple variable models, which include the most important single variable, are shown. Models were not fit for age 1+ hybrids because no models had reasonably good fit.

Species	Model[1]	AIC*c*	ΔAIC*c*	Relative likelihood	Akaike weight (w_i)	R^2	w_I/w_i
Steelhead	BA	47.8	0.00	1.00	0.57	0.28	1.00
	BA, BFW	50.1	2.26	0.32	0.19	0.29	3.09
	BA, G	50.2	2.36	0.31	0.18	0.29	3.26
	BA, BFW, G	52.7	4.90	0.09	0.05	0.29	11.58
	G	55.9	8.11	0.02	0.01	0.13	57.59
	BFW	57.1	9.25	0.01	0.01	0.10	101.97
Cutthroat	BA, BFW	53.6	0.00	1.00	0.45	0.36	1.00
	BA, BFW, G	54.6	1.03	0.60	0.27	0.39	1.67
	BA	55.3	1.76	0.41	0.19	0.28	2.41
	BA, G	56.9	3.32	0.19	0.09	0.30	5.25
	BFW	68.1	14.54	0.00	0.00	0.02	1433.65
	G	68.9	15.33	0.00	0.00	0.02	2131.43

[1] BA = log (contributing basin area), G = channel gradient, BFW = bankfull channel width

Table 2.1. Timing of electrofishing and habitat survey events in three reaches of Rock Creek from 2005 through 2009.

Event Number	Date	Season	Number of Habitat Units Sampled			
			Reach 1	Reach 2	Reach 3	Total
1	8/9/2005[1]	summer 2005	23	16	11	50
2	10/20/2005	fall 2005	23	13		36
3	2/21/2006	winter 2006	19	13		32
4	7/10/2006	summer 2006	23	17	11	51
5	9/25/2006	summer 2006	23	18	11	52
6	3/8/2007	winter 2007	20			20
7	7/24/2007	summer 2007	18	13	12	43
8	9/25/2007	fall 2007	17	13	9	39
9	4/3/2008	spring 2008	19		11	30
10	7/28/2008	summer 2008	18		11	29
11	9/30/2008	fall 2008	18		11	29
12	3/24/2009	spring 2009	16		12	28
13	8/17/2009	summer 2009	15		11	26
14	9/23/2009	fall 2009	16		11	27

[1] During event 1, reach 1 sampling started on 8/9/2005, but reaches 2 and 3 were sampled starting 9/21/2005.

Table 2.2. The number of cutthroat trout tagged each year from 2005-2009 in reaches of Rock Creek and the proportion that were subsequently recaptured or detected by at stationary antennas at the mouth of Rock Creek through the fall of 2010.[1]

	Reach 1			Reach 3			Totals		
Year	Tags	% Detected	%Recap	Tags	% Detected	%Recap	Tags	% Detected	%Recap
2005	182	46	30	99	17	14	281	36	25
2006	118	49	42	153	24	31	271	35	35
2007	120	53	48	103	23	56	223	39	52
2008	204	53	39	81	11	40	285	41	39
2009	195	42	34	219	8	27	414	24	30
Total	819	48	38	655	16	32	1474	34	35

[1] Reach 2 is omitted because sampling did not continue beyond fall 2007 and reach 2 was not included in survival analyses.

Table 2.3. Descriptive statistics for fish and habitat variables used in growth and survival analyses from 2005-2009 in Rock Creek.

Variable	Mean	Min	Max	CV
Cutthroat Trout Length (mm)	113.34	60.00	280.00	0.11
Cutthroat Trout Weight (g)	17.82	1.80	229.40	0.08
Mean Daily Water Temperature (°C)	9.21	0.20	18.07	0.42
Mean Daily Discharge[1] (m/s^3)	3.59	0.26	72.21	1.52
Area (m^2)	48.08	3.64	189.42	0.16
Width (m)	4.60	0.82	15.80	0.11
Max Depth (m)	0.56	0.04	1.40	0.14
Residual Depth (m)	0.36	0.00	1.15	0.17
Coho Salmon Biomass Density (g/m^2)	1.12	0.01	22.37	1.99
Trout Biomass Density (g/m^2)	2.22	0.00	26.76	1.29
Salmonid Biomass Density (g/m^2)	3.00	0.00	29.35	1.29
Coho Density ($\#/m^2$)	0.14	0.00	4.86	2.52
Trout Density ($\#/m^2$)	0.17	0.00	1.35	1.06
Salmonid Density ($\#/m^2$)	0.31	0.00	5.18	1.41

[1] Discharge from USGS 12145500 Raging River near Fall City, WA.

Table 2.4. Best candidate GLMs using environmental and biological factors to explain variability in cutthroat trout parr and fry growth. Signs (+,-) denote the sign of the slope for each covariate and are displayed for univariate models only.[1] Models are listed from most plausible ($\Delta AICc=0$) to least plausible. The Akaike weight w_i indicates the relative likelihood of the best fitting model compared to other models. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best fitting model (w_I) compared to other models (w_i). All of the best multiple variable models and the single variable models for variables which were included in the best models are shown.

Growth Model	AICc	ΔAICc	AIC weight	R^2	w_I/w_i
Cutthroat Parr					
flow, weight, trout density	-2071.01	0.00	0.62	0.08	1.00
flow, weight, temperature, trout density	-2069.88	1.13	0.35	0.08	1.76
flow (+)	-2063.75	7.26	0.02	0.03	37.70
weight (-)	-2062.36	8.64	0.01	0.02	75.32
temp (-)	-2060.90	10.11	0.00	0.02	156.76
trout density (-)	-2060.72	10.29	0.00	0.02	171.19
Cutthroat Fry					
weight, year	-616.03	0.00	0.66	0.34	1.00
weight, year, flow	-613.73	2.30	0.21	0.34	3.16
weight, year, temperature, flow	-612.27	3.76	0.10	0.35	6.57
weight (-)	-609.93	6.10	0.03	0.26	21.10
year (-)	-604.17	11.86	0.00	0.19	375.70
temp (-)	-596.74	19.29	0.00	0.10	15461.30
flow (+)	-592.98	23.05	0.00	0.05	101345.99

Table 2.5. Model structure and relative support ($QAIC_c$ for reach 1 datset, AIC_c for reaches 1 and 3 dataset; see methods) for models of recapture probabilities for coastal cutthroat trout in Rock Creek from fall 2005 through fall 2009. Capitalized model variables were fit as continuous variables and non-capitalized variables were fit as factors. Additive linear models are denoted by +, and multiplicative models (interaction) by :, and combined additive and multiplicative by * (interaction + additive effect). The null model is (.). TSM is the time-since-marking, time is the capture event and season is fall, spring, or summer. Models are listed from most plausible ($\Delta QAICc$ or $\Delta AICc=0$) to least plausible. The Akaike weight w_i indicates the relative likelihood of the best fitting model compared to other models. The number of parameter is denoted by K.

Data Subset	Recapture Model	$QAIC_c$ / AICc	$\Delta QAIC_c$ / ΔAIC_c	w_i	K
Reach 1	TSM + time	723.40	0.00	0.68	14
	time	725.60	2.20	0.22	13
	TSM * time	727.25	3.84	0.10	23
	season	738.88	15.48	0.00	4
	TSM + season	739.68	16.27	0.00	5
	TSM * season	743.42	20.02	0.00	7
	TSM	797.33	73.93	0.00	3
	(.)	806.08	82.68	0.00	2
Reach 1 and 3	reach : time	0.00	1047.35	0.88	14
	time	5.63	1052.98	0.05	8
	reach + time	6.70	1054.05	0.03	9
	TSM + time	7.50	1054.85	0.02	9
	TSM + time + reach	8.51	1055.86	0.01	10
	TSM * time : reach	10.04	1057.39	0.01	25
	TSM * time	15.50	1062.85	0.00	14
	reach + season	29.96	1077.31	0.00	5
	TSM + season + reach	30.75	1078.10	0.00	6
	season	33.19	1080.54	0.00	4
	reach : season	33.47	1080.82	0.00	7
	TSM + season	33.56	1080.91	0.00	5
	TSM * season	37.53	1084.87	0.00	7
	TSM * season : reach	41.03	1088.38	0.00	13
	reach + TSM	118.33	1165.68	0.00	4
	reach * TSM	120.33	1167.68	0.00	5
	TSM	121.72	1169.07	0.00	3
	reach	127.82	1175.17	0.00	3
	(.)	131.41	1178.76	0.00	2

Table 2.6. Model structure and relative support ($QAIC_c$ for reach 1 datset, AIC_c for reaches 1 and 3 dataset; see methods) for temporal models of survival probabilities of coastal cutthroat trout in Rock Creek. Capitalized model variables were fit as continuous variables and lower-case variables were fit as factors. Additive linear models are denoted by +, and multiplicative models (interaction) by :, and combined additive and multiplicative by * (interaction + additive effect). The null model is (.). TSM is the time-since-marking, time is the capture event and season is fall, spring, or summer. Models are listed from most plausible ($\Delta QAICc$ or $\Delta AICc$=0) to least plausible. The Akaike weight w_i indicates the relative likelihood of the best fitting model compared to other models. The number of parameter is denoted by *K*.

Data Subset	Survival Model	$QAIC_c$ / AICc	$\Delta QAIC_c$ / ΔAIC_c	w_i	*K*
Reach 1	(.)	723.40	0.00	0.44	14
	TSM	723.45	0.05	0.43	15
	season	727.26	3.86	0.06	16
	TSM : season	727.69	4.28	0.05	17
	TSM * season	731.62	8.21	0.01	19
	TSM : time	731.81	8.41	0.01	21
	time	733.86	10.46	0.00	22
	TSM + time	736.66	13.26	0.00	24
	TSM * time	754.00	30.60	0.00	33
Reaches 1 and 3	TSM + time	1045.14	0.00	0.23	18
	TSM * time	1046.30	1.16	0.13	22
	TSM : time	1047.02	1.88	0.09	19
	(.)	1047.35	2.21	0.08	14
	season	1047.69	2.55	0.06	16
	TSM	1047.98	2.84	0.06	15
	reach	1048.42	3.28	0.04	15
	TSM * season	1048.51	3.37	0.04	19
	TSM : season	1048.72	3.58	0.04	17
	TSM : reach	1048.79	3.65	0.04	16
	reach + season	1049.22	4.08	0.03	17
	TSM + time + reach	1049.24	4.09	0.03	20
	TSM + reach	1049.47	4.33	0.03	16
	TSM + season	1050.00	4.86	0.02	18
	TSM * reach	1050.81	5.67	0.01	17
	reach : time	1050.86	5.72	0.01	23
	time	1051.11	5.97	0.01	20
	reach : season	1051.69	6.55	0.01	19
	TSM + season + reach	1051.81	6.67	0.01	19
	reach + time	1052.94	7.80	0.00	21
	TSM : season : reach	1053.90	8.76	0.00	20
	TSM : time : reach	1054.54	9.40	0.00	23
	TSM * season : reach	1054.82	9.68	0.00	24
	TSM * time : reach	1058.19	13.05	0.00	32

Table 2.7. Model structure, relative support ($QAIC_c$ for reach 1 datset, AIC_c for reaches 1 and 3 dataset; see methods), and variable coefficients with standard errors and 95% confidence intervals for describing the effect of abiotic and biotic factors on survival probabilities for coastal cutthroat trout in the first period after marking in reach 1 of Rock Creek from fall 2005 through fall 2009. Variables were fit as continuous predictors (slope and intercept); the null model is (.). Models are listed from most plausible ($\Delta QAICc$ or $\Delta AICc=0$) to least plausible. The Akaike weight w_i indicates the relative likelihood of the best fitting model compared to other models. DS denotes the dataset for corresponding models.

DS	Survival Model	$QAIC_c$ / AICc	$\Delta QAIC_c$ / ΔAIC_c	w_i	K	Slope	SE	Lower CI	Upper CI
1	(.)	710.46	0.00	0.27	14	-	-	-	-
	Residual Pool Depth	711.81	1.35	0.14	16	1.71	1.03	-0.31	3.72
	Distance Upstream	712.08	1.62	0.12	16	0.00	0.00	-0.01	0.00
	Maximum Pool Depth	712.32	1.86	0.11	16	1.58	1.00	-0.37	3.53
	ln(Coho Biomass Density)	713.92	3.46	0.05	16	0.40	0.45	-0.47	1.28
	ln (Coho Density)	714.02	3.56	0.05	16	0.15	0.17	-0.18	0.49
	Condition Factor	714.08	3.62	0.04	16	1.77	2.19	-2.53	6.07
	ln (Weight)	714.09	3.62	0.04	16	-0.19	0.23	-0.64	0.25
	ln (Salmonid Density)	714.29	3.83	0.04	16	0.15	0.21	-0.26	0.56
	Pool Area	714.48	4.02	0.04	16	0.00	0.01	-0.01	0.02
	ln (Trout Density)	714.63	4.17	0.03	16	0.07	0.28	-0.47	0.61
	ln (Salmonid Biomass Density)	714.65	4.19	0.03	16	0.04	0.20	-0.35	0.43
	ln (Trout Biomass Density)	714.67	4.21	0.03	16	-0.02	0.20	-0.41	0.38
1&3	(.)	1032.35	0.00	0.26	14	-	-	-	-
	ln (Trout Density)	1034.30	1.95	0.10	16	0.30	0.21	-0.11	0.72
	ln (Weight)	1034.46	2.12	0.09	16	-0.26	0.20	-0.65	0.14
	ln (Coho Density)	1034.51	2.17	0.09	16	0.20	0.15	-0.10	0.50
	ln (Salmonid Density)	1034.77	2.42	0.08	16	0.22	0.18	-0.12	0.57
	ln (Salmonid Biomass Density)	1035.22	2.87	0.06	16	0.20	0.19	-0.18	0.58
	ln (Trout Biomass Density)	1035.45	3.10	0.06	16	0.17	0.18	-0.18	0.52
	Distance Upstream	1035.60	3.26	0.05	16	0.00	0.00	0.00	0.00
	Condition Factor	1035.73	3.38	0.05	16	1.11	1.52	-1.87	4.09
	Pool Area	1035.87	3.53	0.05	16	0.00	0.01	-0.02	0.01
	Residual Pool Depth	1036.18	3.83	0.04	16	0.27	0.83	-1.35	1.90
	Maximum Depth	1036.20	3.86	0.04	16	0.24	0.82	-1.36	1.84
	ln (Coho Biomass Density)	1036.26	3.91	0.04	16	0.05	0.31	-0.55	0.65

Figure Captions

Figure 1.1. Map of Ellsworth Creek, WA within the Willapa Bay watershed. The inset shows the location of the watershed within Washington State and the United States.

Figure 1.2. Length frequency histograms after genotype assignments of all trout sampled (a), steelhead (b), cutthroat trout (c), and hybrids (d) from Ellsworth Creek in June 2008.

Figure 1.3. Frequency distribution of the number of individuals with each number of cutthroat (a) and steelhead (b) markers in Ellsworth Creek.

Figure 1.4. Map of Ellsworth Creek showing the spatial distribution of steelhead (black), cutthroat trout (light gray), and hybrids (dark gray) as proportions of the total number of age 0+ trout in found in a reach. Empty circles are reaches where no age 0+ fish were captured.

Figure 1.5. Map of the Ellsworth Creek showing the spatial distribution of steelhead (black), cutthroat trout (light gray), and hybrids (dark gray), as proportions of the total number of age 1 and 2+ trout in found in a reach. Empty circles are reaches where no age 1and 2+ fish were captured.

Figure 1.6. The proportion of age 0+ and age 1+ cutthroat trout, steelhead, and hybrids in a reach relative to log basin area, showing the modeled relationship from single variable GLMs.

Figure 2.1. Map of the Cedar River, WA and tributaries above Landsburg Diversion Dam. The midpoints of three study reaches shown as solid lines perpendicular to the creek. A stream-spanning 3-antenna PIT tag detection array was located at the downstream boundary of reach 1 at the mouth of Rock Creek. Stream reaches accessible to upstream migrating fishes are solid lines; dashed lines are stream reaches above natural migration barriers.

Figure 2.2. Mean + 1 SE summer coho salmon (white bars) and cutthroat trout (black bars) density in pools of Rock Creek from 2005-2009.

Figure 2.3. The proportion of cutthroat trout movements and stream discharge by month in Rock Creek from summer 2005 through fall 2009. Three movement types are shown: first time emigration of individuals from Rock Creek to the Cedar River (open bars; n = 523), all unique fish movements in a downstream direction (dark gray bars; n= 392), and all unique fish movements in upstream direction (light gray bars; n = 103). Discharge (black diamonds) is measured as monthly means of mean daily discharge from the Raging River, which is representative of the temporal pattern of discharge in Rock Creek.

Figure 2.4. The relationship between fork length at tagging and the amount of time before cutthroat trout were first detected emigrating from Rock Creek (n=523). Larger fish were detected emigrating sooner than smaller fish. Dashed horizontal lines represent one and two years after tagging.

Figure 2.5. Seasonal growth rates of cutthroat trout and trout fry in Rock Creek. There was a significant effect of season on growth rate (Generalized Least Squares ANOVA with unequal variance, $p < 0.001$).

Figure 2.6. Monthly survival estimates of cutthroat trout in reaches 1 and 3 of Rock Creek from summer 2007 through fall 2009 from the best temporal-spatial model (phi~Time since marking + time period) of cutthroat trout. Each series represents survival estimates for fish tagged starting in that period. Error bars are standard errors. Survival in summer 2009 is not shown since this parameter cannot be estimated independent of capture probability in the final inter-capture period.

Figures

Figure 1.1

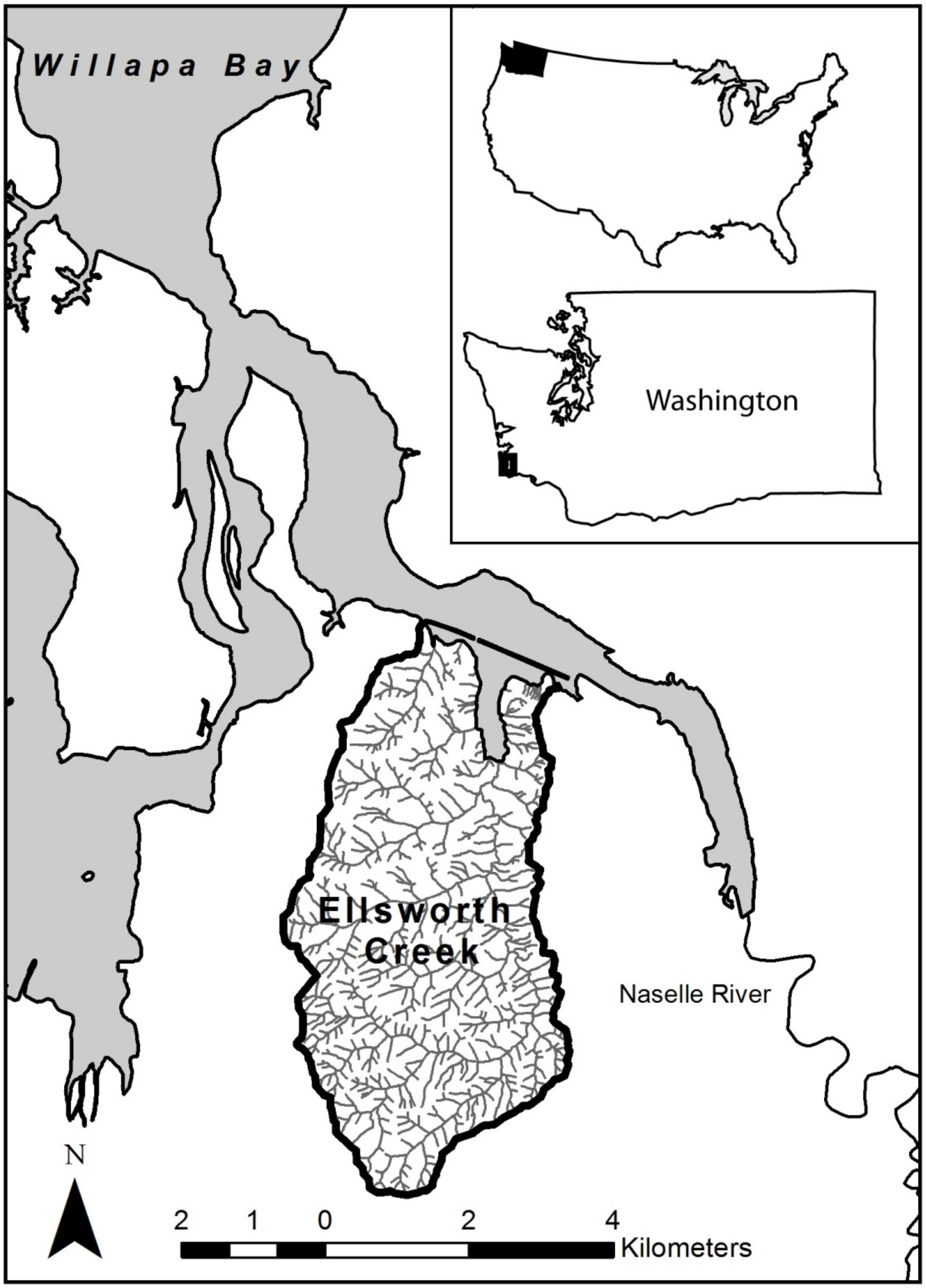


Figure 1.2

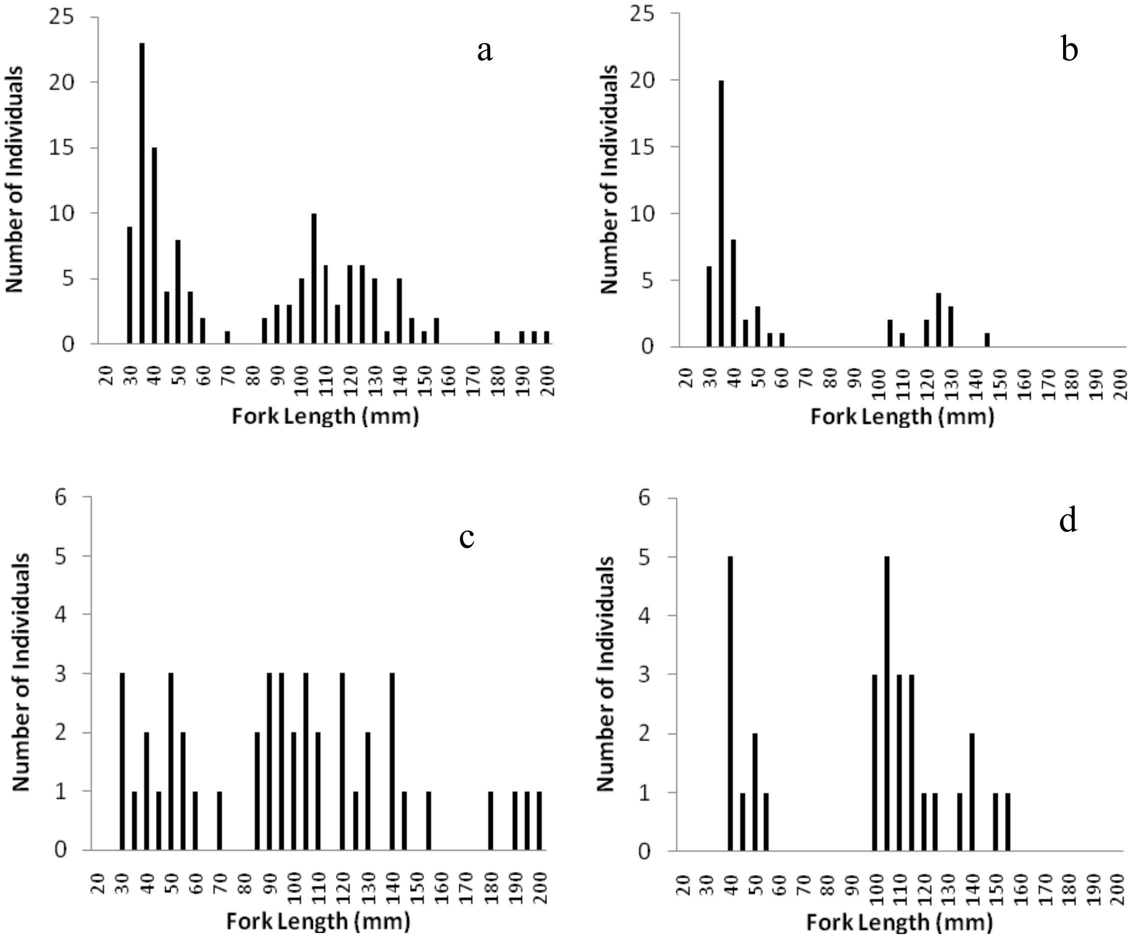

a
b
c
d
Number of Individuals
Fork Length (mm)
0
5
10
15
20
25
0
1
2
3
4
5
6
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200

Figure 1.3

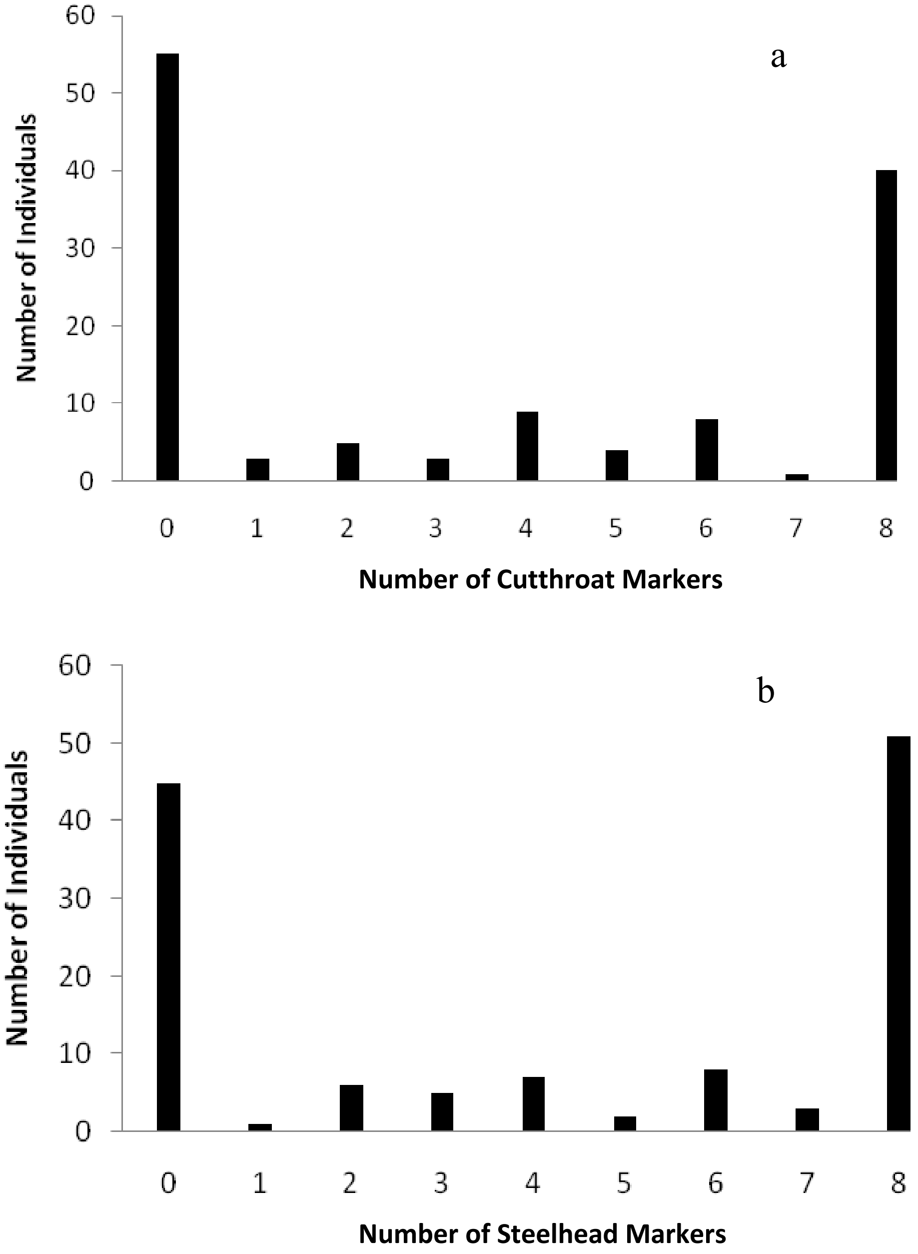

a
Number of Individuals
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
Number of Cutthroat Markers
b
Number of Individuals
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
Number of Steelhead Markers

Figure 1.4

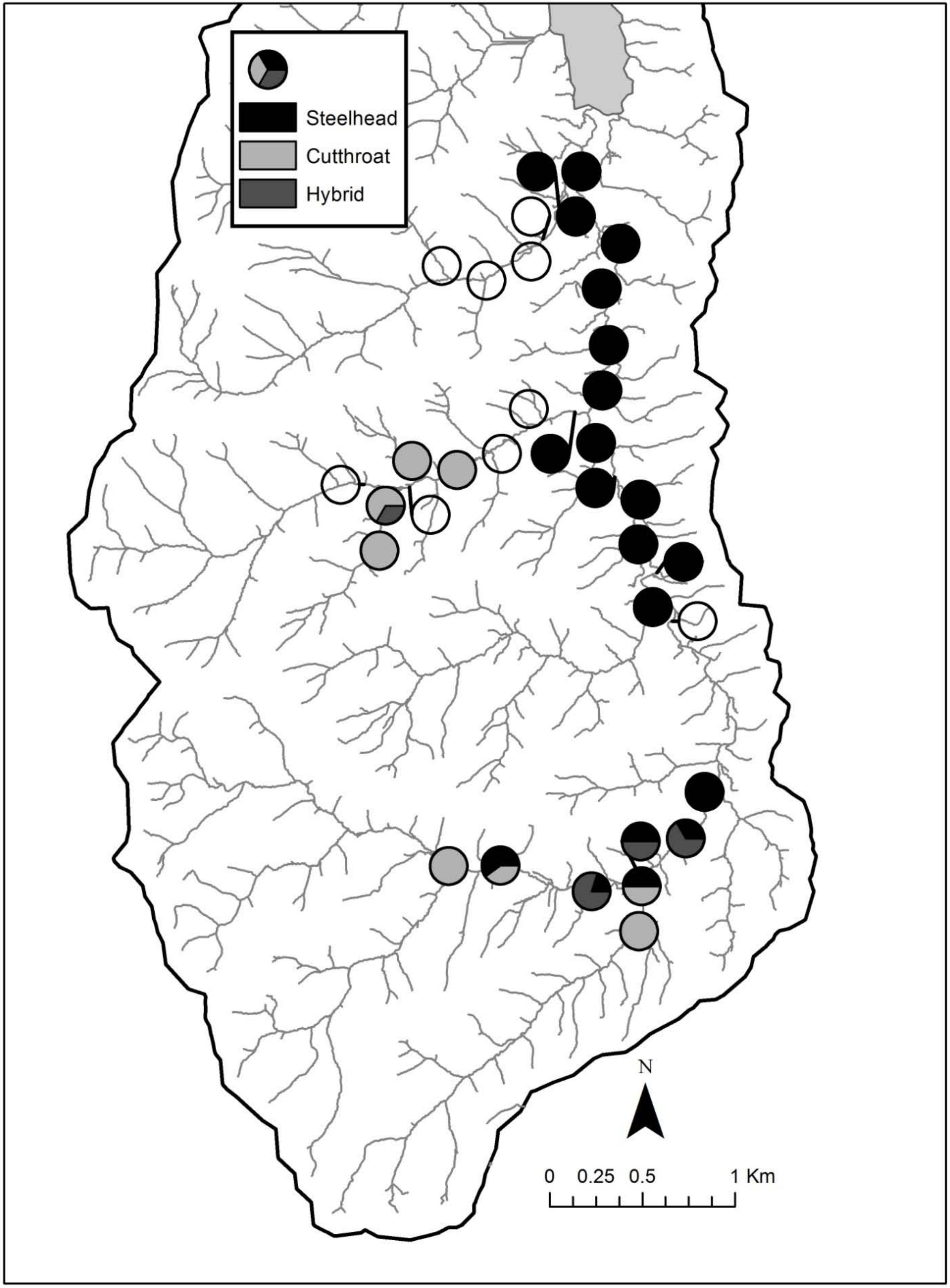


Figure 1.5

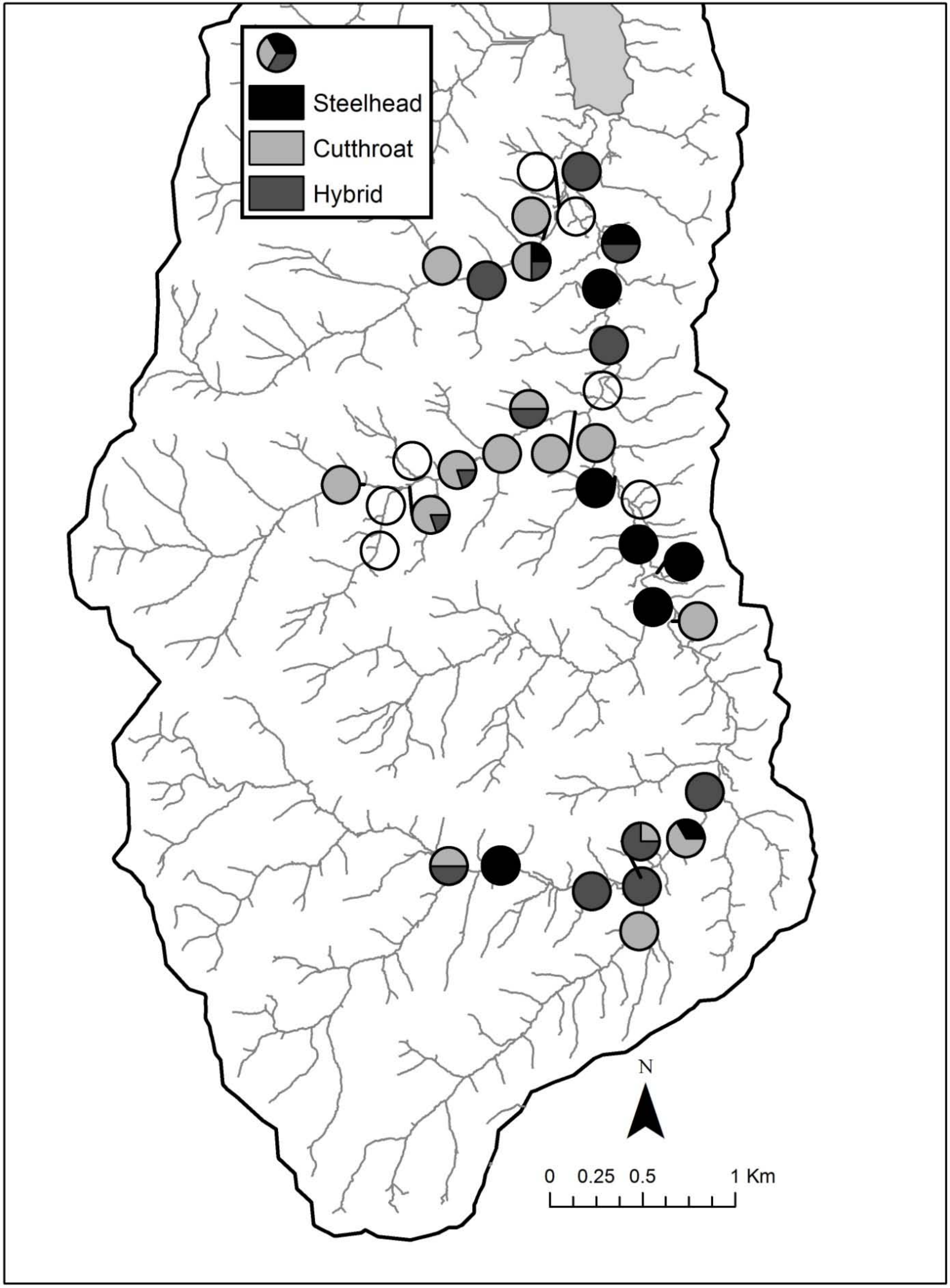


Figure 1.6

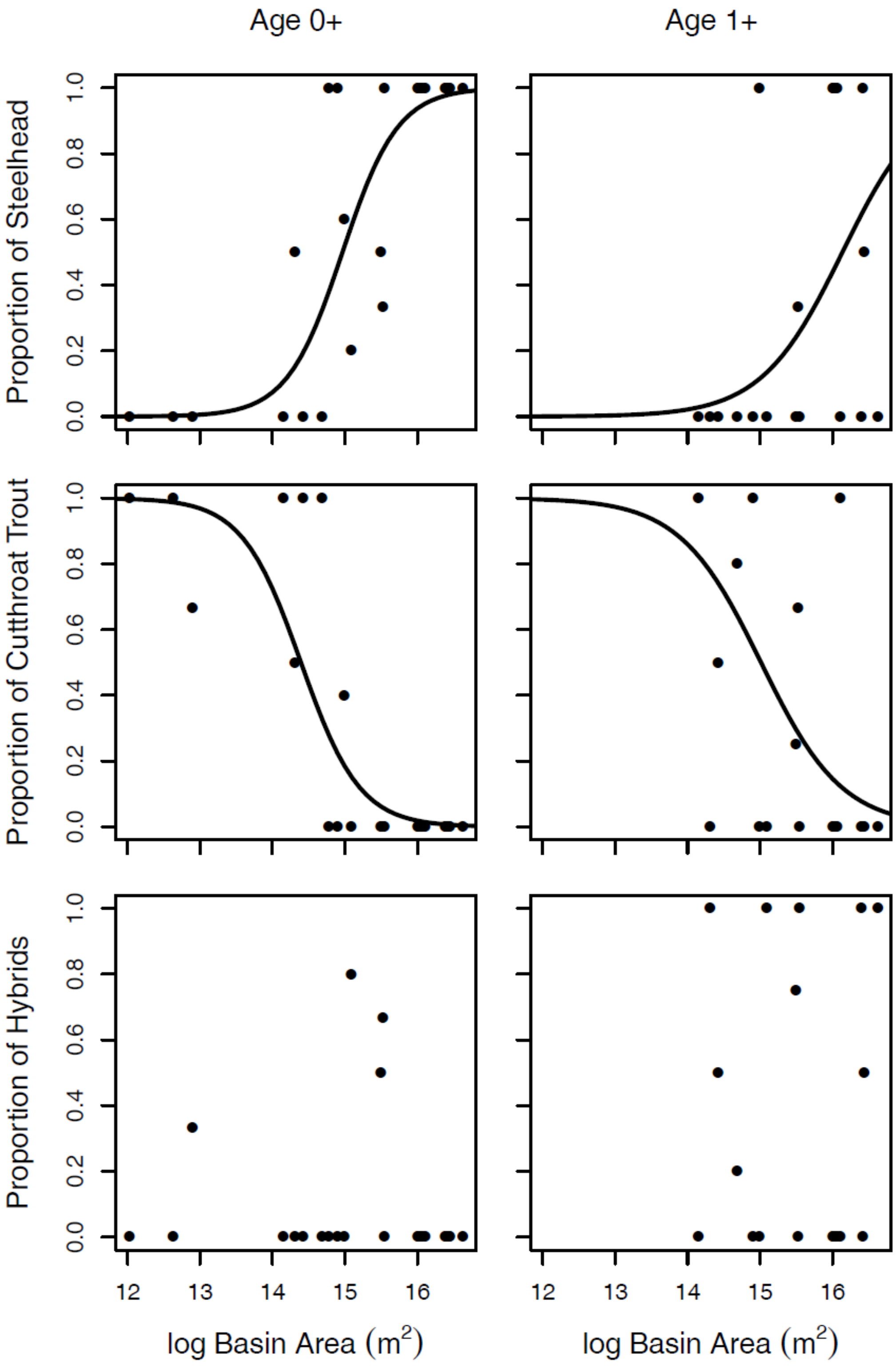

Age 0+
Age 1+
Proportion of Steelhead
Proportion of Cutthroat Trout
Proportion of Hybrids
0.0
0.2
0.4
0.6
0.8
1.0
12
13
14
15
16
log Basin Area (m^2)
log Basin Area (m^2)

Figure 2.1

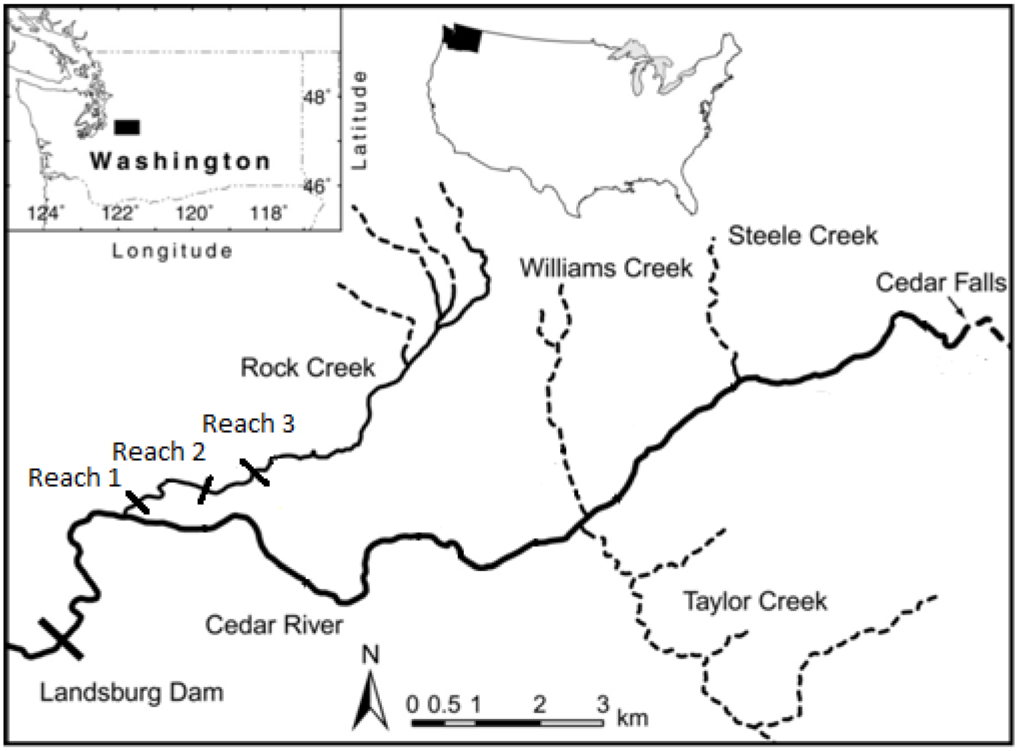

Washington
48°
46°
Latitude
124°
122°
120°
118°
Longitude
Williams Creek
Steele Creek
Cedar Falls
Rock Creek
Reach 3
Reach 2
Reach 1
Taylor Creek
Cedar River
Landsburg Dam
N
0 0.5 1 2 3 km

Figure 2.2

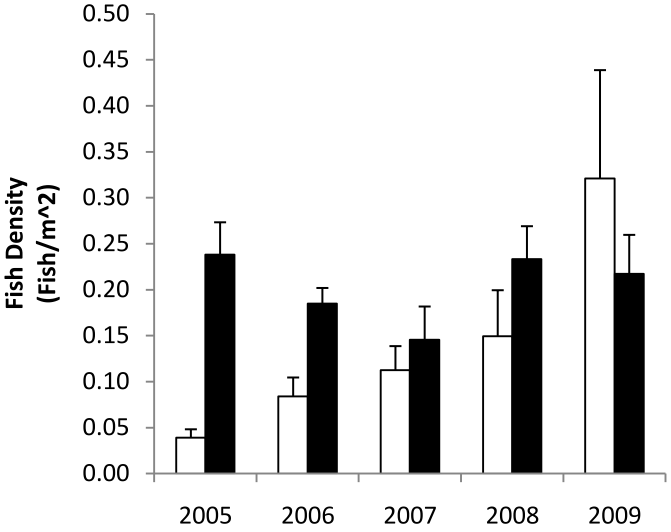

Fish Density (Fish/m^2)
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
2005
2006
2007
2008
2009

Figure 2.3

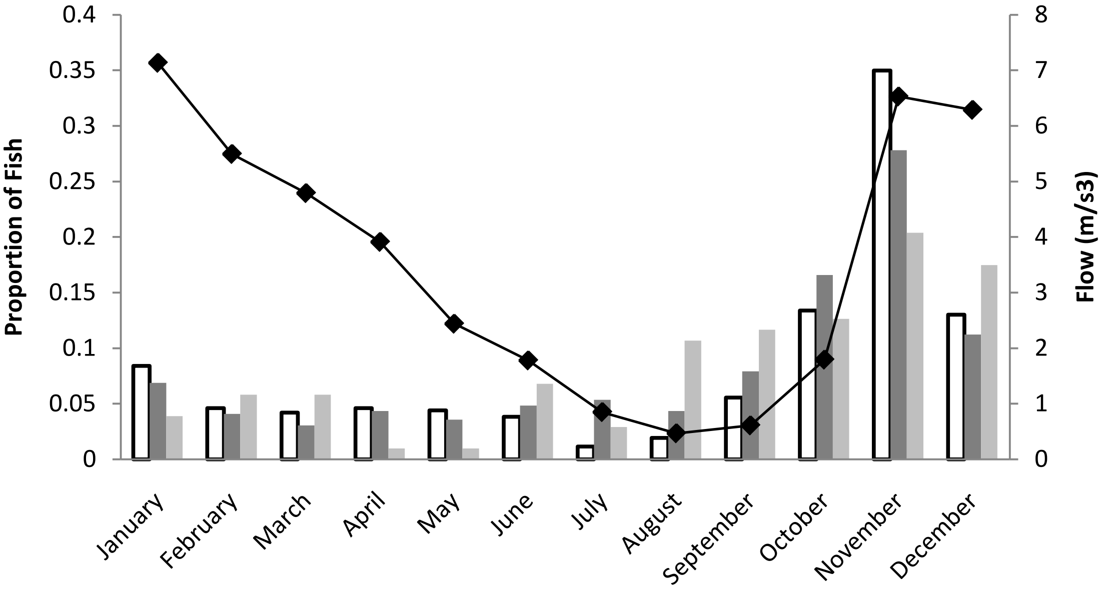

Proportion of Fish
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Flow (m/s3)
8
7
6
5
4
3
2
1
0
January
February
March
April
May
June
July
August
September
October
November
December

Figure 2.4

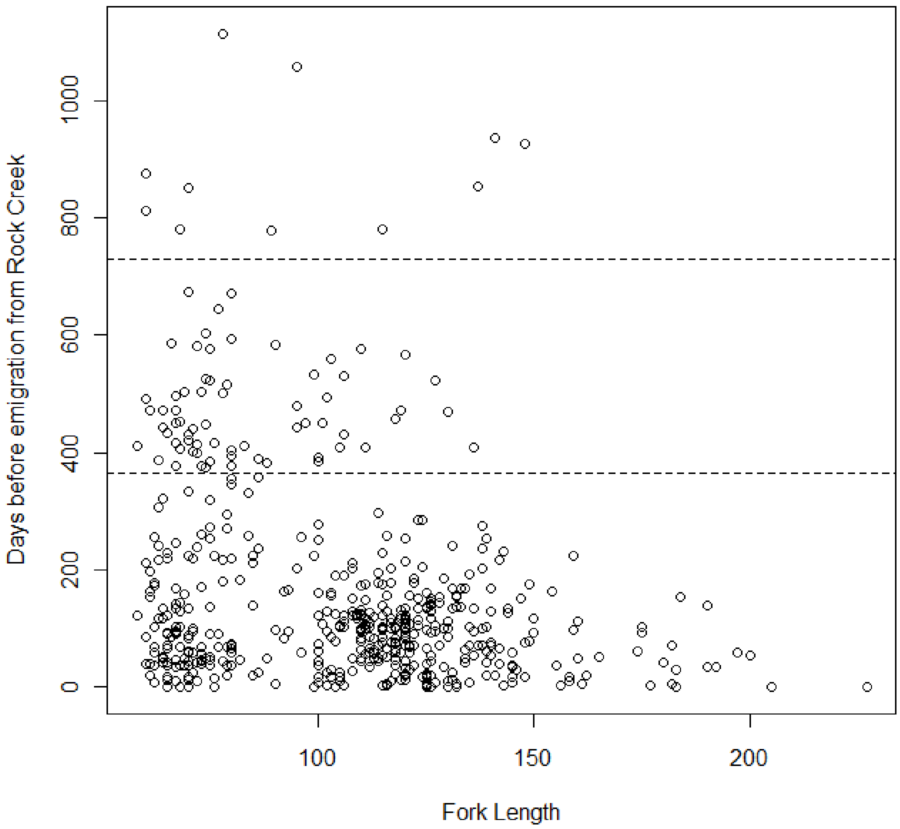

Days before emigration from Rock Creek
0
200
400
600
800
1000
100
150
200
Fork Length

Figure 2.5

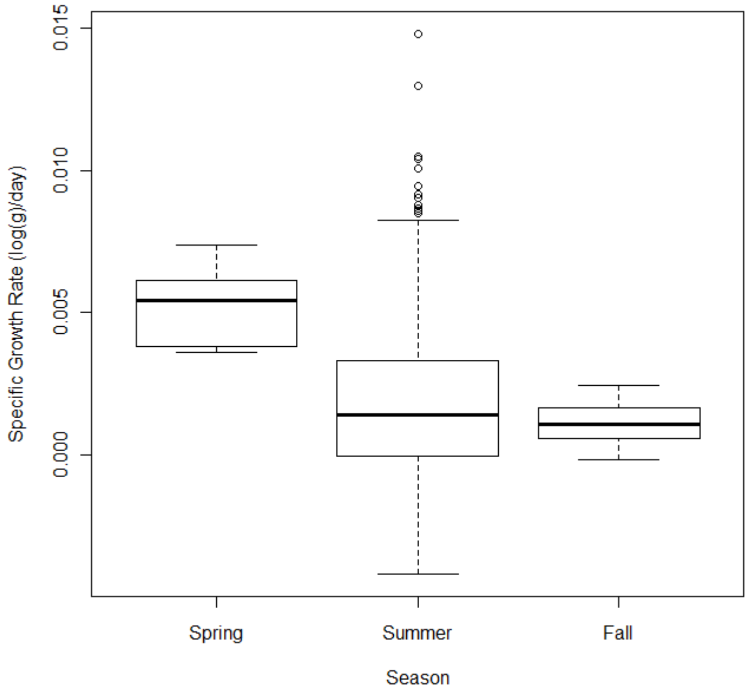
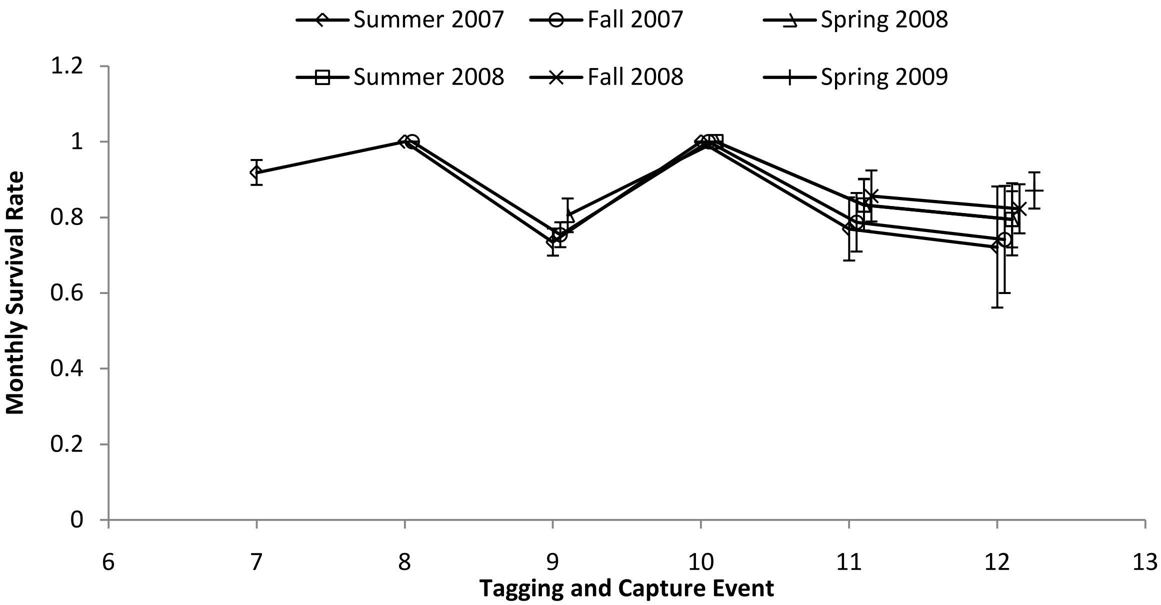

Specific Growth Rate (log(g)/day)
0.000
0.005
0.010
0.015
Spring
Summer
Fall
Season

Figure 2.6


Summer 2007
Fall 2007
Spring 2008
Summer 2008
Fall 2008
Spring 2009
Monthly Survival Rate
1.2
1
0.8
0.6
0.4
0.2
0
6
7
8
9
10
11
12
13
Tagging and Capture Event