Assessment of the causal linkages between forests and fish: implications for management and monitoring.

Kyle D. Martens

Kyle.martens@dnr.wa.gov

Oregon State University

College of Forestry

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Executive Summary

Understanding the causal links between riparian forests, streams, and salmonids is important to help understand the likely effects of forest management practices. Previous studies have identified three major causal pathways (Instream Cover, Light, and Hydrology) through which riparian forests influence streams, and ultimately stream fishes. To evaluate the potential importance of these pathways, I developed a conceptual model of how they can be described. From this I evaluated evidence in support of the influence of these pathways using available data on riparian forest, instream conditions, and size and abundance of age-1 or older coastal cutthroat trout.

These data were derived from monitoring conducted in 50 small watersheds across the 110,000 ha of lands managed by the Washington State Department of Natural Resources on the western Olympic Peninsula. The study domain was centered on the Olympic Experimental State Forest (OESF), where forest conditions primary represent previously harvested younger second growth forests (<80 years old). Additional monitoring data from 11 unharvested watersheds were added from the OESF (n=2), the Olympic National Park (n=4), and the Olympic National Forest (n=5) to increase the range of diversity of forest conditions in the sample. Overall the primary objective of this effort was to evaluate evidence in support of causal pathways through which forest

conditions influence streams and fish in the study area. Insights gained from this effort are intended to inform future monitoring and management within the OESF.

Results of analyses evaluating statistical relationships among available indicators provided support for all three of the pathways (Instream Cover, Light, and Hydrology) in the model as well as the presence of self-thinning (a density dependent process where fish reach an equilibrium between size and abundance) in age-1 and older cutthroat. Stream depth was one of the most important factors for age-1 or older cutthroat trout on the OESF. Overall, the support for the Light Pathway and instream wood of the Instream Cover Pathway were less important than expected. This may be due to the limited range of conditions in canopy coverage (all watersheds had heavy shading) and instream wood (potentially reduced volumes of wood throughout the OESF). The lack of watersheds with lower canopy cover, higher volumes of instream wood, and deeper stream depths may be an indication of the slow rate of recovery under passive restoration alone.

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Introduction

Interactions between forests, streams and salmonid fishes (salmon and trout) have long been a topic of investigation in Pacific Northwest ecosystems (Meehan 1991; Naiman and Bilby 1998; Northcote and Hartman 2008). Many studies have successfully attributed specific ecological responses (e.g., instream wood, canopy closure, and water availability) to forest management (Mellina and Hinch 2009; Kiffney et al 2004). Often multiple factors are influencing salmonids and any management that aims to influence a single factor without addressing the others may not produce desired outcomes. From an applied perspective, it is an understanding of mechanistic pathways that can best inform the myriad of decisions that forest managers face in balancing multiple objectives that include protection and restoration of fishery resources (Beechie et al. 2010).

Understanding the mechanistic pathways that link forests to streams and ultimately salmonids is challenging because fish can be influenced by multiple and sometimes confounding factors (Railsback et al. 2009). The current literature linking fish to forest management in Pacific Northwest streams has focused on three general causal pathways: Hydrology (e.g., stream discharge, surface area, and depths; Perry and Jones 2016), Light (e.g., riparian canopy density; Kaylor and Warren 2017), and Instream Cover (e.g., wood and boulders; Connolly and Hall 1999; Penaluna et al. 2015). Identifying the relative importance of these pathways would be valuable to managers to better understand how different management alternatives could lead to different outcomes and to better anticipate unintended outcomes or “surprises” (Hulse et al, 2016). In addition, many studies have found that fish can also be affected by density-dependent factors that could be important when considering interactions between fish and habitat (Rose et al. 2002). There are many potential ways in which hydrology, light, instream cover, and density dependence can interact to influence fish in streams (Figure 1). As depicted here, these represent different potentially interacting pathways through which forest practices influence forests, streams, and ultimately fish.

The hydrologic chain of causality can be particularly important during low-flow periods, especially in Mediterranean climates where rainfall can be largely absent for (typically summer months (Poff 1996). Smaller streams can become intermittent or experience highly reduced flows when temperatures are at their warmest (May and Lee 2004; Arismendi et al. 2013). These conditions are likely to negatively impact the capacity of streams to support fish. Instream conditions can also be affected by their surrounding riparian forests. Forests that consist of younger trees (typically found in second growth forests) have higher rates of transpiration than older trees (Moore et al. 2004) and have been found to further reduce low-flows periods in the summer (Perry and Jones 2016). As many forests of the Pacific Northwest are currently in this younger stage of development, Perry and Jones (2016) hypothesized this could be associated with widespread reductions in summer flows. These reductions could have a large impact on smaller streams, especially those that lose surface flows. Rolls et al. (2012) hypothesized that stream ecosystems are not affected by low flows until a certain threshold is reached in which negative effects start to occur. Since reduced summer flows are known to negatively impact juvenile salmonids (Berger and Gresswell 2009;

Penaluna et al. 2015; Ohlberger et al. 2018), preventing further reductions or improving summer stream flows could positively impact salmonids.

Light availability (Light Pathway) in streams is another way in which forest conditions can impact fish (Warren et al. 2016). Forest canopies regulate the amount of light available to streams. Second growth forests, which now dominate the landscapes of the Pacific Northwest, can limit the light available to streams and as a result stream productivity is reduced (Kiffney et al 2004; Kaylor et al. 2017). Older forests typically develop (>100 years) to a point where canopy gaps start to open up through competition and disturbance which increases the amount of light in streams (Franklin et al. 2002). In riparian areas where light is limited, increasing the amount of light in the canopy has been shown to be increase density and biomass in salmonids (Wilzbach et al. 2005; Wooten 2012). The amount of light available to streams has been suggested to be the dominant driver of salmonid and invertebrate production (Kaylor and Warren 2017).

Instream cover can regulate fish abundance and is driven by the surrounding environment. Use of fish cover is typically a trade-off between food availability and protection from predators and energy expenditure (Allouche 2002; Harvey and White 2017). Forests help regulate the physical structure of streams by constraining channels, stabilizing banks (which regulates sediment contributions to streams), and through active wood recruitment. Instream wood and sediment structure, typically in the form of boulders and large cobbles, are two common types of cover used by salmonids (Holecek et al. 2009). In addition to direct fish cover, instream wood can also increase the number and size of pools, and help regulate the amount and size of substrate in streams (Montgomery et al 2003). Salmonid declines have been attributed to reduced volumes of instream wood, often associated with past land management activities (McHenery et al. 1998; Fausch and Northcote 1992; Connolly and Hall 1999). The physical characteristics of streams (e.g. channel form, substrate, and instream cover), especially in combination with reduced flows, can be an important factor controlling salmonid biomass (Penaluna et al. 2015).

Forest stage and ultimately stream conditions affect salmonid species and life histories differently. Age-1 and older coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) are likely to be one of the species/age classes most negatively affected by management practices since even anadromous forms typically spend multiple years in freshwater (Wydoski and Whitney 2003). Surface water levels in streams likely affect the abundance of age-1 and older cutthroat trout in streams. As water lowers during the summer, cutthroat trout are either forced to move or become more susceptible to competition for resources and predation. This lowers the carrying capacity of streams (Rolls et al. 2012). Alternatively, as fish get larger they need more food and may favor more productive areas of a watershed (Gowan et al. 1994; Hughes and Grand 2000). If resources are not available these fish likely perish or move (McMahon et al. 2006).

Beyond habitat, the size of the fish in a stream can also affect fish densities through density-dependent processes. The presence of larger fish in streams can limit the number of smaller fish through a process termed self-thinning (Grant and Kramer 1990; Bohlin et al. 1994; Dunham and Vinyard 1997; Harvey and Nakamoto 1997). Under self-thinning population density equilibrates between the size of fish and the amount of fish in a given area. In watersheds with lower food production the equilibrium will be lower and result in a reduced carrying capacity. An example of self-thinning can be found in years with low recruitment, in these years the existing population will either experience increased growth and/or reduced mortality to meet the equilibrium of the site (Bohlin et al. 1994). Overall, both density-dependent and density-independent factors are important for regulating salmonid populations (Honkanen et al. 2019). Therefore both salmonid and stream indicators are needed to fully understand the complex interactions between forests and fish.

In this paper, I use information from watersheds draining highly managed forests as well as a set of unharvested watersheds to evaluate three hypothesized causal pathways (Hydrology, Light, and Instream Cover) and the concept of self-thinning on age 1+ coastal cutthroat trout in a conceptual model (Figure 1). Developing a greater understanding of the importance of these causal pathways can help assure that the desired outcomes for forest, stream and fish population management. Results of this evaluation will provide relevant information on coastal cutthroat trout population dynamics, habitat differences between higher capacity self-thinning watersheds and lower capacity density-independent watersheds, the importance of the causal pathways alternative, and help direct future monitoring and research.

Methods

Background

The Olympic Experimental State Forest (OESF) is a working forest designated to use experimentation to better integrate revenue production (primarily through timber harvesting) and ecological values (primarily habitat conservation; WADNR 2016). Many of the forest practice guidelines for DNR-managed lands in the OESF were established in 1997 as part of the State Lands Habitat Conservation Plan (HCP) and updated through the OESF Forest Land Plan in 2016 (WADNR 1997; WADNR 2016). While DNR policy allows for some forest harvest and thinning in riparian areas, most streams have been left to recover through passive restoration (the use of natural processes of succession and disturbance to alleviate anthropogenic impacts over time). Overall, the HCP allows for certainty in conducting timber harvests while simultaneously protecting sensitive species. In 2012, DNR initiated habitat monitoring through its Status and Trends Monitoring of Riparian and Aquatic Habitat in the Olympic Experimental State Forest program (STRAH) and in 2016 salmonid monitoring through its Riparian Validation Monitoring Program (RVMP). The RVMP, a requirement in the HCP, was designed to evaluate the cause-and-effect relationships between DNR forest management, stream and riparian habitat, and salmonids.

Study Area

The OESF includes approximately 110,000 ha of state lands on the western Olympic Peninsula (Figure 2). The boundaries follow the Olympic Mountain crest as well as the West Twin Creek and Lake Crescent watersheds to the east, the Strait of Juan de Fuca to the north, the Pacific Ocean to the west, and the Quinault River Watershed to the south. Elevations within the OESF range from sea level to 1,155 m. The OESF is a coastal rain forest that receives heavy precipitation (203 to 355 cm per year) with the majority falling in the winter. The OESF contains a diversity of the forests within three vegetation zones (Franklin and Dyrness 1988). The majority of the OESF is within the western hemlock zone (*Tsuga heterophylla*; 150 to 550 m elevation), while the lower elevations (0 to 150 m) are in a Sitka spruce zone (*Picea sitchensis*) and the upper elevations (550 to 1,155 m) are in the Pacific silver fir zone (*Abies amabilis*). DNR-managed forests with the OESF mostly consist of second growth forests as a result of the prior timber harvests with only 19% of the forest older than 100 years as of 1995 (WADNR 1997).

DNR-managed lands contain over 4,300 km of streams including portions of several major rivers such as the Queets, Clearwater, Hoh, Bogachiel, Calawah, Sol Duc, Dickey, Hoko, and Clallam (WADNR 2013). The smallest fish-bearing streams (stream order 1-3; Strahler 1957) typically have some combination of juvenile coho salmon (*Oncorhynchus kisutch*), rainbow trout/steelhead (*O. mykiss*), coastal cutthroat trout, lampreys (*Lampetra spp.*) and/or sculpins (*Cottus spp.*). Coastal cutthroat trout are the most commonly found salmonid species within these smaller streams (Martens 2016).

Approach

DNR's STRAH and RVMP were designed to monitor and track changes in conditions (riparian forests, streams, and salmonids) as a result of DNR management. To accomplish this, DNR monitors 50 of the 244 (20%) smaller watersheds (range 31-789 ha) of the OESF (Figure 2). Watersheds were selected through a randomized stratification design based on the median slope of the watershed and balanced to ensure that all areas of the forest were represented. Six of the original 50 samples were removed from the sample due to the lack of surface waters or fish absence above an obvious physical barrier (e.g. waterfall or a section with subsurface flows). In addition, since most of the 50 watersheds have a majority of the watershed that has been harvested at least once (range 27% to 100%; median 83%), eleven watersheds were added that have likely never been harvested in the OESF (n=2), nearby Olympic National Park (n=4), or National Forest (n= 5). This was done to expand the range of conditions and better understand the effects of DNR management on habitat and salmonids. These watersheds have only experienced natural disturbances and are primarily in the older stages of forest development (range 81 to 100%; median 99%). Sampling occurred in one reach per watershed. The reaches were approximately 100-m in length and located near the streams terminus.

Fish Sampling

Juvenile fish sampling was designed to be completed within one day to maximize the amount of watersheds that could be sampled in a summer. The RVMP calls for twenty of the OESF watersheds to be sampled annually with the remaining watersheds to be sampled on a two-year rotation. Fish sampling used a variable pass (3 to 6 passes) form of multiple pass-removal. This method ensures that all estimates are worthwhile and prevents wasted efforts from population estimates with large confidence intervals.

Some methods of multiple-pass removal have been found to underestimate fish populations (Rosenberger and Dunham 2005; Peterson et al. 2004), however this underestimation can be minimized (Saunders et al. 2011). Increasing the number of passes can reduce the underestimation (Rosenberger and Dunham 2005) while simultaneously lowering the standard error (Connolly 1996). Using the variable-pass method should reduce the underestimation and improve the quality of the estimates by increasing the number of passes when needed. In addition, the variation between watersheds and years is expected to be large enough that the need for more watersheds will likely outweigh any potential accuracy issues created through the use of multiple-pass removal sampling (Larsen et al. 2004; Meyer and High 2011). Poorten et al. (2017) recommended the use of multiple-pass removal electrofishing over single-mark recapture sampling, since single-mark recapture typically takes longer to sample (typically two days which would reduce the sample size in half) and also suffers from accuracy issues when assumptions are violated (which are difficult to determine when using a single-recapture event).

Before initiating electrofishing, seine nets were placed at the top and bottom of a reach to block fish movement. After a reach was blocked, a Smith-Root model 24b backpack electrofisher (https://www.smith-root.com) was used to collect fish with a forward and backward pass through the reach. Electrofishing was typically conducted using a frequency of 20 hertz with 10% duty cycle and voltage ranging from 300 to 600 volts. All sites were sampled with a minimum of three passes and up to six passes. The number of passes were determined through the charts of Connolly (1996) and used as described in Martens and Connolly (2014). All salmonids were anesthetized with MS-222, visually inspected, measured and weighed, and released. Fish population estimates were calculated using the program MARK (Cooch and White 2012) and extrapolated over the length and area of the reaches.

Habitat Sampling

After all passes were completed, a stream habitat survey was conducted. The habitat survey identified habitat units based on the field guide of Minkova and Vorwerk (2015) and measured the lengths, widths and depths of each unit. Additional habitat data were taken from the STRAH, or derived through GIS. Indicators for water depth, stream area, and habitat units were collected during habitat surveys conducted after electrofishing. Data on stream temperature, stream-bed substrate, instream wood, gradient, canopy cover, and riparian forests were taken from the STRAH program. The protocols for collecting these indicators are described in Minkova and Foster (2017). Watershed area and the percent of the watershed consisting of second-growth forests were derived through GIS analysis using ESRI's ArcMap (https://www.esri.com/en-us/home).

Metrics

Twenty metrics were calculated for potential analysis. Three fish metrics were calculated and included: the density of age-1 or older cutthroat trout per square meter (fpm^2), the density of coho salmon (fpm^2) and the average body size of cutthroat trout (mm). Four metrics were calculated to assess stream depth. The stream depth metrics were maximum depth (cm) in a reach, stream depth in non-pool habitat units (cm), average stream depth in pools (cm) and bankfull width to depth ratio. The accumulation of growing season degree days (March through September) was calculated to assess the effect of stream temperatures on cutthroat trout. Five metrics were calculated to assess instream cover including measures of boulders and instream wood. The percentage of boulders included the percent of substrate between 25-399 cm. The four measures of wood included: the number of pieces of wood instream (>10 cm diameter and 1 m length) per 100 meters, key piece density (>45 cm diameter and 1 meter length), the volume of wood per 100 meter and the volume of key pieces per 100 meter. Reach gradient was used as a measure of watershed characteristics. Measures of riparian conditions included stream measurements of closure, riparian measures of forest size and composition, and a watershed measurement of forest age. The stream metrics consisted of the percent of forest canopy was covering the stream (canopy closure). The riparian forests metrics (with 20 meters of the stream) included, the basal area in conifers (m^2/ha), basal area in hardwoods (m^2/ha), and percent of the basal area that consists of hardwoods. Two metrics were derived through GIS (the percent of second growth forest and watershed area). The percent of the watershed with forest less than 88 years of age was calculated to determine the amount of second growth forest in the watershed and watershed area (ha) was calculated as measure of watershed size.

Statistical Analysis

All statistical tests were considered significant at an alpha of 0.05 (Murtaugh 2014). Since the RVMP did not sample all watersheds each year, a linear regression (Fish density [fpm^2] ~ year + average body size [abs] + year*abs) was conducted in the program R (R core team 2013) using the package glm2 to determine whether the data could be combined between years. Since there was no year effect (t = -0.127, P = 0.90), data from 2017 was combined with 2018. If a watershed was sampled in both 2017 and 2018 only data from 2017 was used. A Mantel test was then conducted to determine if there was spatial autocorrelation between fish densities (fpm^2) and the location of the watersheds (Manly 2006). The Mantel test was conducted in the program R using the mantel function in the ecodist package.

To assess whether cutthroat trout on the OESF had a self-thinning relationship between fish size and density, I conducted a series of nonlinear quantile regressions (Cade and Noon 2003). Quantile regressions for the 10th, 25th, 50th, 75th and 90th quantiles were conducted in R using the rq function in the quantreg package. The response variable (fish density) was log-transformed to create non-linear regressions. Watersheds with no age-1 or older cutthroat trout but with other salmonids present (n=6), were removed from the dataset since the zeros skewed the fit of the first two (10th and 25th) quantile regressions. Next, I conducted Pearson and Spearman correlations in Sigma Plot (Systat Software Inc, Chicago IL) between the cutthroat trout watershed capacity, through the use of residuals from the five quantile regressions and 19 potential habitat and 1 salmonid (coho per m^2) metrics. The correlations looked at the importance of each metric in relationship to the size/density residuals and helped to determine the most appropriate metrics for evaluating the conceptual model. Two groups were then created using watersheds with positive residuals from the 75th quantile regression (higher-capacity watersheds) and watersheds with negative residuals from the 25th quantile regression as well as watersheds with no age-1+ cutthroat trout but other salmonids present (density-independent watersheds). The two habitat groups were then compared (watershed comparison) using twelve habitat metrics thought to impact salmonids. Data were compared using either a t-test if the data had a normal distribution or a Mann-Whitney U-test if it did not.

To assess the three pathways in the conceptual model, I used the residuals from the 50th quantile regression (watershed capacity) as the response variable and conducted a series of multiple regression models using six predictor variables. Predictors were limited to six due to the smaller sample size (n=48) and to prevent over parameterization. The predictor variables were determined by their assumed importance to the causal pathways in the conceptual model. The data were standardized by dividing each metric by the relevant range of the data as suggested by Grace and Bollen (2015). In addition the data used in the full model were tested and passed for assumptions of normality, constant variance, and multicollinearity. Akaike's Information Criterion, corrected for smaller samples sizes, (AICc) model ranking was used to determine which pathway or combination of pathways were having the most impact on salmonid populations. All models within two AICc units of the top model were assumed to have substantial support and considered to be impacting salmonids. Models over three AICc units from the top model were considered to have less support and were thought to be of less importance for age-1 or older cutthroat trout (Burnham and Anderson 2003).

Results

There was no yearly effect (*t* = -0.13, *P* = 0.900) or spatial autocorrelation (*r* = 0.10, *P* = 0.143) for fish densities in the dataset. The self-thinning relationship between fish density (fpm2) and average body size (mm) increased as the quantiles increased (Figure 3). The lowest two quantile regressions (10th and 25th) did not have a significant relationship (10th Quantile, *t-value* = -1.53, *P* = 0.133; 25th Quantile, *t-value* = -1.81, *P* = 0.077) between fish density and body size indicating that fish in these watersheds were not subjected to self-thinning. All other quantile regressions showed a significant relationship (50th, *t-value* = -2.14, *P* = 0.038; 75th, *t-value* = -3.07, *P* = 0.004) with the 90th quantile having the strongest relationship (*t-value* = -7.17, *P* = <0.001).

The Pearson correlations with the 50th quantile regression showed positive relationships between the self-thinning residuals with percent boulders (*r* = 0.36, *P* = 0.014) and gradient (*r* = 0.50, *P* = <0.001) and negative correlations with the percent of the watershed in second growth (*r* = -0.32, *P* = 0.026) and bankfull width to depth ratio (*r* = -0.28, *P* = 0.053). The Spearman correlation had positive relationships between the 50th quantile self-thinning residuals and stream depth in non-pools (*r* = 0.29, *P* = 0.048), % boulders (*r* = 0.34, *P* = 0.021) and gradient (*r* = 0.52, *P* = <0.001). The Spearman correlation found negative relationships with the percent of watershed in second growth forest (*r* = -0.39, *P* = 0.006), bankfull width to depth (*r* = -0.29, *P* = 0.045), and coho density (*r* = -0.54, *P* = <0.001). The results of all of the correlations between the quantile regression residuals and the metrics used in the AIC analysis can be found in Appendix Tables 1 and 2.

Stream depth in non-pools, stream temperature, percent boulders, instream wood volume, and gradient had significant differences in our watershed comparison between the higher-capacity and density independent watersheds (Figure 4). Stream measures of % second growth forest, watershed area, canopy closure, maximum stream depth, bankfull width to depth ratio and instream stream key piece density were not significantly different. The average stream depth in non-pools was higher (*t* = -3.31, *P* = 0.003) in the higher-capacity watersheds (mean depth = 11.30 cm) when compared to the density independent watersheds (mean depth = 6.72 cm). Stream temperature was lower (*U* = 31.0, *P* = 0.005) in higher-capacity watersheds (mean GSDD = 2,068 days) when compared to the density independent watersheds (mean GSDD = 2,171 days). The percent of boulders in the reach was higher (*t* = -2.82, *P* = 0.008) in the higher-capacity watersheds (mean = 15.7%) compared to the density independent watersheds (mean = 6.6%). Instream wood (*U* = 70.0, *P* = 0.023) was higher in the higher-capacity watersheds (mean = 42.6) than in the density independent watersheds (mean = 29.9 and 20.19). Finally, gradient was higher (*U* = 31.0, *P* = <0.001) in the higher-capacity watersheds (mean = 9.3 %) when compared to the density independent watersheds (mean = 3.9%).

Fifty-nine regression models using combinations of six variables were used to help evaluate the conceptual model. Six models were found within two AICc units of the top model indicating there was substantial support for these models (Table 1). All of the six models contained stream depth while five models contained gradient. The percent of the watershed in second growth forest (three of the six models) and boulders (three of the six models) were the next most common variables. Canopy closure (the model with the highest AICc score with a Delta AICc less than 2) was the only other variable found in the top models. Wood volume was not found within any of the top models.

Within the stratified random sample of watersheds, all but one of the OESF watersheds contain over 40% of their forest in second growth condition (Figure 5). When the OESF sites were included with the 11 unharvested watersheds (0-27%), there are only two watersheds (19 and 27%) within 10-40% of the watershed in second growth forests.

Discussion

Self-thinning and Habitat Condition

Age-1 or older cutthroat trout populations in the small streams of the OESF showed a pattern that is consistent with the process of self-thinning when an unknown threshold of habitat was present. The self-thinning relationship was significant in the upper quantiles (50th, 75th, 90th) but not in the lower quantiles (10th and 25th) and increased over each quantile. Presumably, this is the result of influences of underlying factors that limit fish density (Cade et al.1999). For salmonids in streams, self-thinning is thought to be a function of density dependence where either food or space limits the capacity of the stream (Chapman 1966; Milner et al. 2003). While self-thinning has been found in some populations of salmonids, others populations are limited by density independent factors, such as temperature (Keeley 2003). It would appear that the lower capacity watersheds are being regulated through density independent factors. As the limiting factors (habitat) improve, the capacity of the stream will be higher allowing for some combination of more or larger fish. Therefore, the degree of self-thinning may be a good indicator of a how a watershed is functioning. This idea is supported by the work of Rosenfeld (2014) who suggested that the patterns of self-thinning could be useful for determining habitat limitations within streams.

With density independent factors potentially limiting age-1 or older cutthroat trout in the lower-quantile watersheds, the question becomes what factor could be the most limiting for age-1 or older cutthroat trout in these watersheds? Indicators for stream depth, instream wood, stream temperature, boulders and gradient were all significantly different when comparing the density independent watersheds to the higher-capacity watersheds. These indicators have also been found to be important for salmonids within other studies. The deeper stream depths in non-pool habitats in the higher-capacity watersheds is consistent with the findings of Heggenes et al. (1991) that found that coastal cutthroat trout had a strong preference for deeper streams. Higher densities of wood volumes in the higher-capacity watersheds was also not surprising as the benefits of instream wood for salmonids has been well documented (Rosenfeld et al. 2000; Roni and Quinn 2001; Mellina and Hinch 2009; Roni et al. 2015). In addition, the importance of having cooler water temperatures is supported by the findings of Berger and Greswell (2009) that found cooler water temperatures increased and warmer waters decreased survival between 2.7-17.3 °C. The importance of boulders as cutthroat trout cover was also documented in both Andersen (2008) and Berger and Gresswell (2009). Overall, my findings are corroborated by other studies that have looked at the connections between cutthroat trout and their environments, and provides additional support for the conceptual model (Figure 1).

Reach gradient could be more of an indirect indicator of different habitat characteristics (such as boulders or deeper pockets of waters) than an indicator of a specific habitat quality (Bisson et al. 2017). Gradient was higher in the higher-capacity watersheds (9.3%) when compared with the density-independent watersheds (3.9%). This may be due to habitat and/or species competition. Some evidence in support of both hypothesis can be found in the correlation data as boulders were typically found in areas with higher gradients and cutthroat trout had higher abundances in areas with fewer juvenile coho salmon. However, Rosenfeld et al. (2000) found that both juvenile coho salmon and cutthroat trout densities were highest in reaches with gradients between 0-5%. The authors were unsure if the preference for lower gradient streams was due to increased areas of spawning gravels, lower extreme flows, or instream wood. Therefore, if cutthroat trout densities are typically highest in lower gradient watersheds, lower gradient watersheds on the OESF may have insufficient levels of instream wood or spawning gravels. The cause of lower cutthroat trout capacities in low gradient streams in the OESF should be further explored.

Evaluation of the Conceptual Model

Most aspects of the conceptual model (Figure 1) could be examined through my analyses. The self-thinning relationship between body size and fish density appears to be strongest when habitat is not limiting but breaks down if habitat is limiting. Since evidence of self-thinning appears to some degree in a number of the watersheds, the use of both fish size and abundance in the conceptual model seems to be appropriate.

Instream Cover Pathway

The Instream Cover Pathway assess the importance of boulders and instream large wood on fish populations (Figure 1). Correlations showed support for gradient and boulders, but not tree size or instream wood volume. Watershed comparisons showed support for gradient, boulders, and instream wood volume. Gradient appears to be one of most important predictors (along with stream depth) for cutthroat trout as it was in five of the top AICc models. Boulders were present in three of the six top models while wood was not found in any of the models. It was mildly surprising that wood volume did not appear in any of the top models as it is often thought of one of the most important aspects of salmonid habitat and is often a target for active restoration (Roni et al. 2015). Gradient and boulders were the only two metrics of the Instream Cover Pathway that were supported in all three analyses. Overall, the three analyses support the importance of the Instream Cover Pathway in the conceptual model (via wood or boulders).

Questions remain whether instream wood or boulders are better habitat for coastal cutthroat trout. The model ranking did not find wood in any of the top models and it was not significantly correlated with the self-thinning residuals, but wood volumes were significantly higher in the watershed comparison. The lack of support for wood in the correlations and AICc model ranking appears to go against most of the common thought on the importance of instream wood for salmonids. This suggests that instream wood is not as important to cutthroat trout as other salmonids or that instream wood levels within the OESF were insufficient to evaluate the full range of potential conditions.

There is some evidence that the unharvested watersheds do not meet the full range of conditions that would be present in the OESF prior to large-scale anthropogenic modifications. An uneven portion of the unharvested watersheds are from higher gradient streams and/or may be from more mature forests (100-200 years) rather than old growth forests (>200 years). Forest succession typically increases light availability and wood recruitment after 200-350 years (Franklin 2002). In a separate analysis of instream wood on the OESF that included four of the unharvested sites in this study, Martens et al. (2019) found that the OESF sites had significantly lower densities and volumes of wood than the reference conditions found in Grette (1985). In addition, the unharvested watersheds wood densities and volumes were not significantly different from those of the OESF watersheds. The unharvested sites used in this comparison had higher average gradients (11.3%) when compared to the reference sites in Grette (1.2%) and the OESF watersheds (3.1%). Therefore, the similar numbers between the current unharvested and OESF watersheds may highlight the limited range of unharvested conditions in the sample.

It is unlikely that wood is not important to cutthroat trout since others studies have documented the benefits of wood for coastal cutthroat trout (Fausch and Northcote 1992; Connolly and Hall 1999; Rosenfeld et al. 2000). Andersen (2008) in a study conducted in a second growth forest, also found that boulders were the most commonly used form of cover for coastal cutthroat trout, and that availability of instream wood was very low. This could be attributed to widespread reductions of instream wood due to previous timber harvest practices (Miller 2010). Similarly, the OESF is a working forest where most of the forests are in second growth due to a long history of extensive forest harvests. In addition, Harvey et al. (1999) found that cutthroat trout without adequate cover commonly moved into habitats with larger boulders. They also found that the cutthroat trout that used boulders moved more often while cutthroat trout inhabiting areas with instream wood were less likely to move. This suggests that while cutthroat trout will use boulders for cover, they may have a preference for instream wood. So while watersheds with higher amounts of boulders had higher densities of cutthroat trout on the OESF, this may be due an overall lack of cover, especially wood, in the lower gradient streams of the OESF.

It could also be that boulders in higher gradient streams are a naturally substitutable type of instream cover for wood in lower gradient streams. Gradient has been found to be negatively associated with instream wood accumulations (Fox and Bolton 2007; Wohl and Cadol 2011). This negative association is likely due to a higher probability of wood movement in higher gradients when compared to lower gradient streams. If wood and boulders were substitutable, this could explain the presence of gradient and boulders in the top models and the lack of importance of instream wood from lower gradient streams. The importance of cover types at higher and lower gradients for cutthroat trout should be further examined.

Light Pathway

The Light Pathway that hypothesizes that primary productivity is limiting fish populations through bottom up controls had the least amount of support of any of the pathways (Figure 1). Canopy closure was not correlated with the self-thinning residuals or different in the watershed comparison. In addition, canopy closure was only found in one of the six models with substantial support. This suggests that canopy closure was at least somewhat important to cutthroat trout. Since other studies have documented that heavy canopy coverage levels limit overall salmonid biomass (Kaylor and Warren 2017) and there was some support for this hypothesis in the analysis, it is likely that increased levels of shading from second growth forests is limiting salmonid productivity. Overall, there was not a lot of variation between canopy closure within the sites (83-95%). The median for the OESF watersheds and unharvested watersheds was 92.5 and 91.9% respectively. This supports the hypothesis that the dataset does not have enough variation to truly assess the impact of more open canopies on fish production.

As is, the question remains whether the current levels of canopy shading differ from pre-settlement conditions and if those differences are currently negatively impacting salmonids. The current group of unharvested watersheds suggests canopy coverage in the OESF watersheds are similar to those in areas that have been never been harvested. Since large areas of old growth are thought to exist on the OESF prior to large-scale forest harvests (WADNR 2016) and old growth forests are known to allow more light into streams (Warren et al. 2016), it is likely that the unharvested sample does not have a similar range in light availability than what existed historically. In addition, results of this study contrast with the findings of Kaylor and Warren (2017) who had a median of 22.4% canopy openness (the inverse of closure) in old growth reaches and 8.4% in second growth reaches. The median canopy closure (91.65%) in the second growth sites from the Kaylor and Warren study is similar to the median value of my sites on the OESF (92.5%) and in the unharvested watersheds (91.9%). The median canopy closure for old growth forests in the Kaylor and Warren study was 77.6% and 77.0% in another study conducted in the nearby Olympic National Park (Hatten and Conrad) while the lowest watershed in the OESF had a 83.3% canopy closure. The similarity in results in mostly second growth forests and the contradicting findings between the Kaylor and Warren's old growth sites and my unharvested sites show that the unharvested sites may be lacking an old-growth component. Due to concerns with the limited range of data in the study, the full importance of the Light Pathway may not be fully assessed in my analysis. Future studies should be conducted to better evaluate the importance of the Light Pathway on salmonids of the OESF. Questions that still need to be addressed should include what is the historical range of canopy closure and whether the current levels of canopy closure are negatively impacting salmonids?

Hydrology Pathway

The Hydrology Pathway assesses the role that water depths have in streams and on fish populations (Figure 1). The percent of second growth forest and stream depth were positively correlated with the self-thinning residuals, but not with watershed area. In the watershed comparison, steam depth was significantly higher than the density-independent watersheds but there was no difference in the percentage of second growth forest or in watershed area. Overall, we found no support that watershed area was important in the conceptual model. Stream depth was found in all six of the AICc models, so it was one of the most important factors for determining the age-1 or older cutthroat trout capacity of watershed. The amount of second growth forest in the watersheds was also found in four of the top six models with substantial support. However, the percentage of second growth forest in the watershed was not correlated with stream depth (Pearson $r = -0.12$, $P = 0.419$) suggesting that while both metrics may be important, the pathway between the two metrics may not be important.

The lack of relationship between second growth and stream depth could be due to the scale or location of these metrics (reach vs watershed). Stream depth is collected near the bottom of the watershed, while the second growth forest can occur anywhere in the watershed. If transpiration is a large driver of water depth in streams, the proximity of the second growth forest to the stream may be important. Riparian forests historically had similar ages as upland forests, but changes in management practices that preserve riparian forests while allowing for forest harvests in the uplands are creating an ever-increasing amount of age-differences between riparian and upland forests. It may also be possible that the percentage of second growth within the riparian forest, rather than the whole watershed, would be a better metric for relating second growth forests to stream depth.

It is not clear whether the metric for second growth forests is the best metric for the Hydrology Pathway. Interpretation of any mechanism through an observational study is tenuous, since the link between the cause and effect are not controlled as in an experimental study. The metric for second growth forests, may be representing an accumulation of human disturbances in the watersheds (e.g. road density is likely to be higher in watersheds with more second growth forests) rather than the direct effect of younger forests on streams. If this were the case, it may explain why there was no correlation between second growth forest in the watershed and stream depth. While the role of forest transpiration on water depth is still unclear, the Hydrology Pathway appears to be one of the more important drives for age-1 or older cutthroat trout on the OESF. Questions remain whether low stream depths on the OESF are caused by increased transpiration in younger forests (the result of historical large-scale forest harvests), reduced structure in streams (lack of instream wood), natural variability between watersheds, climate change, or some combination of these factors. Overall, this pathway should be further explored to separate the impact of anthropogenic changes in water depth from natural variations.

Conclusions

One of the biggest problems associated with large-scale monitoring programs is how to interpret the findings (Nichols and Williams 2006). To fully understand current conditions that have resulted from anthropogenic influences, it is important to understand the full-range of conditions that would have existed without historical large-scale anthropogenic disturbances. To address this issue we added eleven unharvested watersheds, though the sample appears to have a limited range of conditions. Only one of the watersheds had between 20-40% of the watershed in second growth forests (Figure 5), and the unharvested sample may be disproportionately bias towards higher gradient watersheds and mature forests (100-200 years old) rather than old growth forests (>200 years old). The absence of a full range of potential conditions may have reduced the importance of both canopy cover and instream wood in the analyses.

A portion of the watersheds of the OESF appear to be limiting age-1 or older cutthroat trout through density-independent processes rather than density-dependent self-thinning. It is currently unclear how many watersheds were historically regulated through density-independence processes and how many (if any) are degraded due to anthropogenic influences. If limiting habitat conditions within these watersheds improve, the capacity of the watersheds are likely to increase which is also likely to increase the role of density dependence within the watersheds.. As such, the degree of self-thinning may be a useful indicator of watershed condition and has potential for tracking watershed change over time.

The conceptual model may be just as important for identifying what was not found to be important than what was found to be important. The absence of watersheds with lower levels of canopy coverage and potentially higher volumes of instream wood in lower gradient streams may be an indication of the timeline for recovery. Studies have suggested that passive recovery for restoring salmonid populations could take a 100 years or more (McHenry et al. 1998; Connolly and Hall 1999; Kaylor et al. 2017). Given the current conditions (after 20 years of recovery) and the typical timeline for forest recovery under passive restoration, management approaches that combine both active and passive management could be explored to expedite salmonid recovery.

To accelerate salmonid recovery, management should incorporate a landscape approach that creates a diversity in forest conditions. Creating a diversity of habitats, known as the portfolio concept, can help reduce the risk of single events having large effects on a population (Schindler et al. 2015). Pollock and Beechie (2014) suggested that management strategies that create a range of conditions would hedge against unforeseen negative outcomes (e.g. disturbances or unexpected species needs). To maximize diversity in the short-term (<100 years) it is likely that a combination of active and passive restoration is needed. The most successful forms of active restoration would address all three of the pathways (Hydrology, Light, and Instream Cover). For example, riparian thinning that directs a proportion of the larger trees in the stream (tree-tipping) could be employed to address all of the pathways (Benda et al. 2016). This approach would increase light in the stream, instream cover, and potentially stream depth (instream wood can alter flows in streams which could create deeper water; Montgomery et al. 2003). If pathways are ignored, managers risk spending limited resources on costly recovery actions that may not produce the intended results or maximize recovery efforts.

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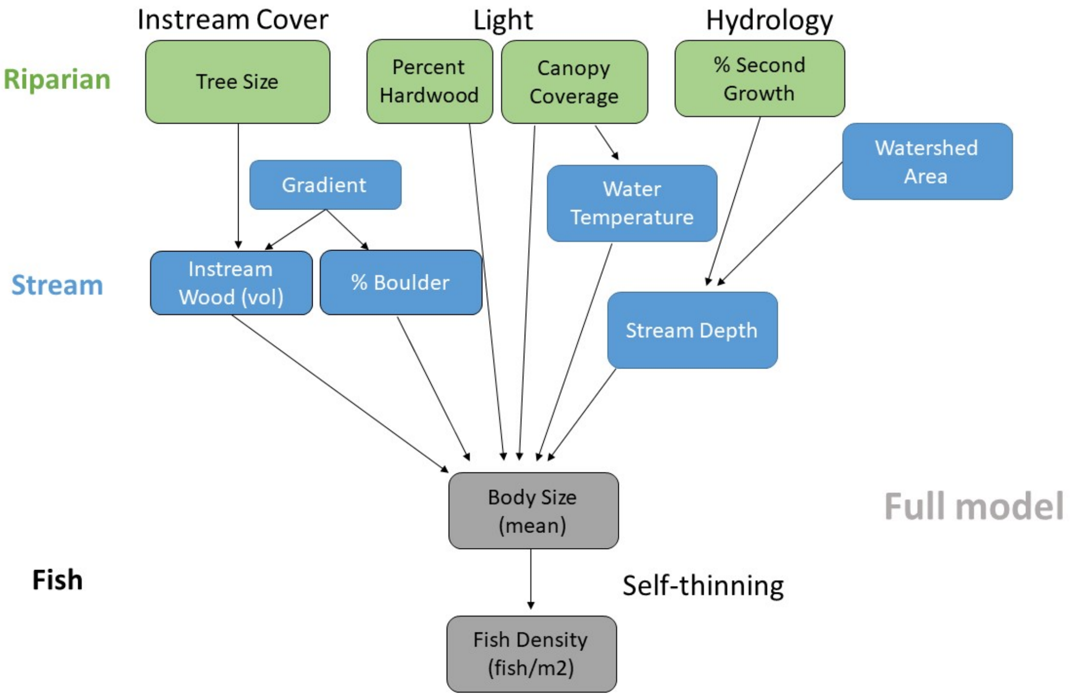

Figure 1. Conceptual model of riparian forests, stream and salmonids interactions.

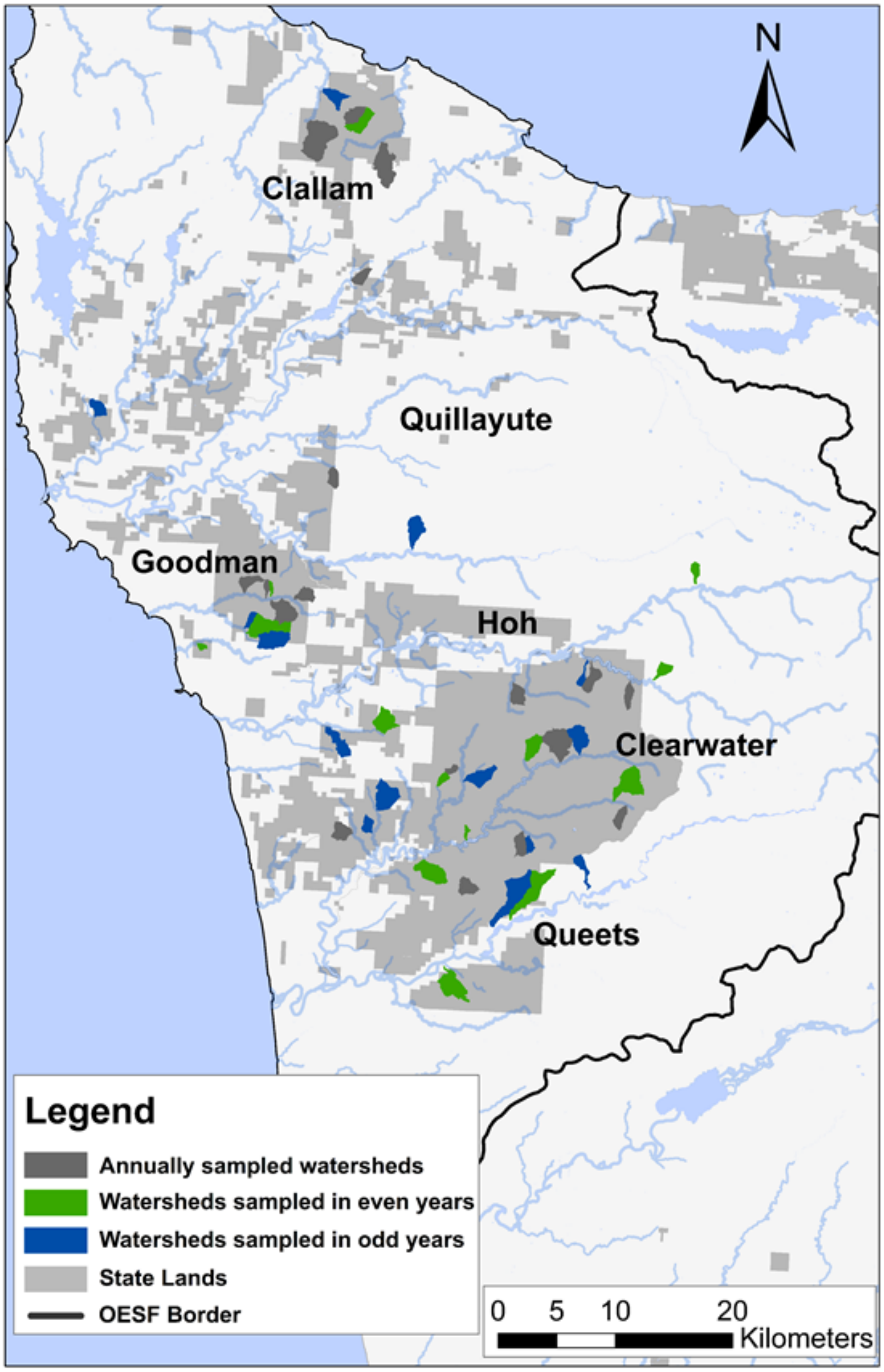

Figure 2. Map of OESF state managed lands and sample watersheds.

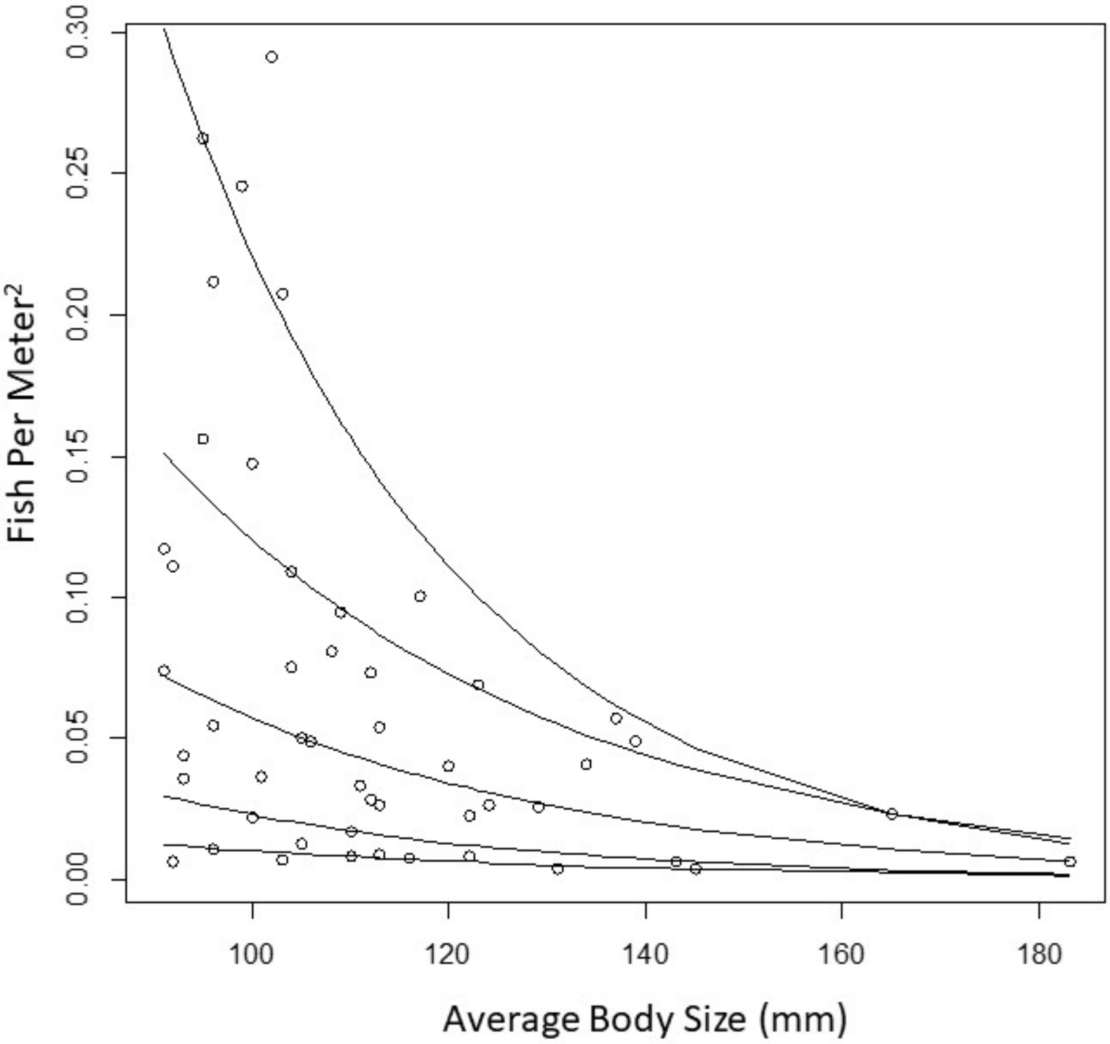

Figure 3. Quantile Regressions (10th, 25th, 50th, 75th and 90th Quantiles) for the relationship between fish density (fish/m^2) and average body size (fork length).

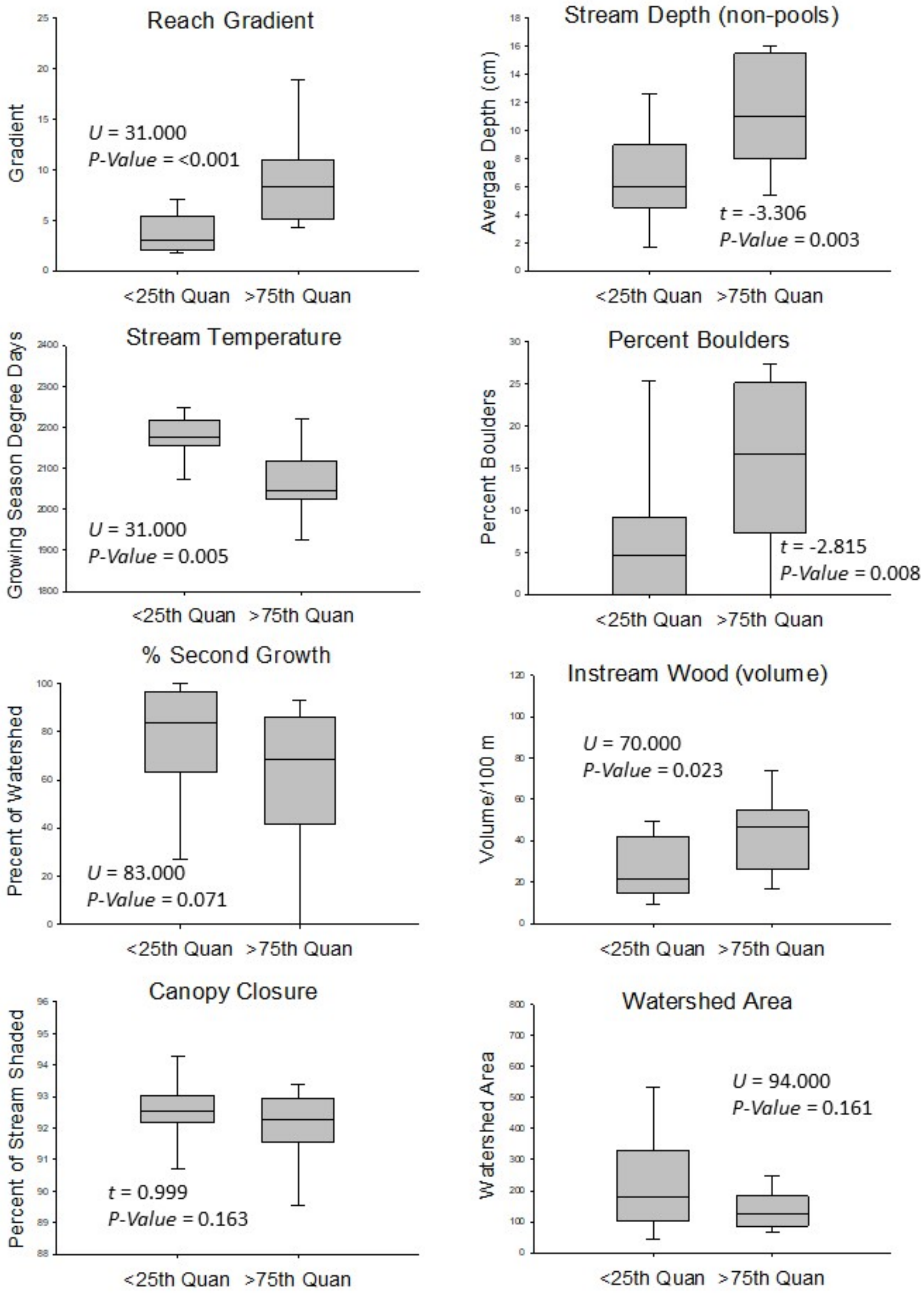

Figure 4. Comparison of watersheds with relatively high numbers of fish (watershed with residuals >75th quantile of a self-thinning regression) and relatively low numbers of fish (watersheds with residuals <25th quantile).

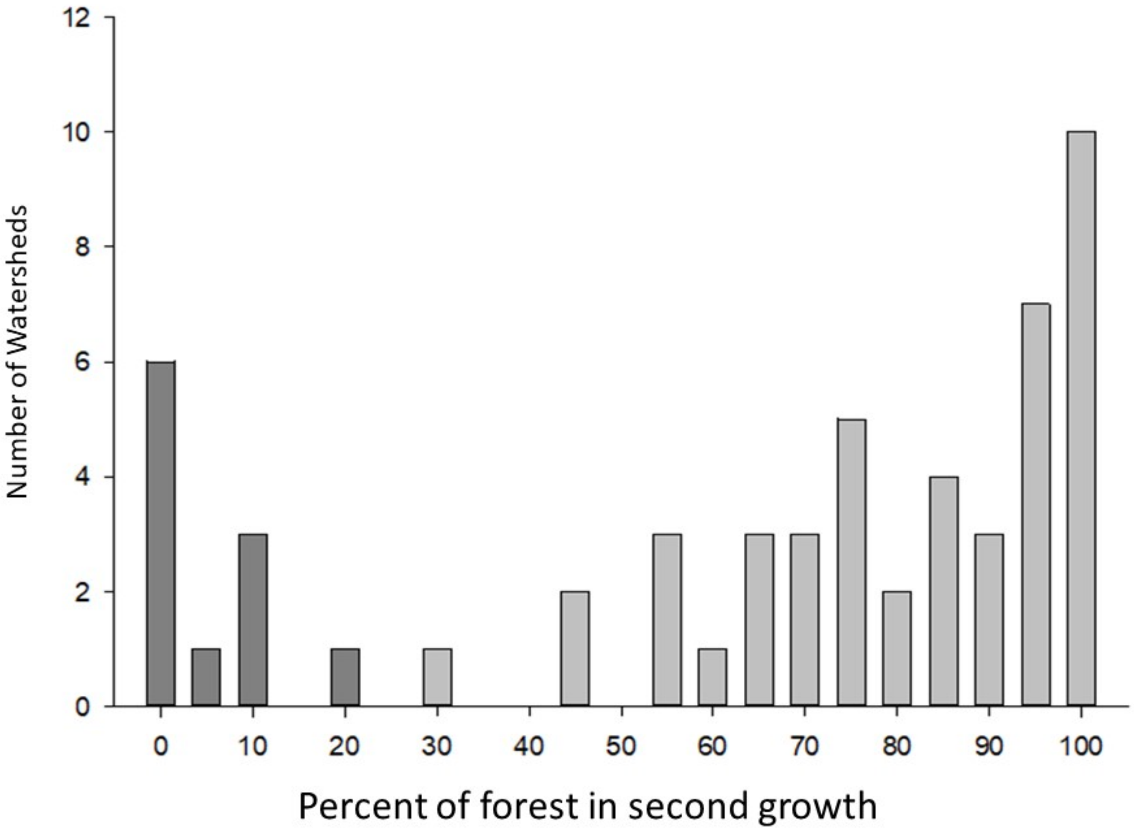

Figure 5. The percent of watersheds within the OESF with forest less than 88 years (Second growth forest) as selected through a random stratification design to represent the smallest fish-bearing streams. The dark grey bars represents the unharvested watersheds, while light grey bar represent the random stratified samples of watersheds on the OESF.

Table 1. Multi-model selection results from the top 20 of the 59 multiple linear regression models for predicting the residual relationship between age-1 or older cutthroat trout through habitat metrics found in the conceptual model. *Canopy = Percent of canopy coverage, Depth = The average depth in non-pool habitat units, 2Growth = The percent of the watershed that is <88 years, Bould = Percent of stream substrate that consists of boulders, Wood = The volume of instream wood, and Grad = stream gradient.*

Model	*K*	*AICc*	*Delta AICc*	*AICc Weight*
Depth + Grad	*4*	*126.84*	*0*	*0.12*
Depth + 2Growth +Bould + Grad	*6*	*126.90*	*0.1*	*0.12*
Depth + 2Growth + Bould	*5*	*127.23*	*0.4*	*0.10*
Depth + Bould + Grad	*5*	*127.27*	*0.4*	*0.10*
Depth + 2Growth + Grad	*5*	*127.76*	*0.9*	*0.08*
Canopy + Depth + Grad	*5*	*128.31*	*1.5*	*0.06*
Canopy + Depth + Bould + Grad	*6*	*129.07*	*2.2*	*0.04*
Canopy + Depth + 2Growth + Bould + Grad	*7*	*129.10*	*2.3*	*0.04*
Depth + Wood + Grad	*5*	*129.33*	*2.5*	*0.04*
Canopy + Depth + 2Growth + Grad	*6*	*129.45*	*2.6*	*0.03*
Depth + 2Growth + Wood + Bould + Grad	*7*	*129.57*	*2.7*	*0.03*
Canopy + Depth + 2Growth + Bould	*6*	*129.80*	*3.0*	*0.03*
Depth + 2Growth + Wood + Bould	*6*	*129.88*	*3.0*	*0.03*
Depth + Wood + Bould + Grad	*6*	*129.90*	*3.1*	*0.03*
Depth + 2Growth + Wood + Grad	*6*	*130.34*	*3.5*	*0.02*
Canopy + Depth + Wood + Grad	*6*	*130.90*	*4.1*	*0.02*

Appendix Table 1. Pearson (top) and Spearman (bottom) Correlations of the Quantile Regressions (Alpha = **.05** AND .10). The upper number is the r-value and lower is the P-value.

Residuals	Stream Depth (zmax)	Stream Depth (non pools)	Stream Depth (mean pool)	Stream Temp. (GSDD)	% Bould	Instm Wood	Key wood	Wood vol	Key vol	Grad	Can Cov	Basal Area conif	Basal Area (hrd)	% BA (hrd)	% 2nd growth	WS Area	Bankfull W:D	Coho fpm2
10th	0.098 0.515	0.268 0.072	0.129 0.393	-0.230 0.158	**0.348** **0.017**	-0.223 0.127	-0.025 0.866	0.164 0.267	0.190 0.197	**0.495** **<0.001**	-0.076 0.608	-0.091 0.546	-0.101 0.503	-0.103 0.497	**-0.313** **0.030**	-0.196 0.182	**-0.306** **0.034**	-0.238 0.103
25th	0.113 0.454	0.272 0.068	0.139 0.356	-0.235 0.149	**0.351** **0.015**	-0.227 0.120	-0.027 0.857	0.167 0.258	0.193 0.189	**0.499** **<0.001**	-0.082 0.578	-0.090 0.551	-0.106 0.483	-0.109 0.473	**-0.317** **0.028**	-0.188 0.201	**-0.295** **0.0417**	-0.247 0.090
50th	0.130 0.389	0.276 0.064	0.151 0.317	-0.241 0.140	**0.356** **0.014**	-0.231 0.113	-0.029 0.846	0.170 0.248	0.197 0.180	**0.503** **<0.001**	-0.090 0.545	-0.089 0.558	-0.111 0.461	-0.115 0.446	**-0.321** **0.026**	-0.178 0.225	**-0.282** **0.053**	-0.257 0.077
75th	0.132 0.382	0.276 0.063	0.152 0.313	-0.241 0.139	**0.356** **0.014**	-0.232 0.113	-0.029 0.845	0.170 0.247	0.197 0.180	**0.503** **<0.001**	-0.090 0.541	-0.089 0.558	-0.112 0.459	-0.116 0.444	**-0.322** **0.026**	-0.177 0.228	**-0.280** **0.054**	-0.259 0.076
90th	0.189 0.208	0.285 0.055	0.190 0.206	-0.257 0.115	**0.363** **0.012**	-0.243 0.096	-0.036 0.809	0.179 0.223	0.207 0.159	**0.507** **<0.001**	-0.115 0.438	-0.082 0.588	-0.129 0.393	-0.137 0.365	**-0.331** **0.022**	-0.141 0.340	-0.228 0.120	**-0.290** **0.046**

Residuals	Stream Depth (zmax)	Stream Depth (non pools)	Stream Depth (mean pool)	Stream Temp. (GSDD)	% Bould	Instm Wood	Key wood	Wood vol	Key vol	Grad	Can Cov	Basal Area conif	Basal Area (hrd)	% BA (hrd)	% 2nd growth	WS Area	Bankfull W:D	Coho fpm2
10th	0.019 0.899	**0.306** **0.039**	0.138 0.358	-0.286 0.077	**0.326** **0.026**	-0.081 0.583	-0.005 0.972	0.261 0.073	0.246 0.092	**0.513** **<0.001**	-0.109 0.460	-0.149 0.322	-0.039 0.794	-0.005 0.972	**-0.376** **0.009**	-0.185 0.206	**-0.296** **0.041**	**-0.522** **<0.001**
25th	0.031 0.839	**0.292** **0.049**	0.136 0.367	-0.294 0.070	**0.326** **0.026**	-0.094 0.522	-0.009 0.949	0.260 0.074	0.245 0.093	**0.513** **<0.001**	-0.100 0.500	-0.149 0.321	-0.043 0.774	-0.009 0.953	**-0.392** **0.006**	-0.188 0.200	**-0.288** **0.047**	**-0.520** **<0.001**
50th	0.052 0.730	**0.293** **0.048**	0.151 0.316	-0.311 0.054	**0.336** **0.021**	-0.100 0.499	-0.001 0.993	0.270 0.063	0.253 0.083	**0.516** **<0.001**	-0.104 0.479	-0.138 0.358	-0.065 0.665	-0.030 0.843	**-0.392** **0.006**	-0.183 0.211	**-0.290** **0.045**	**-0.535** **<0.001**
75th	0.054 0.723	**0.293** **0.049**	0.151 0.316	-0.311 0.054	**0.337** **0.021**	-0.102 0.490	-0.004 0.981	0.270 0.064	0.252 0.084	**0.518** **<0.001**	-0.107 0.468	-0.139 0.357	-0.063 0.678	-0.028 0.855	**-0.389** **0.007**	-0.184 0.211	**-0.285** **0.049**	**-0.535** **<0.001**
90th	0.112 0.457	**0.292** **0.049**	0.180 0.229	-0.306 0.058	**0.326** **0.026**	-0.112 0.408	-0.008 0.959	**0.297** **0.041**	0.271 0.062	**0.496** **<0.001**	-0.149 0.310	-0.129 0.392	-0.089 0.556	-0.050 0.738	**-0.402** **0.005**	-0.145 0.325	-0.242 0.098	**-0.542** **<0.001**

Appendix Table 2. Pearson (top) and Spearman (bottom) correlations of the metrics used in the AICc analysis. The upper number is the r-value and lower is the P-value.

	Stream Depth (non-pools)	% boulders	Wood Volume	Gradient	Canopy Cover	% second growth
Stream depth (non- pools)		0.489 <0.001	0.394 0.007	0.199 0.186	-0.460 0.001	-0.122 0.419
% boulders			0.247 0.095	0.534 <0.001	-0.180 0.227	0.116 0.439
Wood Volume				0.271 0.062	-0.159 0.280	-0.170 0.249
Gradient					-0.239 0.102	-0.282 0.052
Canopy Cover						0.064 0.664

	Stream Depth (non-pools)	% boulders	Wood Volume	Gradient	Canopy Cover	% second growth
Stream depth (non- pools)		0.524 <0.001	0.396 0.007	0.262 0.079	-0.257 0.084	-0.201 0.179
% boulders			0.343 0.019	0.636 <0.001	0.026 0.859	-0.003 0.985
Wood Volume				0.403 0.005	-0.275 0.059	-0.259 0.076
Gradient					-0.015 0.921	-0.280 0.054
Canopy Cover						0.137 0.350