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Evaluating Coexistence of Fish Species with Coastal Cutthroat Trout in Low Order Streams of Western Oregon and Washington, USA

Kyle D. Martens [1,*] and Jason Dunham [2]

[1] Washington Department of Natural Resources, 1111 Washington Street SE, Olympia, WA 98504, USA
[2] U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA; jdunham@usgs.gov
* Correspondence: kyle.martens@dnr.wa.gov

Abstract: When multiple species of fish coexist there are a host of potential ways through which they may interact, yet there is often a strong focus on studies of single species without considering these interactions. For example, many studies of forestry–stream interactions in the Pacific Northwest have focused solely on the most prevalent species: Coastal cutthroat trout. To examine the potential for interactions of other fishes with coastal cutthroat trout, we conducted an analysis of 281 sites in low order streams located on Washington's Olympic Peninsula and along the central Oregon coast. Coastal cutthroat trout and juvenile coho salmon were the most commonly found salmonid species within these streams and exhibited positive associations with each other for both presence and density. Steelhead were negatively associated with the presence of coastal cutthroat trout as well as with coho salmon and sculpins (Cottidae). Coastal cutthroat trout most frequently shared streams with juvenile coho salmon. For densities of these co-occurring species, associations between these two species were relatively weak compared to the strong influences of physical stream conditions (size and gradient), suggesting that physical conditions may have more of an influence on density than species interactions. Collectively, our analysis, along with a review of findings from prior field and laboratory studies, suggests that the net effect of interactions between coastal cutthroat trout and coho salmon do not appear to inhibit their presence or densities in small streams along the Pacific Northwest.

Keywords: Cutthroat trout; coexistence; coho salmon; steelhead; presence; density; headwaters; stream gradient; stream size

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1. Introduction

Many studies of stream fishes involve consideration of just a single species or just a small fraction of the total species assemblage, though it is well-known that interactions within these assemblages can be important [1,2]. A case in point is the host of studies involving influences of forestry on streams and fishes in the Pacific Northwest, USA. In this region, highly valued salmonids are the focus of much policy and research to understand how they are influenced by land management practices [3,4]. With respect to the question of forestry and fish [5–7], the salmonid most often considered is the coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). This is likely because, among Pacific Northwest salmonids, coastal cutthroat trout predominates in smaller streams [8,9] and such streams comprise a vast majority of the length of streams [10].

Although coastal cutthroat trout are more prevalent in smaller streams in the Pacific Northwest, they share these habitats with a host of other species, including congeneric salmonids, especially steelhead (*O. mykiss*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*), as well as sculpins (*Cottus*, sp.), which are often numerically dominant when present [9]. These species can interact ecologically in numerous ways throughout the life cycle, and in the case of steelhead, hybridization is also a possible interaction [11]. Given the number of interactions that are possible among these species, it is impossible to fully consider them in any single analysis. Furthermore, interactions may be dependent on abiotic interaction modifiers [12], lending additional complexity to the problem. In this study, we take initial steps to evaluate the importance of co-occurring fishes in Pacific Northwest streams to address the presence and density of coastal cutthroat trout. Our intent is not to delve deeply into single or multiple sets of processes explaining species coexistence, but rather to evaluate associations as a first approximation of the net effect of these processes on realized occurrence and density of coastal cutthroat trout.

To evaluate associations between coastal cutthroat trout with other fish species we used observations of species presence and fish density (fish/m^2) collected in low-order (4th order or smaller) streams draining coastal forests of the Pacific Northwest USA. We began by quantifying patterns of co-occurrence and prevalence in relation to major environmental gradients. Following this analysis, we evaluated associations between the density of coastal cutthroat trout and coho salmon (the most commonly found salmonids) in more detail, also considering the influences of stream size, stream gradient, and body size of coastal cutthroat trout as covariates in linear models to predict density of both species. Collectively, the results of this work provide insights into how net outcomes from a host of potential interactions and resource selection by these two species result in complementary (allotopic) distributions or density within streams.

2. Results

Four salmonid species, sculpin, and less commonly juvenile lampreys (primarily *Lampetra* spp.) and longnose dace (*Rhinichthys cataractae*) occurred in the study area. coastal cutthroat trout were the most prevalent salmonid followed by coho salmon. Steelhead were found in a much lower percentage of sites (29% in the Siuslaw National Forest (SNF); 18% in the Olympic Experimental State Forest (OESF)) while Chinook salmon were found in 8% of the SNF sites and not found in the OESF (Table 1). Sculpin, the only common non-salmonid, was found in 61% of the sites in the SNF and 73% of the sites in the OESF. All species were more likely to occur at lower stream gradient sites and were less likely to occur as gradients increased (Figure 1).

Table 1. Stream gradient (%) and occurrence of fish encountered in surveys conducted on the Siuslaw National Forest (SNF, n= 226) and Olympic Experimental State Forest (OESF, n= 55). CTT = coastal cutthroat trout, COH = coho salmon, STH = steelhead, CHN = Chinook salmon, SCP = sculpin, NP = not present.

	CTT		COH		STH		CHN		SCP	
	SNF	**OESF**	**SNF**	**OESF**	**SNF**	**OESF**	**SNF**	**OESF**	**SNF**	**OESF**
Min	0.3	1.3	0.3	1.3	0.7	1.7	0.8	NP	0.3	1.3
Mean	6.8	5.7	3.7	3.6	5.2	6.7	2.8	NP	5.2	3.9
Median	6.8	4.5	3.2	3.2	4.3	4.5	1.7	NP	3.7	3.3
95TH %	17.8	16.3	8.9	7.1	12.5	–[a]	–[a]	NP	11.9	8.5
Max	23.9	21.1	11.9	7.1	15.4	21.1	11.1	NP	17.6	16.1
Occurrence (%)	97	93	42	51	29	18	8	NP	61	73

[a] Sample was too small to calculate a 95th percentile.

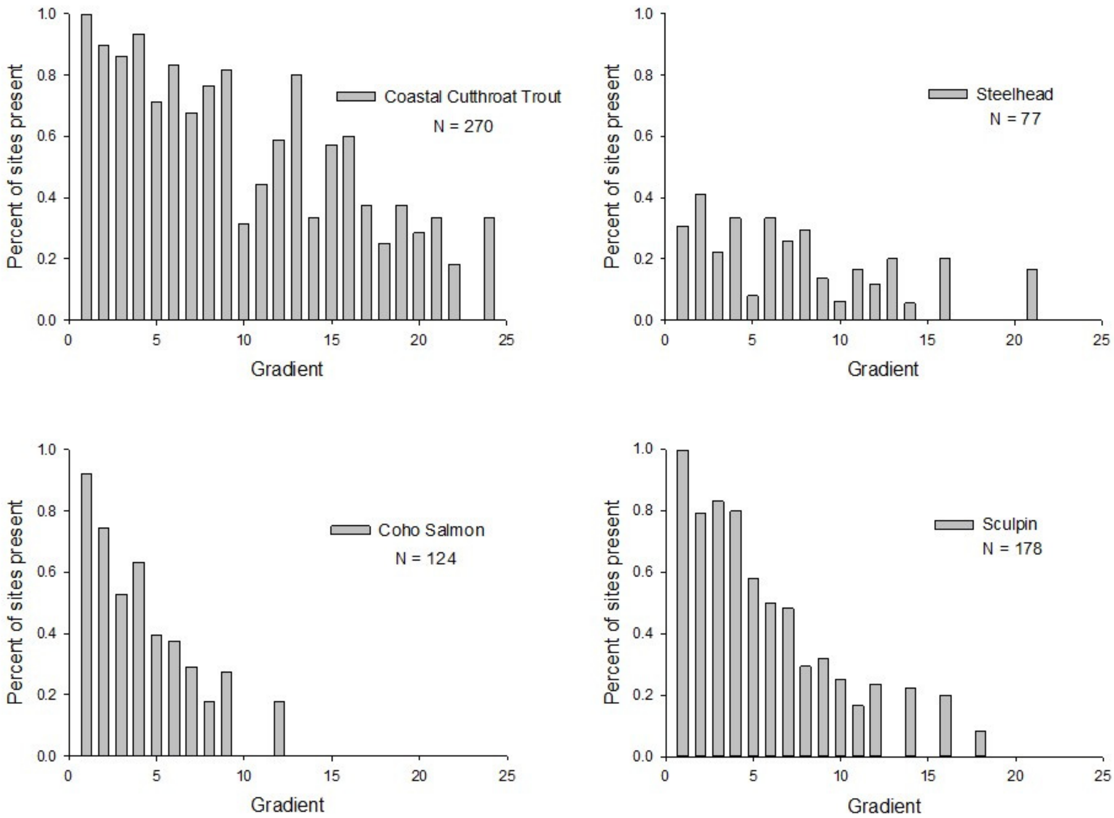

Figure 1. The percent of sites by stream gradient (%) that the most commonly found species (coastal cutthroat trout, coho salmon, steelhead, and sculpin) were encountered on the Olympic Experimental State Forest and Siuslaw National Forest.

Among common fishes in low-order streams in our study systems, coastal cutthroat trout and steelhead occupied the widest range of stream gradients (<1 to 24%). Coho salmon occurred in sites with stream gradients below 11.9% with a median stream gradient of 3.2%. Within lower stream gradient headwater streams (<9%) where coastal cutthroat trout, coho salmon, steelhead, and sculpin often occurred together, and tests for species co-occurrence indicated strong ($p < 0.001$) associations between all species. Associations were positive between coho salmon, coastal cutthroat trout, and sculpin; whereas steelhead was negatively associated with the other three species (Figure 2). No species had a random association. No other species was present frequently enough to determine species associations.

Linear regression models to predict density (fish per square meter) of coastal cutthroat trout ranked seven candidate models using different combinations of biological and physical covariates. The most likely model contained two physical covariates (wetted width and stream gradient) and accounted for 59% of the AICc weight (Table 2). In this model, increasing wetted width was associated with reduced density of coastal cutthroat trout, whereas stream gradient was positively associated with density (Appendix A). The second model, the only alternative with substantial support, contained wetted width, stream gradient, and coho salmon density. In this model, increasing coho salmon density was associated with decreased density of coastal cutthroat trout. This contrasted with a single covariate model where coastal cutthroat trout density had a positive but weak association with coho salmon density ($R^2 = 0.041$; $p = 0.047$; Figure 3). In this instance, the addition of the habitat covariates appears to affect the relationship between the two species. Single-covariate models ranked wetted width as the most important covariate followed by stream gradient and finally coho salmon density.

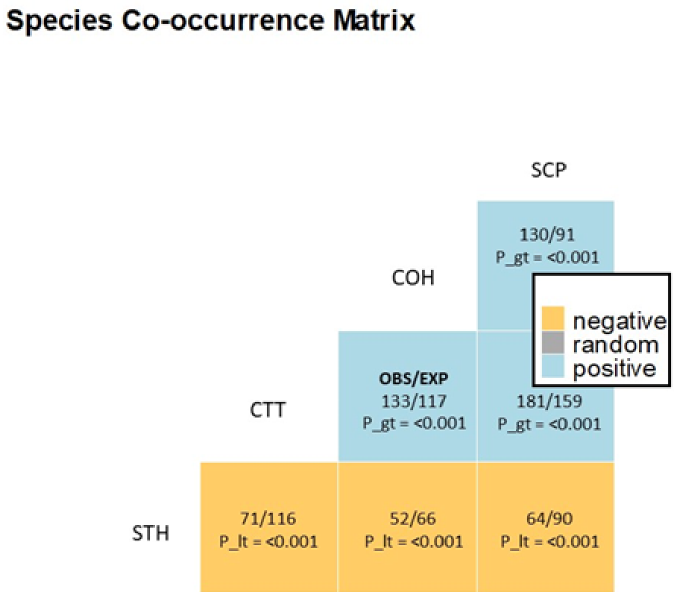

Figure 2. The probability that two species exhibit a positive or negative association within with less than 9% steam gradients. Within each cell the number of observations (OBS) and the number of expected (EXP) occurrences in these streams is indicated. Species codes are as follows: SCP = sculpin, COH = coho salmon, CTT = coastal cutthroat trout, STH = steelhead, P_lt = the probability that two species would be present at a frequency less than expected if the two species were distributed randomly, P_gt = the probability of two species co-occurring at a frequency greater than expected if the two species were distributed randomly.

Table 2. Results of applying model selection to evaluate alternative models of factors influencing coastal cutthroat trout densities in watersheds in SNF and the OESF in watersheds with less than 9% steam gradients. Models within 2 ΔAIC units of the top-ranked model have substantial support and are in bold. CTT = coastal cutthroat trout density (fpm2), COH = coho salmon density (fpm2), WW = wetted width (m), GRAD = stream gradient (percent), ABS = Average body size of coastal cutthroat trout (fork length, mm).

Model	K	AICc	ΔAICc	AICcWT	Cum WT	LL
CTT = WW + GRAD	**4**	**−744.58**	**0.00**	**0.59**	**0.59**	**376.39**
CTT = COH + WW + GRAD	**5**	**−743.33**	**1.25**	**0.32**	**0.90**	**376.82**
CTT = COH*ABS + WW + GRAD	7	−740.70	3.88	0.08	0.99	377.65
CTT = WW	3	−736.61	7.97	0.01	1.00	371.37
CTT = GRAD	3	−712.08	32.50	0.00	1.00	359.80
CTT = COH*ABS	3	−707.28	37.30	0.00	1.00	358.80
CTT = COH	3	−694.05	50.53	0.00	1.00	350.09

Linear regression models to predict density of coho salmon indicated that five out of the nine candidate models tested within two ΔAICc units of the most likely model (Table 3). The most likely model contained wetted width, stream gradient, and the average body size of coastal cutthroat trout and contained 24% of the AICc weight. In this model, increasing wetted width and average body size of coastal cutthroat trout were associated with decreased density of coho salmon, whereas decreasing stream gradient was associated with increased density. In the next most likely model, increasing coastal cutthroat trout density in correspondence with stream gradient, width and average body size was associated with decreased density of coho salmon. Models with single covariates ranked stream gradient as the most important covariate followed by average body size of coastal cutthroat trout, coastal cutthroat trout density, and finally wetted width. Stream gradient was in the top four ranking models. Wetted width, despite being the least important covariate of the single covariate models, was in the two most likely models and three out of the four most likely models. It occurred more frequently within models with substantial support than coastal cutthroat trout density or average body size.

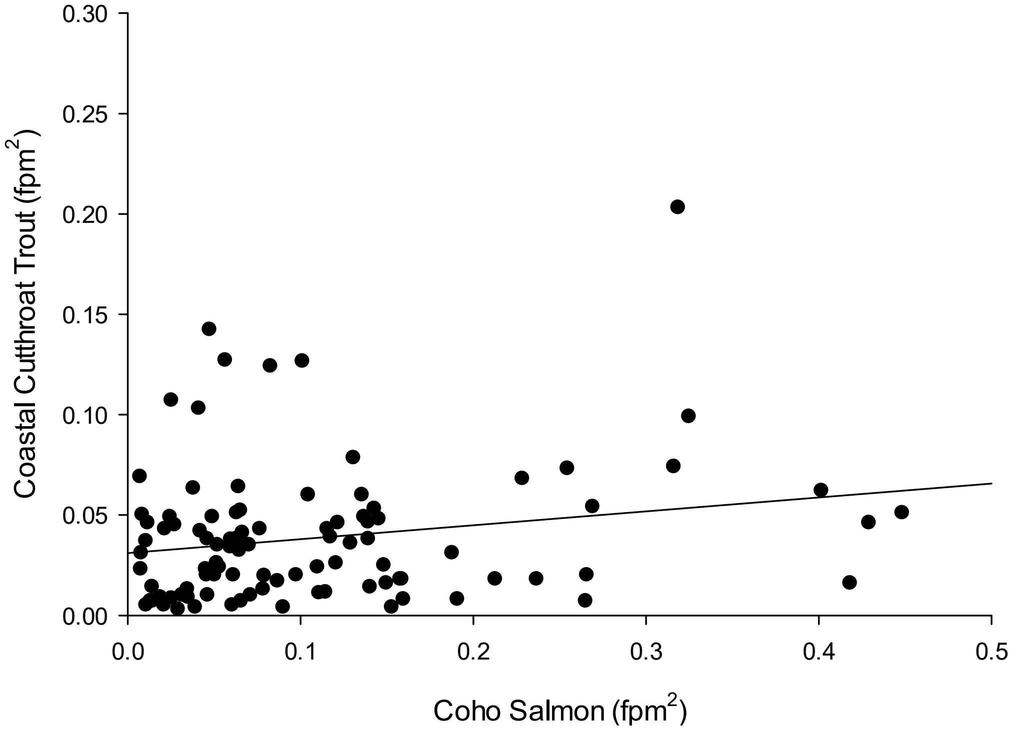

Figure 3. The relationship between fish per meter squared of coastal cutthroat trout and coho salmon when both species were present in streams with less than 9% stream gradient. Sites without coastal cutthroat trout or coho salmon were removed for this analysis. Regression line is presented for visual aid only.

Table 3. Model selection of factors influencing coho salmon densities in watersheds in SNF and the OESF in watersheds with less than 9% steam gradients. Models within 2 ΔAIC units of the top-ranked model have substantial support and are in bold. CTT = coastal cutthroat trout density (fpm2), COH = coho salmon density (fpm2), WW = wetted width (m), GRAD = stream gradient (percent), ABS = Average body size of coastal cutthroat trout (fork length, mm).

Model	K	AICc	ΔAICc	AICcWT	Cum WT	LL
COH = ABS + WW + GRAD	**5**	**−397.50**	**0.00**	**0.24**	**0.24**	**203.91**
COH = CTT + ABS + WW + GRAD	**6**	**−396.55**	**0.95**	**0.15**	**0.39**	**204.49**
COH = GRAD	**3**	**−396.38**	**1.12**	**0.14**	**0.53**	**201.25**
COH = WW+ GRAD	**4**	**−396.28**	**1.22**	**0.13**	**0.66**	**202.24**
COH = CTT + ABS	**4**	**−396.05**	**1.45**	**0.12**	**0.78**	**202.13**
COH = ABS	**3**	**−395.89**	**1.61**	**0.11**	**0.88**	**201.01**
COH = CTT + WW + GRAD	5	395.03	2.47	0.07	0.95	202.67
COH = CTT	3	−392.85	4.65	0.02	0.98	199.49
COH = WW	3	−392.77	4.73	0.02	1.00	199.45

3. Discussion

Spatially segregation or negative pairwise associations of densities of species can potentially signify a host of ecological interactions. Given the number and complexity of potential interactions involving species in this study, we did not expect to arrive at definitive conclusions regarding the specific processes behind patterns revealed herein. Furthermore, it is possible that patterns of presence or density of a given species may be more tied to environmental gradients than to interspecific interactions [13,14], and potentially contextspecific interactions [12]. We included two major factors (stream gradient and wetted width) that are commonly associated with the distribution or density of salmonids, but these variables are also associated with a host of other physical processes that could be more directly driving density [15–17]. Below we discuss the potential implications of our findings with respect to the co-occurrence among species focusing on interactions with coastal cutthroat trout.

3.1. Co-Occurrence among Species

Although our ability to attribute patterns observed here to specific processes is limited, it is widely believed that strong biotic interactions can drive patterns of occurrence and density of vertebrates in small streams, for example fishes and amphibians that specialize in headwater stream habitats [8,18]. In the Pacific Northwest, common salmonid and cottid species are often found together in streams, and typically in a nested fashion, where species richness increases in a downstream direction without loss of headwater species, such as coastal cutthroat trout [9]. In spite of this pattern in our dataset, we found evidence of strong associations across all species of salmonids and sculpin (considered as a group, due to difficulty in identifying species) in lower gradient streams [19]. Interestingly, whereas sculpins, coastal cutthroat trout, and coho salmon were positively associated in terms of occurrence, all three of these species or groups were negatively associated with the presence of steelhead. Our findings are in agreement with Ptolemy [20], who reported that coastal cutthroat trout dominated in smaller streams whereas steelhead dominated in larger streams. Similarly, Rosenfeld et al. [21] found coastal cutthroat trout and coho salmon densities to be highest in smaller streams. Johnson et al. [22] also found lower numbers of steelhead in streams with coastal cutthroat trout and absent in streams with flows less than 0.06 m^3/s.

Among the species considered herein, strong direct interactions may be expected to be more likely between steelhead and coastal cutthroat trout. These two species have more similar ecological characteristics (e.g., spring spawning, flexibility in expression of migratory life histories, and capacity to complete their life cycles in small streams), and can interact evolutionarily via hybridization, where there is potential for outbreeding depression [11]. Within the geographic extent we examined, it is possible that coastal cutthroat trout better adapted to live in low order streams [18], whereas steelhead (potentially due to their larger adult size [20]) are more likely to be present in larger streams: A pattern that is repeated within streams where only *O. mykiss* are present with resident individuals (usually referred to as rainbow trout) occupying headwaters and migratory forms (steelhead) in larger, downstream locations [8,23]. If some of the processes discussed here are in play, the complementary (allotropic) distribution of these two species can indirectly account for other species associations we detected (i.e., the consistent negative or positive association with coastal cutthroat trout and steelhead respectively).

3.2. Density of Coastal Cutthroat Trout and Coho Salmon

Although coastal cutthroat trout and coho salmon commonly co-occur in the streams we studied, the potential for diverse interactions between these species could result in associations evident from examining patterns of density between the species, or in the case of coastal cutthroat trout, the effect of body size on coho salmon. We found that densities of these two species were weakly and positively associated (Figure 3). Similarly, Rosenfeld et al. [21] reported a positive relationship between coho salmon and coastal cutthroat trout density across all sites they studied, but not within a smaller subset of more intensively sampled streams. Buehrens et al. [24] found that coastal cutthroat trout growth, movement, and survival were not influenced by re-establishment of coho salmon. Density of coho salmon in the sites we studied is likely depressed relative to historical levels [25], so potential species interactions could be influenced by these reductions, although a host of outcomes are possible.

Relative to influences considered herein, physical gradients (stream gradients and wetted widths) appeared to be most important for explaining spatial variability in density of both coastal cutthroat trout and coho salmon. The importance of these variables parallels findings reported by Roni [26], who found that large-scale physical variables, such as stream size and stream gradient, were better predictors of fish density than other smaller scale features. Rosenfeld et al. [21] also highlighted the strong association of stream gradient and wetted width with densities of coastal cutthroat trout and coho salmon. Given that stream gradient and wetted widths of streams are commonly associated with variability in hydraulic conditions, channel morphology, and temperature, we suspect that underlying variability in these factors may be important [27,28].

Physical gradients associated with stream gradient and widths, notably local variability in hydraulic factors, depths, or temperatures could be important, adding additional layers of complexity to understanding interactions between coastal cutthroat trout and coho salmon. Juvenile coho salmon are often more abundant in slower moving channel units in streams (e.g., pools and backwaters) whereas similarly-sized juvenile coastal cutthroat trout are more abundant in faster moving units (e.g., riffles or runs) [29,30]. Larger coastal cutthroat trout in smaller streams (similar in size to those considered herein) have been observed to be more closely associated with larger, deeper locations, or locations with available instream cover [30–32]. In this study there was some evidence that increasing body size of coastal cutthroat trout was associated with decreased density of coho salmon, a response that could be mediated by physical conditions that influence density of larger coastal cutthroat trout [33].

Temperature can also play a role in mediating interactions, as indicated by the findings of Glova [34] who studied species interactions at different temperatures. In that study coastal cutthroat trout and juvenile coho salmon exhibited spatial segregation at warmer (13 °C) temperatures, with coastal cutthroat trout sorting into riffles and juvenile coho salmon occupying pools. Habitat use by both species was similar at cooler temperatures [34]. Given that we only considered these species during summer, it is possible that lack of strong relationships between coastal cutthroat trout and juvenile coho salmon were in part mediated by availability increasing hydraulic contrasts (i.e., more distinctive fast and slow-moving units; [30]) among channel units during low flows [35] and seasonally warmer temperatures associated with behavioral segregation of these species [34].

Overall our attempt to predict the density of coastal cutthroat trout resulted in a smaller number of candidate models (Table 2) relative to coho salmon (Table 3; Appendix A). Uncertainty among models predicting density of coho salmon could be attributed to a host of factors, including exclusion of important processes, such as effects of spawning site selection by females [36] and corresponding associations of spawning locations with local densities of juveniles [37,38]. Influences of such factors may be reduced for species like coastal cutthroat trout, which exhibit orders of magnitude lower fecundity and iteroparity (versus semelparity for coho salmon). A potential consequence of the legacy of possible linkages between spawning locations and densities of juvenile coho salmon is higher densities in many locations (e.g., relative to coastal cutthroat trout; Figure 4), with corresponding greater intensities of intraspecific interactions [39,40]. We were not able to account for these factors in this study.

Although we can only draw limited inferences from this observational study, even within experimental settings where conditions can be controlled, the potential effects of competition between co-occurring Pacific salmon and trout can be driven by a host of complex interactions, including size asymmetries, density itself, and spatial scale [14,41,42]. Considering the difficulty of implementing controlled experiments and the complexity of potential interactions through the life cycle, as well as their transferability to field conditions [43], we do not envision clear resolution of species interactions in the near future. For example, the potential influences of natural size asymmetries between juveniles of earlier emerging coho salmon and later-emerging coastal cutthroat trout [41,42] could be reduced if larger resident coastal cutthroat trout also prey on juvenile coho salmon [33,44,45].

Collectively, results from this study and past work do not indicate that coastal cutthroat trout and coho salmon strongly influence each other under field conditions, at least as viewed through the lens of regional patterns of distribution and densities. However, it is important to note that what we were able to observe in the field may be the product of past interactions [30,46]. What is clear from our findings and review of past work is that interactions between coastal cutthroat trout and coho salmon cannot be easily described in simple terms of species interactions (e.g., casting these species as "competitors" or "predators,"; [47]), and that possible interactions could be highly variable, given the dynamic nature of stream ecosystems [48]. Furthermore, the modifying effects of potentially strong interactions with other species, such as steelhead in this work, or a host of other species ranging from prey to predators could be important [49]. Overall, we would expect within-species processes such as density-dependence in demographic rates [39,50,51], prey consumption [52], or migratory life history expression [23] to be more important than interactions among fish species [13].

4. Materials and Methods

In this study we used complementary fish survey data from two locations in forested watersheds along the Pacific Northwest coast (Figure 4), including streams draining the Siuslaw National Forest to the south and Olympic Experimental State Forest in the north. The OESF includes approximately 110,000 ha of state lands managed by Washington State Department of Natural Resources (DNR) on the western Olympic Peninsula. 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 1155 m. The OESF is a coastal rain forest that receives heavy precipitation (200 to 400 cm per year) with the majority falling during winter storms [53]. The OESF has a long history of forest harvests resulting in most of the forest currently in the early to mid-successional stages of development. Small fish-bearing streams (stream order 1–4; [54]) typically have some combination of juvenile coho salmon, rainbow trout/steelhead, coastal cutthroat trout, and/or sculpins. Coastal cutthroat trout are the most-commonly found salmonid species within these smaller streams followed by coho salmon [55]. Starting in 2016, DNR has continuously monitored 100 m reaches in a rotating subset of 45 small fish-bearing streams on state managed lands and another 10 streams with late successional forests in the Olympic National Park and National Forest to assess management impacts as part of their Habitat Conservation Plan [56]. Streams were selected following a random stratified design that selected basins based on stream gradient and balanced over all state-managed lands in the OESF [55].

The SNF includes 254,952 ha of federal lands managed by the U.S. Forest Service on the central Oregon coast range. The SNF is bordered by the Nestucca River Basin to the North and lower Umpqua River Basin to the south. Elevations range from sea level to 1226 m. The Oregon Coast receives around 100–500 cm of precipitation each year. The SNF has a legacy of widespread forest harvest with only 5% of the forest in old growth conditions [57]. Some of the more commonly found species within the smaller streams of the SNF include coastal cutthroat trout, steelhead, coho salmon, Chinook salmon, and sculpins. In 2012, electrofishing surveys were conducted over 30 m reaches in 439 sites across the SNF [9]. Sites were randomly selected near road crossing with a spatially balanced design that ensured one stream was sampled within each sub-network [9].

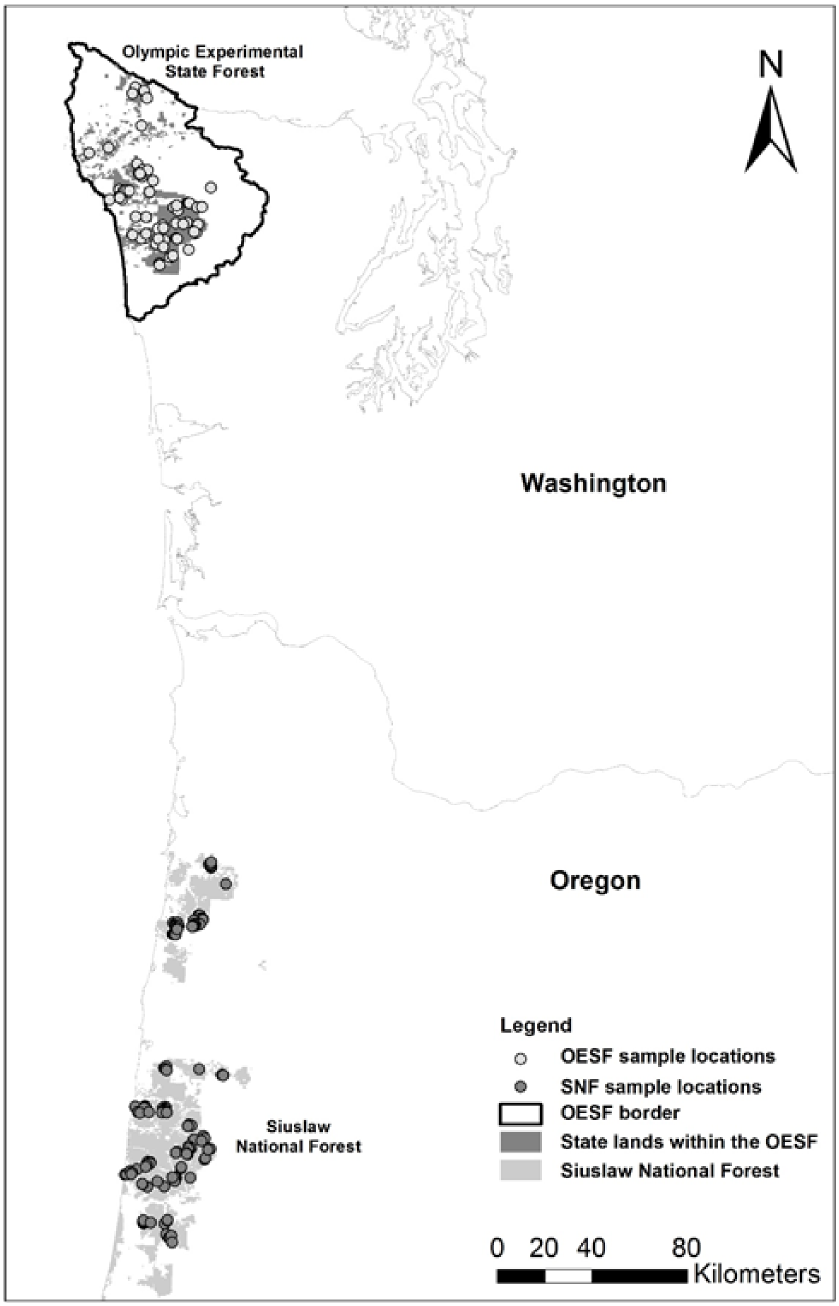

Figure 4. Map of sample sites in the Olympic Experimental State Forest (white dots) and Siuslaw National Forest (dark grey dots).

Data collected from both the OESF and SNF were combined to provide a larger overall sample size and wider geographical inference for evaluating fish species associations with coastal cutthroat trout. Since the SNF surveys included surveys conducted in both spring and summer, we removed all sites sampled prior to July 15th to match the sampling period of the OESF and all streams with no fish resulting in a total of 281 (55 OESF, 226 SNF) sites for combined analyses from both the OESF and SNF. All sites were then analyzed to identify species distributions across stream gradients we calculated the minimum, mean, median, 95th percentile, and maximum values. DNR sampling used a variable-pass method of multiple-pass removal electrofishing [58,59] whereas the SNF dataset relied on estimates from a N-mixture model that used a combination of mark-recapture and single-pass electrofishing [9,55]. To align results from these studies, only data collected during the first pass of each survey were analyzed. Population estimates were not directly compared because the two estimators had vastly different expansion factors casting doubts that the two methods would produce similar estimates. The use of first-pass data was determined to be acceptable after the first-pass data were found to be significantly correlated to the multiple-pass population estimates (R2 = 0.967, $p < 0.001$) from the OESF and the subset of the SNF data where mark-recapture estimates (R2 = 0.705, $p < 0.001$) were conducted. Mark-recapture estimates in the SNF were calculated using the mrN.single function in the "fishmethods" package in the program R [60]. Studies have found that single-pass electrofishing can be an effective method for determining community composition [61–63]. In addition, a comparison of fish presence in sites with multiple-passes revealed that when fish were present, they were collected in the first pass between 95–100% of the time (coastal cutthroat trout—99%, coho salmon—99%, steelhead—95%, Sculpin—100%).

The data set was further reduced to assess species overlap between coho salmon and coastal cutthroat Trout (the two most-commonly found salmonid species) and other species in lower gradient streams. Coho salmon are limited to lower gradient sections of streams [64,65], so we used the 95th percentile of stream gradients with coho salmon to determine areas of potential coexistence between coho salmon and coastal cutthroat trout. This resulted in the removal of all sites with stream gradients over 9%. These sites were removed to insure that streams beyond the range coho salmon accessibility did not overly influence the results. Reductions in the number of sites to ensure similar sampling periods and species overlap resulted in 39 sites in the OESF and 159 sites in the SNF.

Next, we conducted analyses of species associations involving patterns of presence and density. First, we determined whether common fish species were positively, negatively, or randomly associated with each other using a co-occurrence model in the R package "co-occur" [60,66]. Chinook salmon were not analyzed because they were not found in the OESF and only in 17 sites on the SNF. Co-occurrence was measured based on presence/absence data coded "1" for presence and "0" for absence. The model, copied from Griffith et al. [64], uses the formula:

$$Pj = \frac{\binom{N_1}{j} \times \binom{N - N_1}{N_2 - j}}{\binom{N}{N_2}}$$

$$\begin{aligned} N_1 &= the\ number\ of\ sites\ where\ species\ one\ occurs \\ N_2 &= the\ number\ of\ sites\ where\ species\ two\ occurs \\ N &= the\ total\ sites\ sampled \\ j &= 1\ to\ N_1 sites \end{aligned}$$

The co-occurrence model estimated the number of times that two species were observed together (OBS), the probability of occurrence, the expected occurrence (EXP), the probability that two species would be present at a frequency less than expected if the two species were distributed randomly (P_lt), and the probability of two species occurring together at a frequency greater than expected if the two species were distributed randomly (P_gt).

To understand the relative importance of physical features of streams versus species interactions, we used linear regression and AIC model selection. Models were first conceptualized to potentially identify species interactions and habitat data. Physical features of streams were represented by stream gradients (GRAD; %) and the wetted widths (WW; m) of the sites. Stream gradient and wetted width were measured at the stream in the OESF, while stream gradient was estimated by GIS and wetted width was measured at the stream in the SNF [9]. Species interactions were represented by coho salmon (COH) and coastal cutthroat trout (CTT) densities and the average body size based on fork length (mm; ABS) of coastal cutthroat trout. Generalized linear models were then developed to predict both coastal cutthroat trout and coho salmon densities. All models were run in the program

R using the package "glm2" [60]. Akaike's Information Criterion, corrected for smaller sample sizes, (AICc) was used to rank the importance of each model. All models within two ΔAICc units of the most likely model were assumed to have substantial support and considered to have variables important for predicting coastal cutthroat trout or coho salmon densities. Models over three ΔAICc units from the most likely model were considered to have less support and were thought to be of less importance for coastal cutthroat trout or coho salmon [67]. Finally, the top models were tested to assess whether the models would produce results similar to what was found within the datasets (Appendix A).

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Data Availability Statement: Data associated with the SNF have been deposited with the USGS Forest and Rangeland Ecosystem Science Center: htt doi.org/10.5066/F71R6. Data from the OESF are not currently available online and are available on request from the corresponding author. The OESF data are not publicly available because our data sharing resources are currently under development with the goal to make all data publically available in the future.

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Appendix A

Table A1. Predicted fish densities for linear regression models. CTT = coastal cutthroat trout; Coho = coho salmo; fpm2 = fish per meter squared.

Model	Fish Density	Avg. Body Size (ABS) *	Wetted Width (WW)	Stream gradient (GRAD)	Predicted Density
Cutthroat Models					
CTT~WW + GRAD	–	–	2 m	3%	0.0517 fpm2
	–	–	3 m	3%	0.0395 fpm2
	–	–	2 m	4%	0.0550 fpm2
CTT~COH + WW + GRAD	0.100 fpm2	–	2 m	3%	0.0630 fpm2
	0.200 fpm2	–	2 m	3%	0.0550 fpm2
Coho models					
Coho~ABS + WW + GRAD	–	80 mm	2 m	3%	0.0845 fpm2
	–	80 mm	2 m	2%	0.0913 fpm2
	–	100 mm	2 m	3%	0.0717 fpm2
	–	80 mm	3 m	3%	0.0823 fpm2
Coho~CTT + ABS + WW + GRAD	0.100 fpm2	100 mm	2 m	3%	0.0630 fpm2
	0.200 fpm2	100 mm	2 m	3%	0.0447 fpm2

* Coastal cutthroat trout only metric.

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