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Investigation of the relationship between physical habitat and salmonid abundance in two coastal northern California streams

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Understanding the relationship between fish abundance and stream habitat variables is critical to designing and implementing effective freshwater habitat restoration projects for coho salmon (*Oncorhynchus kisutch)* and other anadromous salmonids. In this study, we investigated the relationship between summer coho salmon and steelhead trout (*O. mykiss*) parr abundance and physical stream habitat variables in Caspar and Pudding creeks in Mendocino County, California. Relationships between summer habitat and juvenile abundance were investigated using a stratified random experimental design. Our hypothesis was that one or more of the habitat unit types and variables examined would be associated with salmonid abundance. Habitat differences were examined between the two streams, and we tested our hypotheses regarding habitat variables and salmonid abundance using a variety of statistical tools that included two-way ANOVA, factor analysis, and negative binomial regression modeling. The results indicated that juvenile coho salmon abundance was positively (proportionally) associated with slow water, water volume, and dry large-wood abundance, and negatively associated with fast-water habitat variables. Young-of-the-year steelhead trout were positively associated with water volume and dry large-wood and negatively (or inversely) associated with overhead vegetation and fast water habitats. Older age steelhead abundance was positively associated with slow water, water volume; cover habitat formed by wet and dry wood, and undercut banks. We discuss our findings relative to the use of large wood in anadromous salmonid habitat recovery programs in California coastal watersheds.

Key words: Coho salmon, habitat relationships, large wood, *Oncorhynchus kisutch*, *Oncorhynchus mykiss*, restoration, steelhead trout

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Understanding relationships between fish abundance and stream habitat is important for designing and implementing freshwater habitat restoration projects that improve conditions for fish (Roni and Beechie 2013, Bennett et al. in press). A great deal of study has been directed at understanding habitat requirements for salmonids (Bjorn and Reiser 1991), especially those related to depth and velocity for stream flow evaluations (Bovee 1986). Early works directed at understanding fish habitat requirements were primarily observational (Chapman and Bjorn 1969, Fausch 1993). A number of studies have found correlations between habitat classifications (unit types) and salmonid abundance (Swales et al. 1986, Bisson et al. 1988, Nickelson et al. 1992, Lau 1994, Kruzic et al. 2001, Sharma and Hilborn 2001, CDWR 2004), while others have shown correlations between fish abundance and differing levels of depth, velocity, and complex instream and riparian cover (Butler and Hawthorne 1968, Everest and Chapman 1972, Shrivel 1990, Sutton and Soto 2010). These observations have been supported by field and laboratory experimentation (Bustard and Narver 1972, McMahon and Hartman 1989, Fausch 1993, Kruzic et al. 2001). Few studies have attempted to determine if individual habitat variables are related to fish abundance using multivariate approaches (Kratzer and Warren 2013).

Introducing large wood to improve instream habitat for Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*O. mykiss)* was suggested as part of the recovery strategy for California's coastal coho salmon (*O. kisutch)* (CDFG 2004; NMFS 2013a, b) and steelhead trout (NMFS 2007, 2013c). Following intensive logging, road building, and instream disturbance (Burns 1971, 1972), both Caspar and Pudding creeks experienced large wood removal during the 1970's and 1980's (Allan Grass, CDFW, personal communication). For these reasons, large wood density and abundance is low throughout the Mendocino coast region (Carah et al. 2014).

Solazzi et al. (2000) provided evidence that addition of large wood significantly increased steelhead trout habitat and abundance during summer in two coastal streams in Oregon. Johnson et al. (2005) found that addition of large wood significantly increased coho salmon summer habitat and freshwater survival in Tenmile Creek, a coastal tributary in Oregon. There is also evidence suggesting that a lack of winter habitat may limit coho salmon production in coastal streams (Nickelson et al. 1992). Overwinter habitat limits coho salmon survival in Pudding and Caspar creeks (Gallagher et al. 2012) and summer is the lowest growth season for salmonids in Pudding Creek (Wright et al. 2012).

During the summer of 2013, physical habitat and salmonid abundance data were collected as part of a multiyear before-after-control-impact experiment (Stewart-Oaten et al. 1986) designed to determine if adding large wood to over 80% of the spawning and rearing habitat of a treatment stream (i.e., Pudding Creek) will increase summer and winter stream habitat and improve abundance, growth, and survival of salmonids relative to a control stream (i.e., Caspar Creek). Summer habitat and salmon abundance data were collected in a stratified random experimental design for the purpose of investigating habitat differences and similarities between the two study streams, estimating salmonid abundance, and examining relationships between salmonid abundance and freshwater habitat variables. This is the first study of its kind in California, similar to studies conducted in Oregon, to evaluate the effect of appreciably increasing instream wood to improve habitat condition (i.e., over-summering and over-wintering habitat) and fish abundance.

The purpose of this study was to evaluate relationships between coho salmon and steelhead summer parr abundance and physical stream habitat variables in Caspar and Pudding creeks, Mendocino County, California using multivariate analyses. We hypothesized that one or more of the nine habitat unit types (e.g., cascade, dam pool, plunge pool, riffle, etc.) and some assortment of the 29 habitat variables (e.g., water depth, unit area, percent cover or substrate, etc.) examined would be associated with salmonid abundance (Table 1). We tested our hypothesis that some collection of habitat variables would be associated with salmonid abundance with two-way Analysis of Variance (ANOVA) and negative binomial regression modeling. We conclude with a discussion of whether or not our findings support the supposition that salmonid abundance will increase by addition of large wood to streams.

Table 1.—Detailed habitat variables collected in each selected unit in Caspar and Pudding creeks, Mendocino County, California, during summer 2013.

Habitat Unit Type	Percent Fish Cover	Substrate Composition	Measured Unit Variables	Calculated Unit Variables
Cascade[a]	Aquatic Vegetation	Bedrock	Mean Depth	Residual Pool Depth[b]
Dam Pool[a]	Artificial Structures[a]	Boulders	Bankfull Width	Residual Pool Volume[b]
Dry Units[a]	Dead Woody Debris	Cobbles	Length	Unit Surface Area
Falls[a]	Live Overhanging Vegetation	Course Gravel	Maximum Depth[b]	Unit Volume
Non-turbulent	No Cover	Fine Gravel	Tail Crest Depth[b]	Dry LWD[c] Abundance
Off Channel	Undercut Banks	Fines	Width	Wet LWD Abundance
Plunge Pool		Sand		Dry LWD Density
Rapid[a]		Fines< 2 mm[b]		Wet LWD Density
Riffle		Fines 2-6 mm[b]		
Scour pool				

[a]Few or none encountered; [b]Pools only; [c]Large Woody Debris

Materials and Methods

Physical habitat.—A habitat survey was conducted in July 2013 throughout the anadromous fish habitat in both Pudding and Caspar creeks. During the survey, field staff classified all mesohabitat unit types and collected detailed information on habitat attributes in association with individual units (Table 1). Habitat data were collected in accordance with the Columbia Habitat Monitoring Protocol (CHaMP) (Bouwes et al. 2012), as modified by Holloway et al. (2013). Habitat attributes included unit type, fish cover, substrate composition, depth, wetted length and width, volume, area, and large wood abundance (Table 1). Bouwes et al. (2012) fully describes habitat attributes collected in this study. Due to logistical constraints, all physical habitat variables could not be collected in every unit.

Basic dimensions were measured in every habitat unit, and a systematic sample within the habitat census was used to select habitat units in which additional measures were collected in both streams. These detailed attributes were collected in the first and every 10th habitat unit for each of nine types (Bouwes et al. 2012). To further asses differences between the study streams we evaluated gradient, sinuosity, alkalinity, and stream flow data generated from more detailed CHuMP surveys conducted in August of 2013 in five randomly selected sites in Pudding Creek and four sites in Caspar Creek.

Salmonid abundance.—Salmonid abundance surveys were conducted in a spatially balanced, systematic sample of the units selected for additional measures during the survey. An existing Generalized Random Tessellation Sampling (GRTS) design, developed for regional spawning ground surveys (Gallagher et al. 2013), was employed. Salmonid sampling was conducted in five GRTS reaches in Caspar Creek and eight GRTS reaches in Pudding Creek (Figure 1). Three small gulches, one in Caspar Creek and two in Pudding Creek, were not included due to intermittent summer stream flows. To achieve a balanced design for evaluating fish-habitat relationships, 10 samples of each of the five primary habitat unit types (scour pool, plunge pool, riffle, non-turbulent, and off-channel) were selected in each stream. Dam pools, cascades, and rapid unit types were not included due to their rarity in both streams. Salmonid sampling was conducted in the 10th additional attribute unit of each unit type in each GRTS reach. To achieve the desired number of units, the 30th unit was also sampled in all five GRTS reaches in Caspar Creek and in two randomly selected GRTS reaches in Pudding Creek. Because selecting each 10th unit would not provide the desired 10 plunge pools or off-channel units in either stream, we randomly selected 10 of each of these unit types from the collection of all plunge pools and off-channel units in each stream.

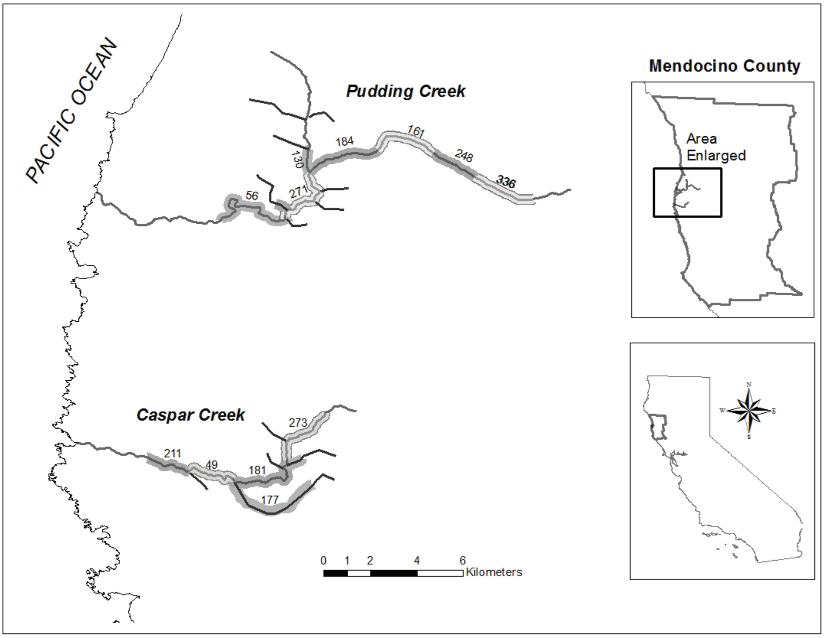

Figure 1.—Location of Caspar Creek and Pudding Creek in Mendocino County, California. Numbers are Generalized Random Tesselation Stratified reaches. The thin lines are stream areas that were not sampled.

Juvenile salmon abundance was estimated by depletion electrofishing in all units less than 1.2 m deep, and by snorkeling in units that exceeded 1.2 m of depth. All selected units were surveyed in July (summer) and again in October (fall) of 2013. Abundance estimates were generated for both summer and fall coho salmon juvenile (parr) and steelhead trout young-of-the-year (YoY), year old (Y+), and two-year and older fish (Y++) in each selected habitat unit (Holloway and Gallagher 2013). Steelhead trout age classes were based on fork length; fish <70 mm were considered YoY, fish between 70 mm and 120 mm were considered Y+, and fish > 120 mm were considered Y++ (Neillands 2003). All captured fish were anesthetized using tricaine methane sulfonate (MS-222), examined for previous marks, weighed, and measured.

Statistical analysis.—The habitat sampling in each selected unit resulted in 23 variables, of which 6 were calculated (Table 1). In pool habitats, we collected data for an additional four, and calculated another two, variables. Bouwes et al. (2012) directs collection of large wood data in a detailed matrix of 32 wet and dry large wood categories. For this analysis, all wood >0.1 m diameter and >3 m length was combined into total dry and total wet large wood for each unit. Unit length, width, and depth measurements were made during the habitat census and again on the day the units were sampled for fish abundance. These measurements were used to calculate unit area, volume, large wood density, residual pool depth, and residual pool volume. The habitat data from 20 replicates of the five predominate unit types in each stream were tested using a two-way Analysis of Variance (ANOVA) design to examine differences in fish habitat variables between streams (factor one) and habitat unit type (factor two). We calculated Shannon's index (*H*') of habitat diversity in the two creeks following Brower and Zar (1984).

Coho salmon and steelhead trout abundance was estimated in each selected unit from depletion electrofishing using the jackknife estimator (Pollock and Otto 1983). For snorkeled units, we used the method of bounded counts to estimate salmonid abundance (Regier and Robson 1967). Unit abundance and total length of stream was then used to estimate total abundance for each stream (Sarndal et al. 1992). Fish density was computed using unit length, width, and depth measurements collected during salmonid abundance surveys. Similar to the habitat evaluation, a balanced two-factor ANOVA was used to examine differences in habitat variables (Table 1), fish density and abundance between habitat unit types and streams. Significant differences found via the ANOVA tests were followed with post-hoc test based on Tukey's all pairwise comparisons to identify specific significant differences at $p < 0.05$ (Glantz 1997).

A negative binomial regression approach was conducted to evaluate relationships between fish abundance and physical habitat variables (Zuur et al. 2009). The habitat data in Table 1 included a large number of variables that were found to be highly correlated. While not an explicit, required assumption of regression, collinearity in multiple regression is a problem because regression evaluates the importance of each variable based on its marginal (or unique) contributions to the dependent variable. When variables are highly collinear, this implies that they are somewhat redundant and thus can cause the coefficients to be unstable, this can create a cancellation effect leading to the variables incorrectly being found insignificant. The first action to address the high correlation among the independent variables was to remove measured variables and substitute them with their corresponding calculated variables. Thus, the original data set was reduced from 28 to 17 variables (Table 2). This reduced variable set indicated that multi-collinearity remained present.

Table 2.—Reduced data set of variables used in factor analysis to evaluate relationships between salmonid abundance and physical stream habitat in Caspar and Pudding creeks, Mendocino County, California, summer 2013.

Unit	Stream	Fish Cover	Substrate[a]	Large Woody Debris
Abundance[b]	Caspar Creek	Aquatic Vegetation	Bedrock	Abundance of Dry
Type	Pudding Creek	Live Overhead Vegetation	Boulder	Abundance of Wet
Volume		No Cover	Course Gravels	
		Overhead Dead Wood	Fine Gravels	
		Undercut Banks	Sand	
			Fines	

[a]Percent; [b]Dependent variable: Coho Salmon, Steelhead YOY, Steelhead Y+, or Steelhead Y++

Factor analysis (FA) is one strategy that can help address multi-collinearity (Williams et al. 2010). FA is a dimension reducing scheme that finds linear combinations of the independent variables representing latent (i.e. underlying) factors. A benefit of FA is that it does not eliminate variables, but results in a variable set with lower dimensions. This produces a reduced data set for use in linear modeling that still contains the original components. Furthermore, by choosing a varimax rotation, FA finds factors that are independent of each other, thereby reducing the multi-collinearity effect (Abdi 2003). Formally, varimax searches for a rotation (i.e., a linear combination) of the original factors such that the variance of the loadings is maximized. In other words, the FA retains all the variables but compresses them into common chucks that yield independent component factor scores necessary for negative binomial regression modeling. The optimum number of factors was determined as those factors that explained ≥70% of the variation in the original variable set, based on principle components analysis. In FA, the factors represent constructs (linear combinations) of all the variables with the highest loadings (absolute correlations between the factors and the variables) helping to define the factors. An absolute correlation (or loading) threshold of 0.3 was selected to identify the variables defining each factor. Studying the variable loadings for the factors helped derive meaningful names for each factor. These factors, along with the original response, became the new basis to determine relationships between habitat (independent variables) and fish abundance (response or dependent variable).

The final FA results found that the total variation explained was low. Furthermore, the factors yielded asymmetrical distributions. To address this new issue, we had to conduct an additional statistical revision; the factors were natural log transformed. Since zeros were present, prior to log transforming, a constant was added to the factors. The transformations were found to improve the amount of total variation explained (Chi-square > 0.10). Since the response variable (i.e., fish abundance) was a count type variable, Poisson regression was used to gain understanding of the relationship between abundance and habitat factors. However, due to excessive zeroes in the response variable, a negative binomial regression approach was used to understand the relationship between abundance and the habitat factors (Zuur et al. 2009). Excessive zeros inflate the variance and the negative binomial is one approach than can deal with such a situation. All statistical analyses were performed in program R (R Development Core Team, http://www.r-project.org/). Statistical significance was accepted at $P < 0.05$.

RESULTS

Physical habitat.—We observed only two cascade and dam pool units in Caspar Creek, and three rapid units in Caspar Creek and one in Pudding Creek. There were a total of 34 dry units in both streams in summer 2013. These unit types were not sampled for fish density or included in further analysis. In both streams, the predominant habitat types were scour pools, riffles, and non-turbulent units (e.g. runs). The frequency of habitat types was not different between the two streams (Figure 2); both streams had similarly low proportions of off-channel and plunge pool habitat types. Habitat diversity in Caspar Creek (H'= 0.50) was nearly identical to that of Pudding Creek (H' = 0.51).

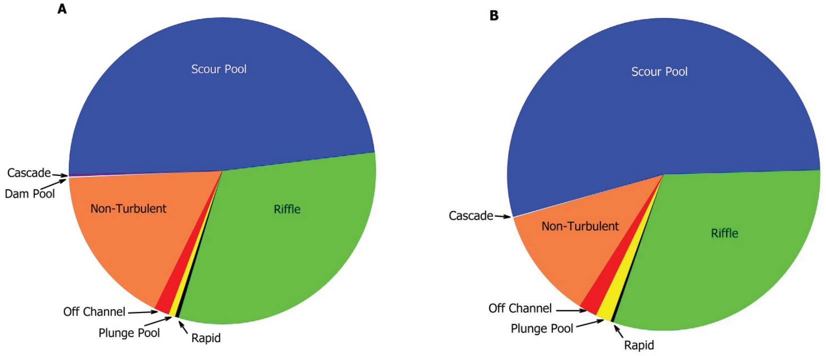

FIGURE 2.—Proportion of habitat unit types in (a) Caspar Creek (a) and (b) Pudding Creek, Mendocino County, California, during the summer of 2013. There were no dam pools in Pudding Creek.

As we expected, many of the habitat variables differed among habitat units (Table 3). Generally, units associated with moving water had higher percentages of coarse stream substrate than units associated with slow water. The percentage of fine sediment was highest in slow water units and decreased with higher velocity unit types (e.g. off channel> pool> non-turbulent > riffle). Slow water units generally had more overhead fish cover than did fast water units. Both plunge pools and scour pools had more undercut banks than other unit types. Plunge pools were deeper, had more volume, and had higher percentages of pool tail fine substrate than scour pools. And pools were deeper and had more volume than off channel units, which were deeper and had more volume than non-turbulent units. Riffles were the shallowest units with the lowest volume.

Eleven of the 29 (38%) variables we examined with ANOVA were significantly different between the two creeks in summer 2013 (Table 3). Notably, cover variables and large wood density and large wood abundance were not different between the two streams. The number of pieces of wet large wood/100 m averaged 21.76 (*SE* = 5.06) in Caspar Creek and averaged 28.17 (*SE* = 6.90) in Pudding Creek. Pudding Creek is a longer stream with a larger drainage area than Caspar Creek and, thus, had more surface area and volume of fish habitat. Pools were deeper and had more residual pool volume in Pudding Creek than they did in Caspar Creek. Caspar Creek had more boulder and cobble substrate than Pudding Creek; whereas Pudding Creek had more coarse gravel and sand substrate and more fines in pool tails than did Caspar Creek.

Table 3.—Results of two-factor ANOVA between stream, habitat unit type, and habitat variables. NS = not significant; NT = non-turbulent; OC = off channel; PP = plunge pool; RI = riffle; and SP = scour pool. Degrees of freedom for the F statistic are 4, 401. Caspar and Pudding creeks, Mendocino County, California, summer 2013.

		Significant Differences			Group Differences	
Habitat Category	Variable	Unit	Stream	Interaction	Habitat Types	Stream Differences[f]
Substrate	Bedrock	NS	NS	NS	None	None
	Boulders	NS	F=10.4; P=0.002	NS	None	C=3.2, P=1.3
	Cobbles	F=3.6; P=0.007	F=27.3; P<0.001	NS	RI>OC, PP, SP	C=12.3, P=4.4
	Course Gravel	F=46.1; P<0.001	F=27.3; P<0.001	NS	RI>PP,SP,NT; NT>SP,PP,OC	C=26.1, P=32.9
	Fine Gravel	F=3.1; P=0.02	NS	NS	NT>OC	None
	Sand	F=20.04; P<0.001	F=6.07; P=0.01	NS	OC,SP>RI	C=21.2, P=25.1
	Fines	F=16.8; P<0.001	NS	NS	OC>PP>SP>NT>RI	None
	Fines<2 mm[a]	F=202; P<0.001	F=6.46; P=0.001	NS	PP>SP	C=13.2, P=22.3
	Fines 2-6 mm[a]	F=2.13; P=0.09	NS	NS	PP>SP	None
	Artificial Structure	Not observed	Not observed	Not observed	Not observed	Not observed
Fish cover	Aquatic Veg.	NS	NS	NS	None	None
	DWD[b]	F=12.1; P<0.001	NS	NS	OC>NT,PP,RI,SP	None
	LOV[c]	F=5.67; P<0.001	NS	NS	OC>NT,PP,RI	None
	No Cover	F=19.19; P<0.001	NS	NS	RI>NT,PP; OC<NT,PP,RI,SP	None
	Undercut Banks	F=6.86; P<0.001	NS	NS	SP,PP>RI,NT	None
Measured metrics	Average Depth	F=63.3, P<0.001	NS	NS	PP>SP>OC>NT>RI	None
	Bankfull Width	F=20.35; P<0.001	F=6.45; P<0.001	NS	OC>NT,PP,RI,SP	C=5.7m, P=5.2 m
	Max. Depth[a]	NS	F=6.26; P=0.007	NS	None	C=53.3 cm, P=59.1 cm
	Tail Crest Depth[a]	NS	NS	NS	None	None
Calculated metrics	Residual Depth[a]	F=3.09; P=0.05	F=10.34; P=0.001	NS	PP>SP	C=40.0 cm, P=55.0 cm
	Residual Volume[a]	F=5.29; P<0.001	F=9.52; P=0.002	NS	PP>SP	C=16.2 m^3, P=24.7 m^3
	DLWD[d] Abund.	NS	NS	NS	None	None
	WLWD[e] Abund.	F=4.8; P<0.001	NS	NS	PP,SP>NT,RI	None
	DLWD[d] Density	NS	NS	NS	None	None
	WLWD[e] Density	F=8.65; P<0.001	NS	NS	OC>NT,RI,PP; PP>NT,RI,SP	None
	Unit Volume	F=13.22; P<0.001	F=8.13; P=0.004	F=3.43; P=0.008	SP>OC,NT,PP,RI	C=4.2 m^3, P=9.4 m^3
	Unit Surface	F=12.56; P<0.001	F=9.00; P<0.001	F=2.58; P=0.04	SP>NT,OC,PP,RI	C=28.8 m^3, P=49.9 m^3

[a] Measured or calculated only in pool units; [b] DWD=Dead Woody Debris; [c] LOV=Live Overhanging Vegetation; [d] DLWD=Dry Large Woody Debris; [e] WLWD= Wet Large Woody Debris; [f] C=Caspar Creek, P=Pudding Creek

The average gradient of Caspar Creek (0.40, SE = 0.13) was not significantly different from that of Pudding Creek (0.69, SE = 0.15). Caspar Creek's average sinuosity (1.16, SE = 0.02) was not different than Pudding Creek's (1.38, SE = 0.20). Both streams had average summer daily mean water temperatures between 11ºC and 16ºC. Caspar Creek's average alkalinity of 167 (SE = 6.3) and average conductivity of 52 (SE = 10.4) was similar to Pudding Creek (250, SE =55.2, 64 SE = 9.8, respectively). Stream flows during summer 2013 were less than 1 cfs in both streams.

Salmonid abundance.—Coho salmon abundance differed among habitat units in both summer and fall and was significantly higher in pools than in off-channel units and riffles (Table 4) and not different among the other unit types examined. Steelhead trout YoY were more abundant in non-turbulent units and scour pools (fall only) than in plunge pools and off-channel units in both summer and fall. Similarly, steelhead trout Y+ abundance was significantly higher in scour pools than in the other unit types during summer and fall. Older steelhead trout (Y++) abundance was significantly higher in scour pools and plunge pools (fall only) than in the other unit types during both seasons.

Coho salmon and steelhead trout YoY and Y+ density was not significantly different among habitat unit types in summer 2013. In fall, coho salmon density was significantly higher in plunge pools than it was in riffles and off channels, whereas steelhead trout YoY and Y + density was not different among unit types during fall 2013. The density of steelhead trout Y++ was significantly higher in plunge pools than in all other unit types during both summer and fall 2013.

Table 4.—Results of two-factor ANOVA between stream, habitat unit type, and salmonid abundance and density. NS = not significant; NT = non-turbulent; OC = off channel; PP = plunge pool; RI = riffle; SP = scour pool. Degrees of freedom for the *F* statistic are 4, 401. Caspar and Pudding creeks, Mendocino County, California, summer 2013.

Season	Abundance [a] or Density[b] of Salmonids	Significant Differences			Group Differences	
		Unit	Stream	Interaction	Habitat Types	Stream[d]
Summer	Coho Salmon Parr Abu.	F = 4.53; P = 0.0002	F = 18.73; P < 0.001	F = 2.47; P = 0.049	SP> PP,OC,RI	C = 4.78, P = 42.82
	Coho Salmon Parr Den.	NS	F = 38.54; P < 0.001	NS	None	C = 0.09 m^2, P = 1.22 m^2
	Steelhead YoY Abu.	F = 3.26; P = 0.01	F = 9.44; P = 0.003	NS	NT> PP,OC[c]	C = 5.64, P = 20.18
	Steelhead YoY Den.	NS	F = 15.37; P < 0.001	NS	None	C = 0.14 m^2, P = 0.60 m^2
	Steelhead Y+ Abu.	F = 6.36; P < 0.001	NS	NS	SP> NT,PP,OC,RI	None
	Steelhead Y+ Den.	NS	F = 5.06; P = 0.02	NS	None	C = 0.04m^2, P = 0.08 m^2
	Steelhead Y++ Abu.	F =8.31; P < 0.001	NS	NS	PP, SP> NT,OC,RI	None
	Steelhead Y++ Den.	F = 4.92; P < 0.001	NS	NS	PP> NT,OC,SP,RI	None
Fall	Coho Salmon Parr Abu.	F = 4.79; P = 0.001	F =16.65; P < 0.001	F=2.69; P = 0.03	SP>OC,RI	C = 3.60, P = 28.90
	Coho Salmon Parr Den.	F = 5.62; P < 0.001	F = 122.1; P < 0.001	F = 3.33; P = 0.006	PP>OC,RI	C = 0.06m^2, P = 0.70 m^2
	Steelhead YoY Abu.	F = 4.01; P = 0.005	NS	NS	NT,SP>PP,OC.	None
	Steelhead YoY Den.	NS	NS	NS	None	None
	Steelhead Y+ Abu.	F = 7.64; P < 0.001	NS	NS	SP> NT,PP,OC,RI	None
	Steelhead Y+ Den.	NS	NS	NS	None	None
	Steelhead Y++ Abu.	F = 5.35; P < 0.001	NS	NS	SP> NT,OC,RI	None
	Steelhead Y++ Den.	F = 5.72; P < 0.001	NS	NS	PP> NT,OC,SP,RI	None

[a] Abu.=Abundance; [b] Den.=Density; [c] Tukeys pairwise comparison p < 0.10; [d] C=Caspar Creek, P=Pudding Creek

In summer and fall 2013, coho salmon abundance and density were higher in Pudding Creek than in Caspar Creek (Table 4). Steelhead trout YoY abundance and density were also significantly higher in Pudding Creek than in Caspar Creek during summer, but not in fall 2013. Older age steelhead trout abundance was not different between the two streams in either season. However, steelhead trout Y+ density was significantly higher in Pudding Creek than in Caspar Creek during summer 2013. The ANOVAs indicated a significant interaction between stream and habitat type for summer and fall coho abundance and fall coho salmon density (Table 4). The interaction for coho salmon abundance and density was due to differences in riffles between the two streams (Figure 3). During summer and fall 2013, only a few coho salmon were captured in two riffles in Caspar Creek, whereas coho salmon were captured in all riffles in Pudding Creek.

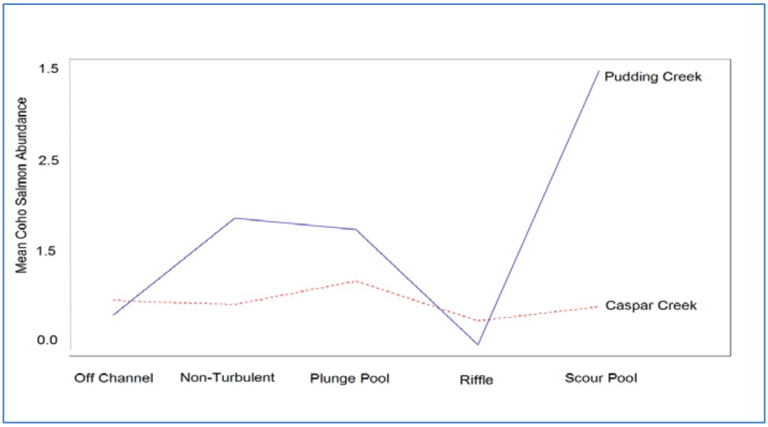

Figure 3.—Interaction plot of mean coho salmon (*Oncorhynchus* kisutch) abundance and habitat unit type in Caspar Creek and Pudding Creek, Mendocino County, California summer 2013.

Coho salmon and steelhead trout total abundance was significantly higher in Pudding Creek than in Caspar Creek during summer and fall 2013. The estimated summer coho salmon abundance in Pudding Creek of 83,306 (95% *CI*, 57,452-107,161) was 13.2 times higher than the 6,306 (95% *CI*, 2,635-9,975) estimated in Caspar Creek. The large difference in stream abundance was similar (13.9 times higher) between the two creeks in fall. In Pudding Creek, we estimated 61,353 (95% *CI*, 43,301-79,905), and in Caspar Creek, we estimated 4,393 (95% *CI*, 960-7,825) coho salmon. During summer 2013, there were five times as many steelhead trout YoY in Pudding Creek (42,335: 95% *CI*, 27,445-57,275) than the estimate of 8,471 (95% *CI*, 4,675-12,267) in Caspar Creek. In fall 2013, there were twice as many steelhead trout YoY in Pudding Creek, where we estimated 10,454 (95% *CI*, 6,709-14,200) steelhead trout YoY versus 5,145 (95% *CI*, 2,879-7,412) in Caspar Creek. Steelhead trout Y+ and Y++ were between 1.7-2.6 times more abundant in Pudding Creek than in Caspar Creek during summer and fall 2013, respectively.

Relationships between salmonid parr abundance and fish habitat.—Factor analysis on 17 salmonid habitat variables (Table 2, excluding unit abundance) revealed seven significant factors (Chi-square 42.24, *df* = 38, *P*=0.29) accounting for >56% of the variation in the data set (Table 5). Based on examination of the variables that were highly correlated (r>0.30) to each of the factor loadings (these define the factors), two factors were associated with cover, two were associated with volume, three were associated with wood, one was related to slow water, and two were related to fast water. Three of the 17 habitat variables (i.e., aquatic vegetation cover, percent bedrock, and unit type) were not found to have significant loadings in any of the seven factors. All of the 14 habitat variables, that were important loadings for the seven factors, contributed significantly to one or more of the factors (Table 5).

Table 5.—Factor names, factor loadings (variables), and loading coefficients (>0.30) resulting from factor analysis of 17 salmon stream habitat variables. Bold font indicates statistically significant loading coefficients for each factor. Caspar and Pudding creeks, Mendocino County, California, summer 2013.

	Factor Names						
Variable	VDLW[a]	Wood	OV[b]	TWSDLW[c]	SWV[d]	FW[e]	UB[f]
Bedrock							
Boulders				**0.59**			
Cobbles				**0.89**			
Coarse Gravels					-0.38	**-0.74**	
Fine Gravels						**-0.46**	
Sand					**0.96**		
Fines						**0.64**	
Large Wood Wet		**0.75**					
Large Wood Dry	0.31	**0.47**		0.34			
Overhead Vegetation Cover			**0.76**				
Overhead Wood Cover		**0.72**					
Aquatic Vegetation Cover							
Undercut Banks							**0.98**
No Cover		**-0.43**	**-0.86**				
Unit Type							
Unit Volume	**0.79**				0.32		
Stream				**0.33**			

[a] Volume and dry large wood; [b] Overhead vegetation; [c] Turbulent water stream and large dry wood; [d] Slow water volume; [e] Fast water; [f] Undercut banks

The negative binomial regression modeling of the scores of the seven habitat factors and coho salmon unit abundance revealed that three factors were significant for predicting coho salmon abundance ($z>3.12$, $P<0.001$). Coho salmon were positively associated with volume, slow water, and dry large wood, and negatively associated with fast water (Tables 5 and 6). Overhead vegetation cover, undercut banks, and wood were not important factors for predicting coho salmon abundance. Steelhead trout abundance was significantly associated with all seven factors ($z>2.17$, $P<0.03$). Steelhead trout YoY were associated two of the same factors as coho salmon and also were associated negatively with overhead vegetation cover and turbulent water. Like coho salmon, older age steelhead trout were positively associated with volume and dry large wood. Steelhead trout Y+ and Y++ were positively associated with the factor wood. Steelhead trout Y+ were positively associated with slow water, volume, and undercut banks, and negatively associated with fast water and overhead vegetation, while steelhead trout Y++ did not have these positive or negative associations.

Table 6.—Habitat factors associated with salmonid abundance. Positive and negative refer to the sign of the regression coefficient for each factor that was significant for predicting salmonid abundance. NS = not significant. Caspar and Pudding creeks, Mendocino County, California, summer 2013.

Salmonid Abundance	Factor Names						
	VDLW[a]	Wood	OV[b]	TWSDLW[c]	SWV[d]	FW[e]	UB[f]
Coho Salmon	+	NS	NS	NS	+	–	NS
Steelhed YOY	+	NS	–	–	NS	–	NS
Steelhead Y+	+	+	–	–	+	–	+
Steelhead Y++	+	+	NS	NS	NS	–	NS

[a]Volume and dry large wood; [b]Overhead vegetation; [c]Turbulent water stream and large dry wood; [d]Slow water volume; [e]Fast water; [f]Undercut banks

DISCUSSION

The differences among habitat units fit the hydraulic and geomorphic theories underpinning the classification scheme from which they were derived. As such, it is not surprising that we found differences in physical habitat variables among unit types. Units associated with moving water had higher percentages of coarse substrate than those associated with slow water. Off-channel units had higher percent overhead cover and the least amount of "no cover" when compared to other units because they are in the riparian zone of the stream. Scour pools had the most undercut banks because the substrate degradation processes that form them are the same that create undercut banks. Pools are, by definition, deeper than the other unit types and plunge pools are deeper than scour pools because of the geomorphic and hydraulic forces that form them. Dry large wood abundance and density were not different among unit types, probably because large wood is rare in coastal California streams (Carah et al. 2014). The reason the number of pieces of large wood in the water was higher in both pool types than in riffles and non-turbulent units is likely due to the fact that large wood is generally responsible for forming and maintaining pools, but not riffles and non-turbulent units.

Salmonid freshwater habitat was similar in Caspar and Pudding creeks during summer 2013. The percentage of habitat unit types in both streams was not different, and habitat diversity indices were nearly identical. Both streams had few dam pool, off-channel, and plunge pool units. The gradient, sinuosity, alkalinity, and conductivity of the two streams were not different, and while stream flows were very low, stream flow and water temperatures were not appreciably different. Of the physical habitat variables we examined, 38% differed among the two streams. None of the fish cover or large wood variables was different between the two streams. This is probably because overhead fish cover and large wood abundance was similar in both streams. Average total fish cover was 22.6% (*SE* = 3.25%) in Caspar Creek and 20.3% (*SE* = 3.08%) in Pudding Creek. Cover percentages in our study streams were higher than Justice (2007), who estimated cover values between 5%-14% in two coastal California coho salmon streams in Humboldt County. Large wood abundance averaged 21.7 (*SE* = 5.05) pieces per 100 m in Caspar Creek and 28.2 (*SE* = 6.88) pieces per 100 m in Pudding Creek. These values are much lower than the 100-800 pieces of large wood per 100 m, reported by Bilby and Ward (1989) for undisturbed streams of variable sizes in western Washington.

Of the variables that differed between the streams, many are likely not biologically meaningful and others were within our measurement error. For example, the five substrate categories differed by less than 10% (two differed by less than 5%). These categories were estimated in the field in 5% increments such that a difference of <5% may be an artifact of our field methods. The reason Caspar Creek had higher percentages of boulder and cobble substrate than Pudding Creek may be because the sediment dams in the north and south forks of Caspar Creek have been removing fine sediment as part of the State Experimental Forest's studies on sediment and logging for over 50 years (Cafferata et al. 2011). Our results suggest that Pudding Creek had more spawning substrate (i.e., coarse gravel), and that the creek may be a slower stream, as indicated by the higher percent finer substrate materials compared to Caspar Creek. It is clear that Pudding Creek was deeper and had more surface area and volume of salmonid habitat than Caspar Creek. An average difference of 15 cm in residual pool depth and 8.5 m^3 in residual pool volume suggests that Pudding Creek provides a great deal more pool habitat than does Caspar Creek. These differences may help explain why Pudding Creek produces more coho salmon smolts than Caspar Creek (Gallagher et al. 2012).

It is not surprising that coho salmon were more abundant in pool habitats than in riffles and off-channel units, because it is well known that coho salmon prefer pools in summer (Bisson et al. 1988). Nickelson et al. (1992) found that coho salmon were more abundant in pools than other unit types in coastal Oregon streams during summer. Sharma and Hilborn (2001) found that watershed pool density was a good predictor of smolt density; a greater number of pools was associated with higher smolt production. Coho salmon density was not significantly associated with any habitat type in summer. In fall, as stream flows dropped and fish became more concentrated, coho salmon density was significantly higher in plunge pools than in riffles. Similar to our results, Lau (1994) found summer coho salmon density was significantly higher in pools than in riffles in Caspar Creek.

Unlike other studies (Everest and Chapman 1972, Bisson et al. 1988, CDWR 2004) that found steelhead trout prefer riffles and other high velocity areas over pools, we found that steelhead trout were significantly more abundant in pools in both summer and fall

2013 than in the other units we examined. This may be because we report fish abundance by age-class, whereas other researchers did not. Also, both Caspar and Pudding creeks are small streams with little stream flow in summer; riffles, although having moving water, did not have "high" velocities (i.e., riffle velocities were < 0.10m/s). In addition, 2013 was a drought year with very low summer flows. The density of YoY and Y+ steelhead trout was not different among habitat units in both summer and fall 2013. This finding corresponds with Lau (1994) who found no significant difference in steelhead trout density among habitat types in Caspar Creek. However, we found steelhead trout Y++ density was significantly higher in plunge pools than in the other unit types during both summer and fall 2013.

Coho salmon abundance and density were higher in Pudding Creek than in Caspar Creek in both summer and fall. While Pudding Creek was 25% longer than Caspar Creek and had deeper pools and more volume of stream habitat, it produced 13 times more parr. This difference is probably attributable to the fact that adult Coho salmon escapement was approximately 28.3 (95% *CI*, 14.4-53.3) times higher in Pudding Creek than in Caspar Creek during winter 2013 (Gallagher et al. 2013). Stream flows in the winter and spring of 2013 were low, so it is likely that redd scour was correspondingly low resulting in high egg-to-emergence survival in both streams. This could explain why coho salmon parr abundance in Pudding Creek during fall 2013 was well above the 2006-2013 average, even though adult escapement in 2013 (i.e., 248 coho salmon) was well below the 12 year average of 462 spawners (Gallagher et al. 2013). In Caspar Creek, escapement of coho salmon and resultant parr abundance in fall 2013 were both below the 12 year average. The magnitude of difference between proportion of spawners (28.3 times higher) and that of parr (13 times higher) in Pudding Creek is likely a result of density-dependent factors (Gallagher et al. 2012). Therefore, the difference in abundance between the two streams may be a synergy of differences in parental spawner abundance, habitat differences, and low winter and spring streamflow conditions during 2013. The difference in abundance between the two streams was also a result of the interaction of stream and habitat abundance (Figure 3), there were few coho salmon captured in riffles in Caspar Creek, whereas many riffles in Pudding Creek supported coho salmon.

Steelhead trout YoY abundance was significantly different between Caspar and Pudding creeks in summer but not during fall 2013. In contrast, steelhead trout YoY density was not significantly different between steams in either season. The reasons for the observed difference in abundance are likely similar to our explanation for coho salmon. There were approximately 4.85 times more steelhead trout adults in Pudding Creek than in Caspar Creek during winter 2013. This is similar to the difference we found between the two streams in summer steelhead trout YoY abundance. There was no difference in steelhead trout YoY abundance in fall 2013 between the two streams, as Pudding Creek only had approximately 1.8 times more fish than Caspar Creek. Apparent summer-to-fall survival of steelhead YoY was different between the two streams; it was much lower in Pudding Creek than in Caspar Creek (e.g., 0.25 vs 0.68, respectively). Steelhead trout mortality may have been due to competition with, and/or predation by, the high density of coho salmon in Pudding Creek during summer and fall 2013. That older age steelhead abundance was not different between the two streams is likely due to a lack of difference in adult escapement in the two streams in earlier years. From 2009 to 2012, steelhead trout escapement and redd estimates were not different between the two streams (Gallagher et al. 2013).

Our approach to understanding relationships between physical stream habitat and salmonid abundance differs from many previous studies in that we used a balanced sampling design and multivariate analyses. Factor analysis and negative binomial regression modeling allowed us to evaluate 17 variables commonly collected during stream habitat evaluations (Ropper et al. 2010, Bouwes et al. 2012) and reduce them into seven composite factors. Previous studies of relationships between physical stream habitat and salmonid abundance primarily used habitat classifications as sample units and correlation for determining significant relationships. These studies all suggest that coho salmon prefer pools, and steelhead trout prefer riffles (Swales et al 1986, Bisson et al. 1988, Nickelson et al. 1992, Lau 1994, Kruzic et al. 2001, CDWR 2004). Our ANOVA results, which also used unit type as the sampling unit, support these findings for coho salmon but not for steelhead. However, factor analysis did not indicate unit type as an important variable in any of the factors.

The factor names are generalizations of the combinations of variables comprising the loadings of the factors (Table 5). In other words, all the factors are a linear combination (i.e., construct) of all the variables, but some variables within the construct are more influential. The focus is on the most influential variables within a factor. Thus, factors are latent (un-observed) that define an underlying concept made up of phenomena that we are able to measure. Three of the 17 variables did not play a significant role in any of the factors: aquatic vegetation, percent bedrock, and unit type. Because previous research identified differences in abundance and density between habitat types (discussed above), we expected habitat unit type to be an important variable loading in the factors and to be associated with salmonid abundance. Unit type was probably not important, because most of the other variables were found in all unit types and pools were deeper, more voluminous, and contained more wet large wood than other unit types. Both bedrock and aquatic vegetation cover were not important because they were rare in both streams. Of the 100 units we sampled, only three had either bedrock or aquatic vegetation.

In the field, the variable dry large wood was defined as either single pieces of wood in the bankfull channel or dry log jams within and above the channel. The factor we called *volume and dry-large-wood* was made up primarily of log jams, which generally cause scour during winter; thus, the association between volume and large wood. The factor *wood* is composed of both wet and dry large wood and overhead wood cover, whereas the factor called *overhead vegetation* is made up of vegetation within 1 m of the water surface (Bouwes et al. 2012). Shrivel (1990) defined cover objects as things that provide fish protection or shelter and cover habitat as preferred levels of velocity, depth, light intensity, reduced social interaction, and reduced predation. The factor we called *wood* potentially contains all these elements of cover habitat, the factor *overhead vegetation* only provides reduced light intensity to the aquatic habitat. Increased light intensity is thought to increase predation risk (Shrivel 1990).

We interpreted the inclusion of fines and cobbles (negative coefficient) to indicate slow water in the factor we called *slow-water volume*. Similarly, we interpreted the loadings of fines and coarse and fine gravel to indicate *fast-water* in that factor. The association between fast water and dry wood in the factor *turbulent-stream and dry large wood* is likely due to the boulder and cobble variables being significantly different between the two streams. Consequently, we assumed the large wood component is related to bankfull wood deposited during high flows in faster water areas. The use of turbulent is slightly misleading, because both steams are low gradient and had drought-caused, very low stream flows in summer 2013.

The negative binomial regression modeling showed coho salmon abundance was positively associated with factors generally attributed to pools (i.e., *slow-water volume*) and negatively associated with factors related to riffles (i.e., *fast-water*) (Tables 5-6). Using correlation analysis, Bisson et al. (1988) found that coho salmon selected pools (i.e., deep, slow moving areas) over riffles (i.e., fast water). Kruzic et al. (2001) used multivariate analysis to show that coho salmon growth was significantly higher in pools than in riffles, which they primarily attributed to difference in water depth, a component of volume in our factor analysis. In our study, unit type was not statistically significant in any of the factors associated with coho salmon abundance, but unit volume was, probably because we found coho salmon in all habitat unit types and they were more abundant in pools compared to riffles (Table 4). Sutton and Soto (2010) found that coho salmon were congregated in cold-slow-water habitat with abundant, complex cover. Similar to Fausch (1993), we found that coho salmon were not associated with cover habitat. Young (2004) found that coho salmon occupied low-velocity pools and displaced steelhead trout into high-velocity riffles. Our results suggest that YoY steelhead trout prefer deep water areas with dry large wood and were negatively associated with fast water and overhead vegetation cover. Contrarily, Fausch (1993) found that age-0 (YoY) steelhead trout preferred areas of overhead cover. Steelhead YoY might select low-velocity areas due to metabolic needs if temperatures are high and food input limited by to low flows. However, water temperatures in both streams were below 16ºC, so high temperature is not likely why YoY steelhead selected low-velocity, high-volume areas in our study.

Older age steelhead trout were associated with the factors *volume and dry-large-wood* and *wood* (Table 6). They were either not associated with (Y++), or negatively associated with (Y+), the factors f*ast-water* and *turbulent-stream and dry large wood*, which are factors related to riffle habitats. Steelhead trout Y+ were also positively associated with slow water. As discussed above, this differs from other studies that found steelhead trout were primarily associated with riffles. The difference may be related to stream size; in larger streams and rivers, riffles have deeper water and larger substrate in which steelhead trout hide (Everest and Chapman 1972). Both Caspar and Pudding creeks are small streams with relatively shallow riffles. Bisson et al. (1988) found that steelhead trout preferred riffles but also used deep pools with high velocities in the center of the channel. Consistent with this finding, our results showed that steelhead trout abundance was significantly higher in pools than other unit types (Table 4), and they were associated with the factor *volume and dry-large-wood*. Unlike coho salmon and steelhead trout YoY, older steelhead trout were positively associated with the factor *wood*, and Y+ were positively associated with the factor *undercut banks*. These findings are consistent with other studies that found steelhead trout preferred both overhead and velocity cover (Butler and Hawthorne 1968, Fausch 1993).

Our results suggest that increasing low-velocity, high-volume habitat areas and decreasing high-velocity areas should provide more preferred habitat for coho salmon and steelhead trout in small coastal streams such as Pudding and Caspar creeks. It should be noted that 2013 was a drought year, conducing this study over multiple years might help elucidate if drought conditions influence habitat use by coastal salmonids. In particular, we found that plunge pools were, although rare, important for salmonids as streams dried in fall. These unit types are formed by large wood, and we anticipate an increase in this unit type resulting from large wood additions. Addition of large wood has increased habitat for salmonids and increased smolt production in most of the places it has been evaluated. Kratzer and Warren (2013) found that trout biomass could be expected to increase with increasing wood habitat in Vermont. Solazzi et al. (2000) increased salmonid habitat and smolt production by adding large wood to a coastal Oregon stream. Similarly, Johnson et al. (2005) found increases in habitat and salmonid abundance resulting from the addition of large wood. Treating a large portion of a salmonid stream by adding large wood (Roni et al. 2010) significantly increased the low-velocity, high-volume salmonid habitats (Jones et al. 2014) in coastal Oregon. These were the habitats that we found were preferred by salmonids in coastal California. We have shown that habitat associated with, or created and maintained by, large wood had higher abundance of salmonids in Caspar and Pudding creeks. In particular, we expect large wood additions to create more low-velocity-high volume areas for coho salmon, reduce fast water areas for both species, and provide more wood and undercut bank cover for steelhead trout.

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