

**Habitat Restoration and Channel Complexity in Lagunitas Creek, CA:
Implications for Endangered Coho Salmon (*Oncorhynchus kisutch*)**

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ABSTRACT

Habitat diversity is an essential component of healthy freshwater ecosystems. Streams with diverse physical and structural elements effectuate local habitat heterogeneity, which promotes adaptive divergence and resilience in fish populations. Urbanization and other human activities homogenize stream habitat, resulting in uniform physical and biological conditions frequently linked to declines in native fish populations. Recovery efforts employ in-stream restoration to artificially enhance habitat complexity, though the construction of off-channel habitat as a specific mechanism is less explored. To assess the effects of off-channel habitat on stream complexity and endangered coho salmon in Lagunitas Creek, California, I sampled four treatment sites (main channel with adjacent side channel) and their corresponding controls (main channel only). For each pairing, I gathered data to compare habitat heterogeneity, invertebrate and fish diversity, and coho salmon population density. Physical and structural habitat variation and fish diversity were generally higher at treatment sites than controls, but invertebrate diversity did not exhibit a clear differential trend. These results indicate that off-channel habitat is associated with enhanced channel complexity and biodiversity, which are conducive to maintaining stream habitat suitable for coho salmon. Accordingly, I found that treatment sites — particularly those with constructed side channels — supported substantially higher coho densities within paired sites and across all sites. Collectively, my results suggest that off-channel habitat as an approach to in-stream restoration may enhance physical and biological diversity and generate habitat favorable to endangered coho salmon.

KEYWORDS

restoration ecology, habitat heterogeneity, biodiversity, in-stream restoration, off-channel habitat

INTRODUCTION

Urban development has precipitated large-scale land use change and necessitated the application of restoration ecology across a range of wildlife habitats. In freshwater environments, native fish abundance and diversity are diminished by human activities that homogenize stream habitat (Moyle and Mount 2007, Poff et al. 2007, Goertler et al. 2018). Habitat complexity is an essential driver of adaptive divergence, a process in which heterogeneous environmental conditions stimulate phenotypic variation and adaptive capabilities in fish populations. Diverse phenotypes lead to diverse survival strategies within the same landscape, increasing the likelihood that some populations will persist anthropogenic stressors and ensure species preservation (Hendry 2001, Elmqvist et al. 2003, Bottom et al. 2009, Thorson et al. 2018). Stream restoration is a well-established approach to improve ecosystem health and stability, but specific execution methods are highly situational and remain debated. Homogenized stream systems reduced to uniform physical, structural, and biological features are often recovered using in-stream restoration, a method that artificially recreates habitat heterogeneity (Penaluna et al. 2018). While popular in practice, the efficacy of in-stream restoration in enhancing native fish populations has been questioned by a number of studies. Any form of human interference with natural systems, even well-intentioned restoration efforts, can neglect ecological intricacies and generate adverse effects. Evaluating the capacity of in-stream restoration to create local habitat complexity and support native fish communities is crucial to informing future management efforts.

Many studies that assessed in-stream methodology documented positive outcomes on stream habitat and, by extension, stream biodiversity. Restoration involves the manual placement and rearrangement of physical elements within a stream reach — often in mimicry of undisturbed reaches — with the ultimate goal of increasing reach-scale structural complexity. This approach includes the installation of in-stream structures such as woody debris, sediment, and boulders; the propagation of native riparian vegetation; the reconfiguration of straightened channels; and the construction of off-channel habitat (Roni 2019). Some research found this approach to benefit native fish species, either through direct increases in population abundance or diversity at the restored reach (Smith and Mather 2013, Shirey et al. 2016, Walrath et al. 2016), or by indication of improved water quality and resource availability (Verberk et al. 2006). These findings support

my hypothesis that in-stream restoration can generate diverse environmental conditions conducive to restoring native fish populations.

Other evidence questions the effectiveness of in-stream restoration and even suggests a hindrance to population recovery if artificial complexity fails to mimic natural stream dynamics. One study, for example, found that fish assemblages in a reconfigured stream channel were more homogenized than those at an unrestored control site, which implies decreased adaptive diversity and resiliency (Clark and Montemarano 2017). Some research suggests that structural complexity is only beneficial if applied at a scale relevant to target biological communities (Lepori et al. 2005), which is not always accomplished with in-stream restoration (Palmer et al. 2010). Further concerns have been raised about whether studies citing increased fish abundance or density in restored areas are simply reflecting congregations rather than actual population increases (Roni 2019). Research discrepancies emphasize the need for continued exploration of how habitat enhancements impact native fish in stream systems, including different mechanisms for implementation.

The utilization of off-channel habitat to increase reach-scale diversity presents an evident research gap in stream restoration ecology. Off-channel habitat includes side pools and side channels, which parallel the mainstem of a stream and provide diverse ecological niches for freshwater species to exploit. Side habitat differs from main channel habitat in a range of chemical and physical properties including channel depth, flow velocity, temperature, and dissolved oxygen content (Sobotka and Phelps 2017). Native fish can exploit the diverse habitat features offered by side channels to improve population abundance and diversity (Huang et al. 2019), as well as reap the long-term benefits of adaptive divergence and enhanced resiliency. Despite these advantages, drastic structural change like off-channel habitat construction can impede salmon populations in unforeseen ways as they carry out their complex migratory life cycle. The current body of research lacks comprehensive evaluation of the relationships between side channel habitat, stream heterogeneity, and the vitality of native fish communities—a gap that my research will address.

This study investigates the influence of off-channel habitat on stream complexity at natural and constructed side channel sites in Lagunitas Creek, California, and the resulting implications for a resident population of endangered coho salmon. To evaluate these impacts, I address the following research questions:

1. *Have physical and structural complexity been enhanced by off-channel habitat?*
2. *Does off-channel habitat improve creek biodiversity?*

3. *How has habitat complexity influenced coho salmon population densities?*

Question (1) will quantify and contrast stream channel complexity at sites with and without adjacent off-channel habitat. I will measure several physical and structural in-stream elements to assess heterogeneity: channel width, channel depth, volume of large woody debris (LWD) structures, conductivity, and temperature. I expect greater variation in these metrics at sites with off-channel habitat. For question (2) I will gather abundance data to calculate macroinvertebrate and fish diversity, both of which I expect to be higher at channels comprising side habitat due to increased niche availability and stream integrity. Question (3) will analyze coho salmon population densities to reflect species habitat preference. I predict higher densities at reaches with side channels because they offer diverse physical and biological features favorable to coho health and resiliency. My study examines the effects of off-channel habitat on stream complexity, biodiversity, and coho densities in Lagunitas Creek, California. Results will elucidate the efficacy of in-stream restoration and inform future management plans to support the preservation of a native, endangered, and ecologically valuable coho salmon population.

METHODS

Study site and species

Located in Marin County, California, the Lagunitas Creek Watershed stretches 22 miles from Mount Tamalpais to Tomales Bay and is home to one of the largest remaining coho salmon populations in the state (ESA 2018). As an anadromous species, coho require access to healthy freshwater streams for the rearing and spawning stages of their life cycle. Lagunitas Creek and its tributaries provide this critical habitat for a highly endangered population of coho salmon designated the Central California Coast Evolutionary Significant Unit (ESA 2018). However, the watershed has historically been and continues to be impaired by a number of anthropogenic disturbances, including urban residential development, dam construction, water diversions, channel reconfiguration, loss of floodplain connectivity, and removal of complex structural elements such as large woody debris (Carlisle et al. 2018, ESA 2018). Substantial habitat loss and homogenization resulting from these disturbances have triggered drastic declines in the abundance of coho salmon and other native fish in the region (ESA 2018).

The chief limiting factor for coho populations in Lagunitas Creek is inadequate winter habitat, given the greatest declines in abundance are observed between fall and spring (ESA 2018). Off-channel habitat is an important component of stream systems because it offers diverse habitat niches that can be exploited by fish, including refuge from high winter flows with velocities that may overpower juvenile salmonids. With coho populations nearing extinction levels (ESA 2018) and the ecological integrity of the watershed at stake, recent restoration projects at Lagunitas Creek have focused their efforts on reconstructing off-channel habitat for increased stream complexity. Consequently, the creek provides an ideal study system for executing my research objectives.

Sampling regime and response variables

Fieldwork took place over four days in September, each reserved for data collection at one of four designated study areas along Lagunitas Creek. I selected each study area based on the presence of a suitable treatment site — one that encompassed off-channel habitat — and a corresponding control site with enough geomorphological similarity to account for relevant confounding variables. Each treatment site comprised one main channel and one adjacent off-channel area, either a side channel or side pool (see Appendix A for example site map), with the exception of Site T3 which included two segregated off-channel habitats. Side habitat was naturally occurring at two of the four treatment sites, sites T1 and T2, whereas the other side channels were artificially constructed to increase stream complexity. In total I sampled 13 locations within Lagunitas Creek (see Appendix B for site photos and summary table) and gathered data for each of eight quantitative response variables: channel width, channel depth, temperature, conductivity, per unit volume of large woody debris (LWD), macroinvertebrate diversity, fish diversity, and coho salmon population density. I compiled main channel and side channel datasets for each treatment site, such that results were representative of comprehensive habitat conditions available in treatment areas and could be directly compared to control site results.

Quantifying physical and structural habitat complexity

At each sampling location I used a standard field tape measure to determine total length (m) of the defined reach as a sum of its pool and riffle segment lengths, then placed evenly

distributed transects throughout. I recorded channel width (m) at each transect and used a handheld YSI Professional Plus multiparameter sensor to survey water metrics at three evenly spaced points across the breadth of the transect line. Water quality data included channel depth (cm), temperature (°C), and conductivity ($\mu\text{S}/\text{cm}$). To quantify variability of LWD structures, I measured the length (m) and diameter (cm) of all fully or mostly submerged woody debris pieces, then performed cylindrical volume calculations to obtain a distribution of per unit volumes (m^3).

To compare physical and structural heterogeneity across study sites, I used R to generate summary statistics for each of the five habitat variables at all treatment/control site pairings. Calculations were based only on data from pool transects to account for the large amount of variation expected between riffle and pool habitats. In addition to mean and standard deviation, sites were assigned a coefficient of variation (CV) that I used to assess whether some or all of the habitat features exhibited greater diversity in treatment reaches.

Macroinvertebrate sampling

To assess macroinvertebrate diversity, I collected a composite D-net sample at each stream reach. After surveying the area, I identified distinctive microhabitats within the channel that could shelter diverse macroinvertebrate communities (see Appendix C for microhabitat descriptions) and sampled each of them, working downstream to upstream to minimize disturbances. To collect each subsample, I placed a 500 μm mesh D-net immediately downstream of a 1x1 ft area within the microhabitat. If medium to large sized rocks were present, I used my hands to remove debris and guide it into the collection net, then discarded the rocks outside of the sampling area. I disturbed the streambed for 60 seconds, either by gently patting it with my hands in slow moving waters or vigorously rearranging sediment in high velocity areas. Following the disturbance, I surfaced the D-net and dipped it in the stream to consolidate all debris to its bottom portion, careful not to take in any new material. For each channel, I rinsed the contents of the net from all microhabitat subsamples into the same storage container with 70% ethanol solution to assemble a composite D-net sample.

Due to time constraints, composite samples were processed for only four of the eight study sites— C1, T1, C2, and T2. I chose to analyze samples from the two treatment sites with naturally occurring side habitat, as opposed to those with constructed side channels, because there was

greater opportunity for invertebrates to colonize the area. In the lab, I ran samples through a 250 μm sieve to discard fine sediment and used a plankton splitter to subset each sample into halves. I randomly selected one of the halves for further processing with the goal of reaching 500 individuals, in accordance with the California SWAMP protocol for sampling macroinvertebrates. I used a Leica S6 Stereo Zoom microscope at medium to high magnification to sort and identify all individuals to Order (see Appendix D for equipment photos). After recording abundance values for each group, I stored the invertebrates in 70% ethanol preservative solution.

To compare macroinvertebrate diversity between composite samples from treatment and control sites, I generated diversity scores in R using the Shannon Index calculation. This metric is used frequently in ecological literature because it accounts for both evenness and abundance within communities.

Surveying fish community composition

I used video footage to gather data for my analysis of fish diversity and coho salmon population density. To capture maximum fish activity at each sampling location, I deployed a total of four underwater GoPro cameras in areas of the stream where coho and other resident species tend to congregate. Dependent on channel depth and lighting in deployment locations, I sometimes stacked two camera lenses on top of one another for improved visibility. After 30 minutes, I removed all cameras from the stream in the same order that I had placed them. Footage had already been collected for several locations over the summer using identical sampling methodology, so I recorded videos only in the remaining reaches.

To quantify fish diversity in each stream, I calculated Shannon Index scores based on maximum abundance by species obtained from the video footage. The four native fish species observed in this study were coho salmon (*Oncorhynchus kisutch*), steelhead trout (*Oncorhynchus mykiss*), California roach (*Lavina symmetricus*), and three-spined stickleback (*Gasterosteus aculeatus*). I also detected individuals in the subfamily Cottoidea, but because sculpin are bottom-dwelling they could not be identified to species with the dimly lit streambed footage. That said, to maintain coherence in my discussion of taxonomic diversity, I will group sculpin with the other fish groups and refer to it as a species.

For each individual or stacked camera unit in the channel, I pulled a consecutive five-minute sample clip from the full 30-minute recording that showed the highest level of fish activity or abundance. I divided the sample clip into ten 30-second segments and within each segment selected one freeze frame that featured the greatest number of fish. I identified and recorded species counts in each freeze frame to determine maximum abundance by camera, then selected the highest abundance value for each species across all cameras in the channel. Representative of community composition in the stream reach, those maximum abundance values were used to calculate Shannon Index scores at each site.

Assessing coho salmon densities

To assess differences in coho salmon population density between treatment and control sites, I evaluated the same video footage used in my fish diversity analysis. Additionally, at each filming location in the stream reaches, I used a meter stick to record volumetric dimensions captured by the camera's underwater field of view. I applied the volume formula for a triangular prism to account for angle distortion and generated estimated channel volumes (m^3) at each camera site. Using counts from the fish diversity dataset, I divided maximum coho salmon abundance by estimated channel volume to obtain a population density for each camera unit. I then averaged all of the individual camera densities to generate an average coho density value for each stream reach.

RESULTS

Physical and structural habitat variables

I found that stream habitat at treatment sites exhibited greater physical and structural complexity compared to control sites. Although the data did not show greater variation for all habitat variables at all treatment sites relative to their controls, there was a strong trend indicating an association between side channel presence and habitat heterogeneity.

Channel width, channel depth, and per unit volume of large woody debris (LWD) had higher coefficients of variation (CVs) at treatment sites within each of the four treatment/control pairs (Tables 1a, 1b, and 1c). I also found that for each of these variables average CV was higher

at treatment sites than control sites (Table 1d). These results are reflected in boxplots for each variable displaying larger spreads at treatment sites than the corresponding controls. (Figure 1).

Table 1. Summary statistics and average CV for channel width, channel depth, and LWD volume. Mean, standard deviation, and coefficient of variation for (a) channel width, (b) channel depth, and (c) per unit volume of LWD across all study sites. Table (d) shows higher average CVs at treatment sites for all three variables.

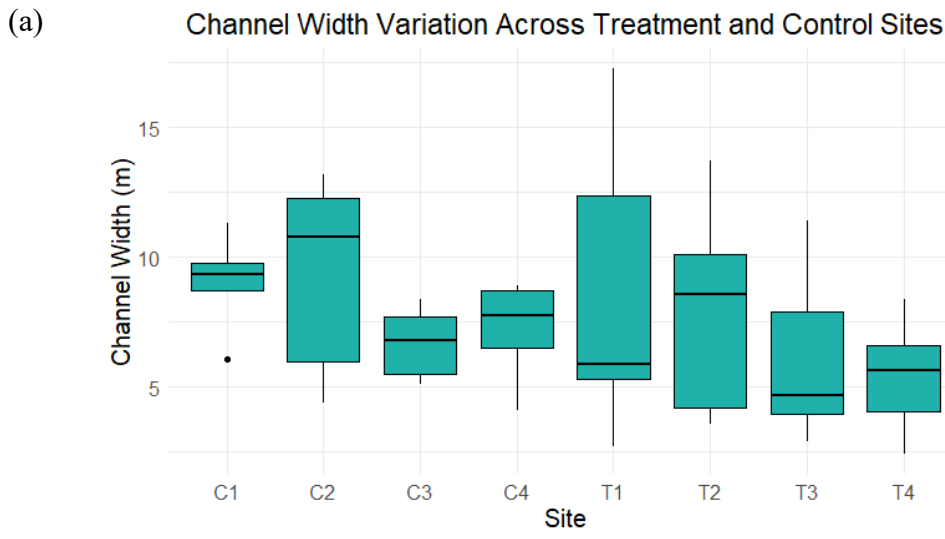
(a)	Site	Mean	Std. Dev.	CV
	C1	9.3000	0.449242	0.048305570
	T1	6.6500	2.986491	0.449096440
	C2	11.775	1.111203	0.094369710
	T2	8.1000	3.451956	0.426167400
	C3	7.4250	0.830252	0.111818430
	T3	6.5294	2.744971	0.420400980
	C4	7.6750	0.836796	0.109028770
	T4	5.9875	1.831206	0.305838150

(b)	Site	Mean	Std. Dev.	CV
	C1	56.2500	13.081041	0.232551800
	T1	58.5417	25.774911	0.440283200
	C2	52.1667	17.351098	0.332608900
	T2	40.4762	15.718203	0.388332100
	C3	28.9167	11.919871	0.412214600
	T3	10.2500	8.258604	0.805717500
	C4	42.1667	13.189757	0.312800600
	T4	42.3750	20.921827	0.493730400

(c)	Site	Mean	Std. Dev.	CV
	C1	1.1063	2.463364	2.226688000
	T1	0.8695	2.992005	3.441111000
	C2	0.0538	0.092380	1.717109000
	T2	0.4720	1.499600	3.177271000
	C3	0.0020	N/A	N/A
	T3	0.5225	1.092770	2.091576000
	C4	0.0502	0.065033	1.294796000
	T4	0.0158	0.038432	2.438172000

(d)	Variable	Avg. CV (T)	Avg. CV (C)
	Channel width	0.4003757	0.090881
	Channel depth	0.5320158	0.322544
	LWD Volume	2.7870325	1.884349

T = treatment C = control



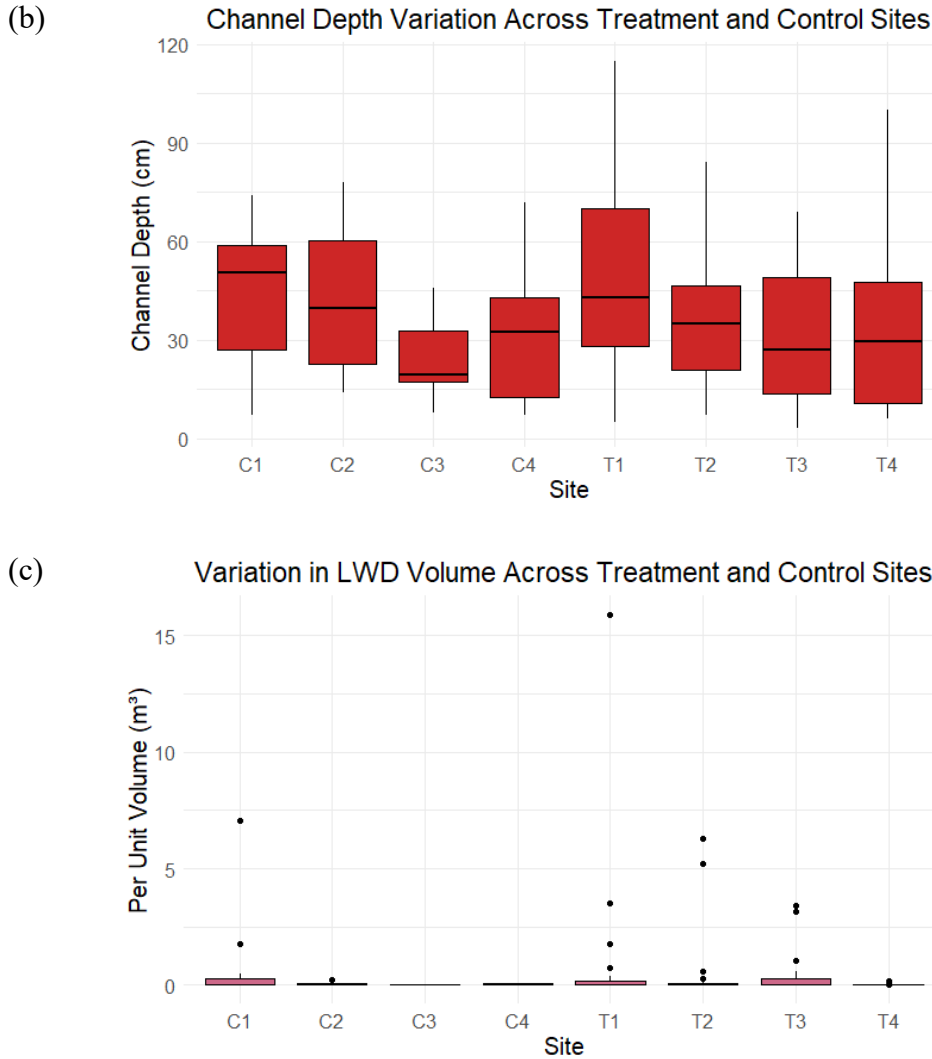


Figure 1. Variation in channel width, channel depth, and LWD volume. Boxplot comparisons of (a) channel width, (b) channel depth, and (c) per unit volume of LWD showing greater variation at treatment sites.

Conductivity and temperature data were not as consistent as other habitat metrics but still suggested an association between the presence of off-channel habitat and enhanced habitat complexity. CVs for conductivity were higher only at sites T1, T2, and T3 relative to their controls; however, the difference in variation between sites C4 and T4 was minimal (Table 2a). Additionally, average CV for conductivity at treatment sites (0.00891) was higher than that at control sites (0.00287). I detected greater thermal variation only at sites T1 and T3 relative to their control channels (Table 2b), but like the other habitat variables, temperature demonstrated higher average CV at treatment sites (0.01441) than controls (0.00929). Differences in variation by site are also shown in boxplot spreads for the variables (Figure 2).

Table 2. Summary statistics for conductivity and temperature. Mean, standard deviation, and coefficient of variation for (a) conductivity and (b) temperature across all study sites.

(a)	Site	Mean	Std. Dev.	CV	(b)	Site	Mean	Std. Dev.	CV
	C1	139.1333	0.177525	0.001275935		C1	13.5667	0.049237	0.003629233
	T1	138.6792	1.461678	0.010540000		T1	13.3125	0.287890	0.021625512
	C2	130.8167	0.689972	0.005274339		C2	11.6417	0.223437	0.019192899
	T2	130.2095	1.430351	0.010984997		T2	11.4000	0.181659	0.015935002
	C3	144.0583	0.206522	0.001433603		C3	13.7250	0.045227	0.003295206
	T3	143.2265	1.606862	0.011219029		T3	13.5971	0.200734	0.014763042
	C4	144.9667	0.505125	0.003484423		C4	13.6417	0.150504	0.011032684
	T4	145.2500	0.425288	0.002927970		T4	13.5500	0.072232	0.005330739

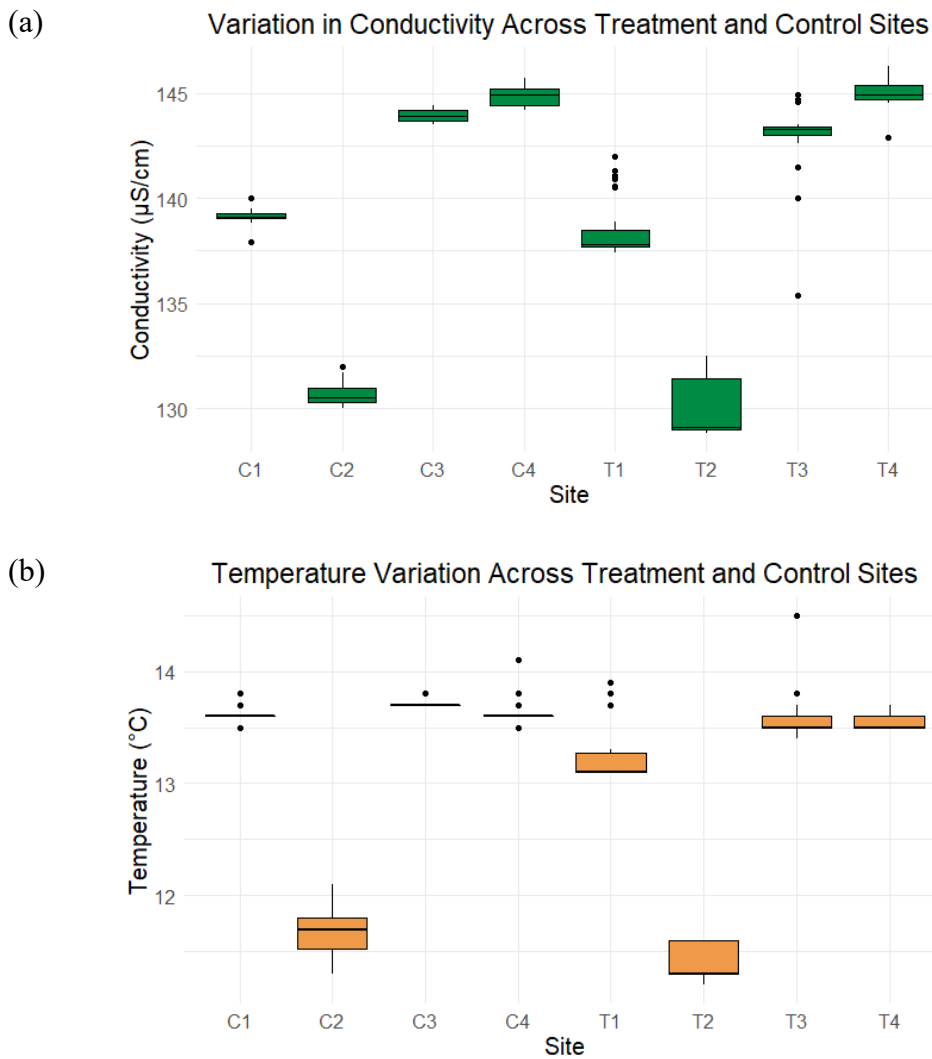


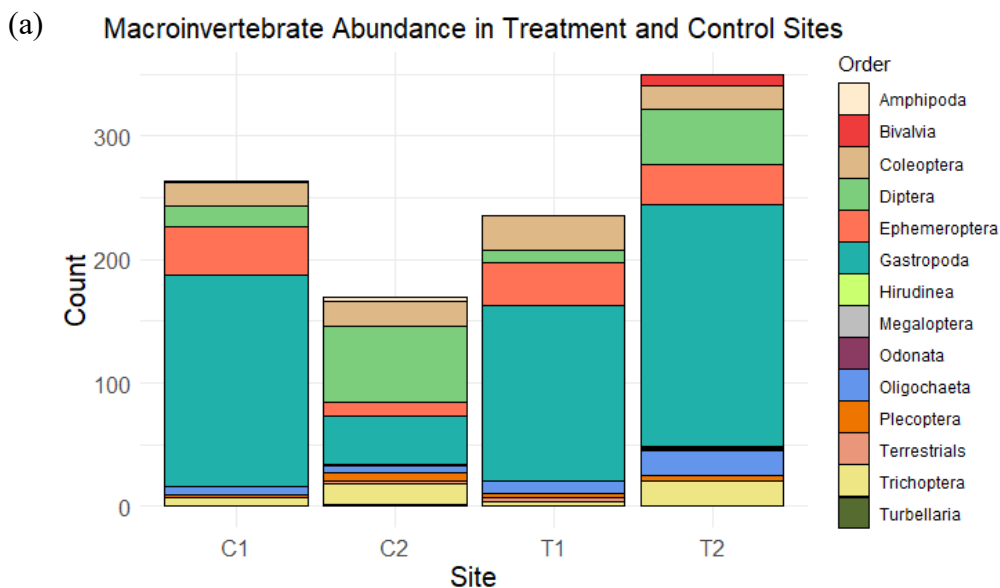
Figure 2. Variation in conductivity and temperature. Boxplot comparisons of (a) conductivity and (b) temperature showing greater variation at most treatment sites compared to their control reaches.

Diversity in macroinvertebrate and fish communities

I determined that treatment sites generally exhibited higher biodiversity when accounting for both fish and macroinvertebrate communities, though not all individual channels followed this trend. Shannon Index scores based on invertebrate abundance by Order were higher at sites T1 and C2 than their respective paired reaches (Table 3), meaning there was no clear association between macroinvertebrate diversity and off-channel habitat at treatment sites. Average diversity based on Shannon Index scores was lower for the two treatment reaches (1.3771955) than for the respective controls (1.4686015). I visualized community diversity in two stacked bar charts— one with all invertebrate Orders identified from the stream samples (Figure 3a) and one with Gastropoda excluded (Figure 3b). Abundance values for Gastropoda were exceedingly high relative to other Orders, so the latter bar chart better distinguishes variation in abundance across species.

Table 3. Macroinvertebrate diversity across four study sites. Shannon Index scores quantifying invertebrate diversity at treatment and control sites within study areas 1 and 2.

Site	Shannon Index Score
C1	1.177803
T1	1.266334
C2	1.759400
T2	1.488057



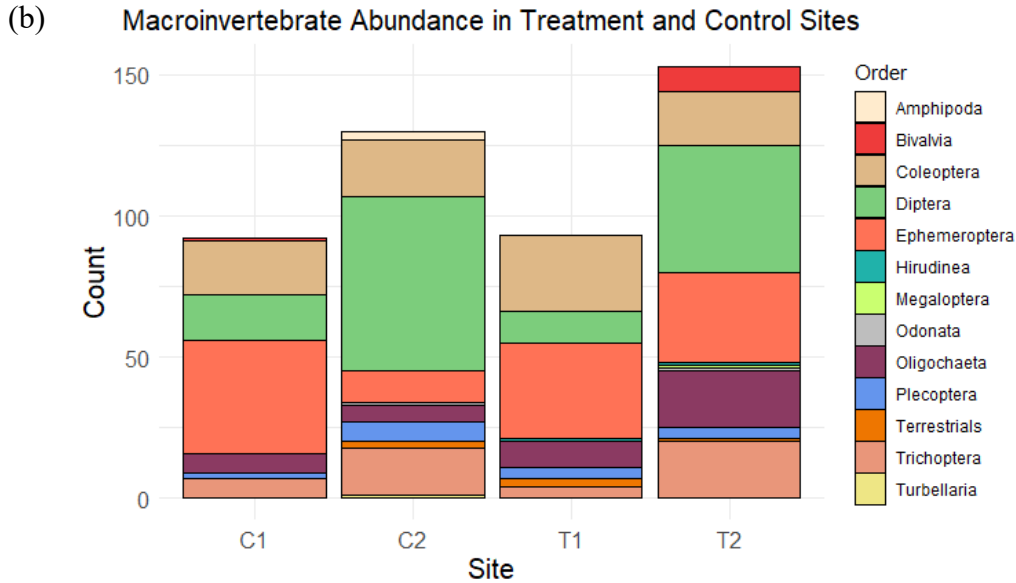


Figure 3. Macroinvertebrate abundance by Order. Stacked bar charts (a) including and (b) excluding the Order Gastropoda to visualize variation in invertebrate abundance across treatment and control sites.

I detected greater fish diversity at most treatment sites relative to their paired control channels. Shannon Index scores calculated from maximum abundance across five native fish species demonstrated higher diversity at all but one treatment site, T2 (Table 4). The average diversity score for treatment sites (1.179846) was slightly greater than that for the corresponding control reaches (1.130701). I displayed results for fish diversity in a stacked bar chart to illustrate overall variation in abundance between sites (Figure 4).

Table 4. Fish diversity and maximum abundance by species. Maximum abundance values represent the highest number of individuals by species that I detected in sample clips across all cameras deployed in the study site. I used these values to calculate Shannon Index scores to quantify fish diversity across all eight study sites.

Site	Max Coho	Max Roach	Max Steelhead	Max Stickleback	Max Sculpin	Shannon Index Score
C1	2	11	2	5	0	1.135901
T1	5	14	3	8	2	1.393497
C2	2	2	1	5	0	1.220607
T2	2	10	1	3	0	1.040840
C3	1	1	3	1	0	1.242453
T3	16	36	6	14	1	1.262166
C4	2	10	0	5	0	0.923841
T4	9	43	2	20	0	1.022882

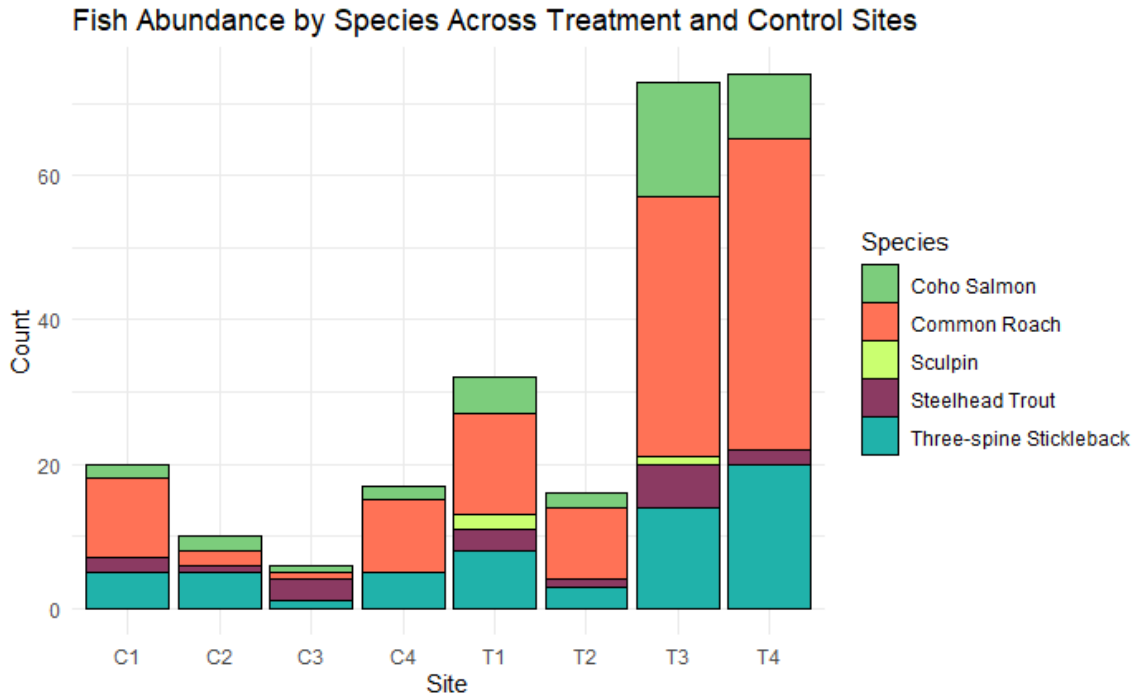


Figure 4. Fish abundance by species. Stacked bar chart showing variation in fish abundance across study sites.

Coho salmon population densities

Across treatment sites, I observed a much larger presence of coho salmon in regard to both relative and absolute comparisons. All four treatment areas exhibited higher population densities than their respective control reaches (Table 5), and the average of all averaged densities across treatment reaches (9.32 individuals/m³) surpassed that of control reaches (1.78 individuals/m³) profusely. For visualization I partitioned the data by channel rather than site to highlight the significant contrast between coho densities at control sites and individual treatment reaches, particularly the constructed side channels at sites T3 and T4 (Figure 5).

Table 5. Average coho salmon population density by channel. I used maximum coho abundance values to calculate average population density (# individuals/m³) first by individual camera, then by channel.

Channel	Avg Density
C1	1.91
T1-M	2.30
T1-S	9.17
C2	1.59
T2-M	2.49
T2-S	4.45
C3	1.36
T3-M	6.16
T3-S-SM	4.72
T3-S-LG	24.20
C4	2.27
T4-M	6.17
T4-S	24.26

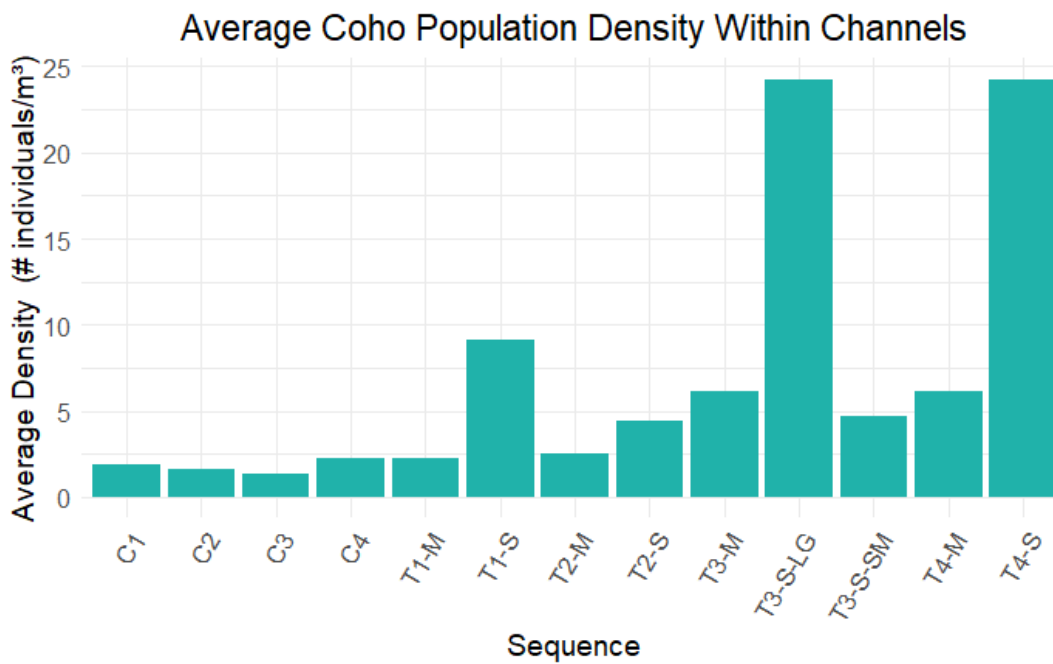


Figure 5. Average coho salmon densities. Average coho population density at control sites and individual treatment channels. Averages were significantly higher at treatment sites than controls, especially the constructed side channels T3-S-LG and T4-S.

DISCUSSION

Freshwater habitats homogenized by human activity can debilitate stream biota (Moyle and Mount 2007, Poff et al. 2007, Goertler et al. 2018) and are often remediated by artificially restoring channel complexity. It is important to assess the effects of habitat heterogeneity on stream systems in order to preserve ecological integrity and provide habitat conditions that support native fish populations. I gathered quantitative data on direct and proxy indicators of coho salmon health in Lagunitas Creek at sites both enhanced and unenhanced by off-channel habitat. My results showed that treatment sites generally encompassed greater physical and structural habitat complexity as well as higher biodiversity and coho salmon population densities. This suggests that side channel habitat which augments stream heterogeneity may benefit endangered coho populations in Lagunitas Creek, and that in-stream restoration should be considered for future management projects to promote species resiliency amid pervasive urban land-use disturbances.

Physical and structural habitat complexity

I found from analyzing several physical and structural stream elements that sites comprising off-channel habitat tend to exhibit greater heterogeneity than those with one channel only. Three habitat variables — channel width, channel depth, and volume of large woody debris (LWD) — produced higher coefficients of variation (CVs) at all individual treatment sites and a higher average CV for treatment sites than for controls. These results suggest that coho salmon in Lagunitas Creek, as an endangered evolutionary significant unit, may benefit from adaptive divergence induced by complex habitat features at side channel sites. For instance, studies have cited population declines in coho and other salmonids during high winter flows in streams that provide limited overwinter habitat (McMahon and Hartman 1989, ESA 2018). Woody debris that varies in size and spatial distribution creates a mosaic of structures that offer coho refuge from high velocity flows and potentially from larger predators (McMahon and Hartman 1989). The high level of variation that I detected in LWD volumes at treatment sites could therefore be exploited by juvenile coho to enhance overwinter survivability and long-term capacity for adaptive divergence.

Conductivity and temperature data were overall less diverse than that of the other habitat variables but still trended towards higher variation at treatment sites compared to controls. I expected these habitat metrics to vary the least because they normally fluctuate between larger landscape areas, such as stream networks or entire watersheds, but were measured only at reach scale. My results confirmed this prediction— CV values for both conductivity and temperature were definitively low. This could be a result of small sample size, as reach-scale sampling may not have captured more widely dispersed variation in these variables. Additionally, CVs for conductivity were higher only at three of the four treatment sites and temperature only at two of the four. It is possible that site T2, one of the treatments that did not demonstrate higher thermal variation, was influenced by its being located in a redwood canyon with high canopy cover, which may have created homogenous cool water temperatures. The summary statistics I calculated show that site T2 had the lowest average temperature of all eight study sites (Table 2b). Although the data did not agree comprehensively across treatment sites, conductivity and temperature both had higher average CVs at treatment sites than controls which provides physical habitat complexity for coho salmon to exploit. Armstrong et al. (2013) showed that coho utilize thermally heterogeneous waters to maximize their digestive capacity and increase overall growth rates.

My results demonstrate an association between off-channel habitat, in-stream complexity, and biological diversity. Studies show that diverse fish communities are positively associated with variation in both conductivity (Huang et al. 2019) and water depth (Gorman and Karr 1978, Walrath et al. 2016, Huang et al. 2019). Likewise, I found that treatment sites trending towards higher CVs for conductivity, channel depth, and other habitat conditions also encompass higher fish diversity. This is beneficial to coho salmon because biodiversity is a well-documented facet of healthy aquatic ecosystems.

Macroinvertebrate and fish biodiversity

Treatment sites produced higher biodiversity than their controls when collectively accounting for both macroinvertebrate and fish community diversity. My results coincide with those of numerous other studies that cite greater biological diversity in streams naturally or artificially enhanced by habitat variation (Miller et al. 2010, Kail et al. 2015, Walrath et al. 2016, Huang et al. 2019). This evidence supports my hypothesis that physical and structural

heterogeneity generated by off-channel habitat contributed to greater biodiversity within Lagunitas Creek, and consequently to improved ecological stability supportive of coho salmon and other native fish populations.

I was surprised to find that Shannon diversity scores for macroinvertebrates were higher only at one of the two treatment sites for which samples were processed. This outcome contradicts multiple studies that detected greater invertebrate diversity in areas where in-stream restoration generated supplemental habitat heterogeneity (Verberk et al. 2006, Miller et al. 2010, Kail et al. 2015). The discrepancy could very well be the result of small sample size, as time restrictions prevented me from processing composite samples from all 13 stream reaches. My results could also convey that not all off-channel habitats have the same capacity to foster biodiversity. Sites T1 and T2 were the treatment areas with naturally occurring side channel habitat, but only T1 surpassed its control channel with a higher diversity score. Photos of each side channel (see Appendix B, Figures B2a and B2c) reveal that T2-S is a small side pool while T1-S is a much wider and deeper pool area, potentially with greater resource and spatial capacity to support more diverse invertebrate communities. This offers an important insight for guiding off-channel restoration efforts in Lagunitas Creek: not all natural side habitat is created equal, and the construction of artificial side habitat should mimic in-stream dynamics proven to promote macroinvertebrate diversity in natural side channels.

Fish communities reflected higher Shannon Index scores at three of the four treatment sites than at the corresponding controls, as well as a higher average diversity at treatment sites. My results align with many other studies that found greater variation in fish assemblages at stream sites that exhibit heterogeneity in substrate, channel depth, flow velocity, woody debris, and other habitat metrics (Smith and Mather 2013, Walrath et al. 2016, Huang et al. 2019). A possible explanation for outlier site T2, which did not exhibit a higher Shannon Index score, is that the video footage used to obtain species counts failed to reflect all diversity present in the stream. While the videos are meant to be representative of the entire reach, they only completely display diversity in channel areas that fall within the collective fields of view of the deployed cameras. Streams with larger main channels such as T2, which had among the highest channel width and channel depth averages (Tables 1a and 1b), may have exhibited lower diversity because not all fish activity was captured by the cameras.

Although invertebrate diversity was not consistently higher at treatment sites, I speculate that overall biodiversity was enhanced after factoring in the diversity of fish assemblages detected at treatment areas. Aquatic invertebrates and fish are both prevalent indicators of stream health and local biodiversity owing to their long life cycles, significant ecological value, and sensitivity to water quality conditions (Hyatt and Godbout 2000, Deborde et al. 2016). As biodiversity is regarded a fundamental component of robust and resilient freshwater ecosystems (Lepori et al. 2005, Poff et al. 2007, Palmer et al. 2010), it follows that my detection of increased diversity among fish and invertebrate communities at treatment sites may enhance stream habitat on which local coho populations rely. This finding importantly coincides with my analysis of habitat heterogeneity in Lagunitas Creek. Stream reaches encompassing side channel habitat generally demonstrated greater physical and structural complexity and heightened biodiversity, both of which generate habitat conditions conducive to coho salmon survival and resilience.

While my results indicate an association between reach-scale habitat heterogeneity and stream biodiversity, some research suggests that in-stream restoration is inadequate when applied at such a small scale. Several studies found that there is no statistically significant difference between macroinvertebrate and fish diversity at stream sites enhanced and unenhanced by habitat complexity (Lepori et al. 2005, Palmer et al. 2010, Verdonschot et al. 2016), and one even documented lower diversity at treated areas (Clark and Montemarano 2017). The authors concluded that scale is extremely important in determining the efficacy of in-stream restoration, and Lepori et al. (2005) asserted that habitat complexity will not promote biodiversity if implemented at a landscape scale which fails to enhance target biological communities. Most in-stream restoration occurs at reach scale, as did the Lagunitas Creek project in 2018. However, some research contends that management efforts should prioritize catchment-scale solutions that promote recovery within the entire watershed (Palmer et al. 2010), rather than reach-scale restoration that may yield biodiversity incapable of supporting aquatic communities holistically or in the long term (Rubin et al. 2017). While critical to addressing widespread homogenization in stream systems, catchment-scale restoration is often timely, expensive, logistically challenging, or otherwise infeasible. Existing literature augmented by my empirical findings demonstrate the benefits of reach-scale restoration sufficiently enough, I surmise, to defend off-channel habitat construction at Lagunitas Creek for diversifying habitat conditions favorable to endangered coho salmon.

Coho salmon densities

In congruence with results from my previous two research questions, I found that all treatment sites reflected higher coho salmon population densities than did their corresponding control reaches. Other studies have presented analogous evidence. Roni and Quinn (2001), using an experimental design similar to my own, found higher population densities of coho juveniles at stream sites where habitat had been augmented with large woody debris structures. One study monitored long-term effects of enhanced habitat heterogeneity on local fish communities and found that restoration not only increased fish counts but also prompted a shift in community composition from nonnative to native fish species (Shirey et al. 2016). This suggests that coho salmon native to the Lagunitas Creek Watershed may benefit from in-stream restoration through both increased population abundance and decreased competition with nonnative species.

Although I predicted the data to reveal higher coho densities at treatment areas, I was surprised to observe such a substantial deviation from those values at control reaches—the average of all average coho densities was over five times greater at treatment sites than at controls. When I analyzed density by individual channel rather than site, I found that T3-S-LG and T4-S were the two largest contributors to such a high average across treatment sites. This is an exciting outcome, as both channels were constructed with the primary goal of enhancing habitat heterogeneity to support local coho in Lagunitas Creek. This demonstrated success can inform future projects about specific habitat features that will improve restoration outcomes.

It is important to note that accuracy of my results is restricted by the dubiety of my video analysis methodology. The underwater footage I used to determine population density at each site provided conclusive data only for stream areas captured in each camera's field of view. Those values do not definitively describe density throughout the entire channel, though the deployment of multiple cameras in areas of concentrated fish activity was intended to reflect holistic community composition as best as possible. The results of a study by Roni (2019) also expressed concern that observed increases in population density at treatment sites could be reflecting congregations of coho salmon, rather than genuine population recovery. Even so, increased coho densities at treatment sites implies that the population prefers stream reaches supplemented by side channel habitat. Physical and structural heterogeneity at these sites offer coho the chance to diverge

for niche specialization and increased species resiliency; therefore, I argue that habitat complexity bolsters coho survivability, even if population densities may reflect superficial congregations.

As the response variable in this study that most directly measures the impacts of habitat heterogeneity on coho salmon, it follows that population density coincided with the outcomes of other proxy variables which I argue have probable positive influence on local populations. This sustains my hypothesis that physically and biologically diverse off-channel habitat may provide habitat more suitable for coho than do homogeneous control channels.

How does off-channel habitat impact stream complexity and endangered coho salmon?

My results collectively showed that enhanced habitat complexity associated with off-channel habitat in treatment areas contributes to the establishment of physical, structural, and biological conditions favorable to native coho salmon populations. Coho can exploit habitat variation to promote short-term survival, such as taking refuge from high velocity flows or maximizing growth rates, as well as long-term survival through an enhanced capacity for adaptive divergence that promotes resiliency in a landscape vulnerable to human disturbances. Habitat complexity also promotes the development of diverse ecological niches and biodiversity that help establish robust stream ecosystems supportive of coho population recovery. My final finding — that treatment sites reflected higher coho population densities than controls — revealed species preference for stream reaches comprising off-channel habitat. This outcome elucidates the associations between side channels, habitat complexity, biodiversity and coho health and thereby indicates that in-stream restoration can improve reach-scale survivability for endangered coho in Lagunitas Creek.

I found that cross comparisons of the eight datasets generated in my research highlighted two study sites that provide two important insights for stream restoration. The first is site T2 which: did not demonstrate the highest coefficient of variation (CV) for any habitat variable, produced lower Shannon diversity scores than its control for both fish and invertebrate communities, and had one of the lowest coho salmon densities out of all treatment sites. Compared to other treatment areas, T2 fared poorly in promoting physical and biological diversity favorable to coho populations. This outcome shows that side habitat is not innately beneficial, and that naturally occurring side channels should be a precedent for determining the best approaches to in-stream

restoration. Conversely, site T3: yielded the highest CVs for multiple habitat metrics, produced one of the highest fish diversity scores across all sites, and supported remarkably high coho densities compared to other control and treatment areas. I was unable to analyze macroinvertebrate diversity for T3 due to time restrictions, but perhaps it would have demonstrated higher relative diversity as well. Both a small and large side channel were constructed at this site 2018, and their success in fostering coho populations offers valuable insight for future restoration at Lagunitas Creek.

Limitations and future directions

My findings are subject to several methodological and inferential limitations. Due to time restrictions, underwater video footage was collected in the summer for some sampling sites and in the fall for others. This inconsistency could skew results for the two variables reliant on video data, as seasonality is an important determinant of local fish assemblages. Additionally, my study omits analysis of certain habitat metrics included in similar studies — including substrate (Shirey et al. 2016, Walrath et al. 2016), velocity (Walrath et al. 2016), and turbidity (Huang et al. 2019) — which may impede a comprehensive display of differences in habitat complexity between treatment and control sites. Field data collection was also somewhat subjective— for example, in deciding the number of distinct microhabitats in each reach and determining the start and end of each riffle and pool section. Perhaps the most important limitation of this study is small sample size, as the Shannon Index and CV formulae used to analyze multiple response variables are largely dependent on sufficient sample data to produce meaningful results. Another consideration is error in biological data analysis. Macroinvertebrates with torn or missing appendages sometimes limited identification to higher taxonomic levels, which may have obscured diversity truly present in certain stream reaches. Video analysis could have also produced distorted species counts from double counting individuals or misidentifying species due to poor lighting or cloudiness. Finally, this study cannot be generalized to areas outside of the Lagunitas Creek Watershed without antecedent investigation due to regional exclusivity in hydrology, ecology, and geomorphology.

Future research can address some of the aforementioned limitations as well as investigate new aspects of this study system. Although my results demonstrate correlation between habitat heterogeneity and the presence of off-channel habitat, future studies could gather data from a larger

and more stringent selection of treatment/control pairs to produce more conclusive, comprehensive, and generalizable results. Similarly, the connection between site-specific habitat heterogeneity and the exploitation of specific habitat features by coho salmon should be explored, as my study only infers the potential for these behaviors. The possibility that coho population densities reflect congregations rather than true populations enhancements at side channel reaches should be addressed through robust abundance estimates within and between sites. Future studies should also analyze inter-species competition; while outside the scope of this study, it should be recognized that increased biodiversity could hinder coho populations if it drives competition for resources such as prey and spawning territory. The importance of scale in determining restoration efficacy implores replication across multiple scales to compare the effects of habitat variation on diversity at, for example, microhabitat and reach scales.

Management implications

My research presented informative connections between environmental variables that may influence endangered coho salmon occupying Lagunitas Creek in Marin County, California. Stream reaches augmented by natural or constructed side channel habitat were generally, though not exhaustively, associated with greater variation across five habitat metrics and within two essential biological communities. Coho salmon exhibited a strong and exhaustive preference for these reaches, which suggests that off-channel habitat generates diverse stream conditions that promote survivability and long-term resiliency in native coho populations.

Implications of this study are relevant to the management of endangered coho salmon in the Lagunitas Creek Watershed and possibly for stream restoration ecology at large. I observed greater reach-scale diversity at sites with natural and constructed side habitat, implying that both types can serve as models for side channel construction projects in the future. Research should explore the feasibility and efficacy of specific natural and artificial channel features — particularly their connection to indicators of coho salmon health — and use the findings to inform management plans. As urban development continues to homogenize watersheds and surrounding landscapes, it becomes increasingly important to understand the influence of restoration approaches on vulnerable and ecologically valuable species. Existing literature and my own findings suggest that off-channel habitat can restore stream complexity to enhance short-term survival strategies and

long-term adaptability in coho salmon residing in Lagunitas Creek. Therefore, in-stream restoration should be considered a viable approach to guide future management decisions, especially those that impact this particular study system.

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APPENDIX A: Site Map

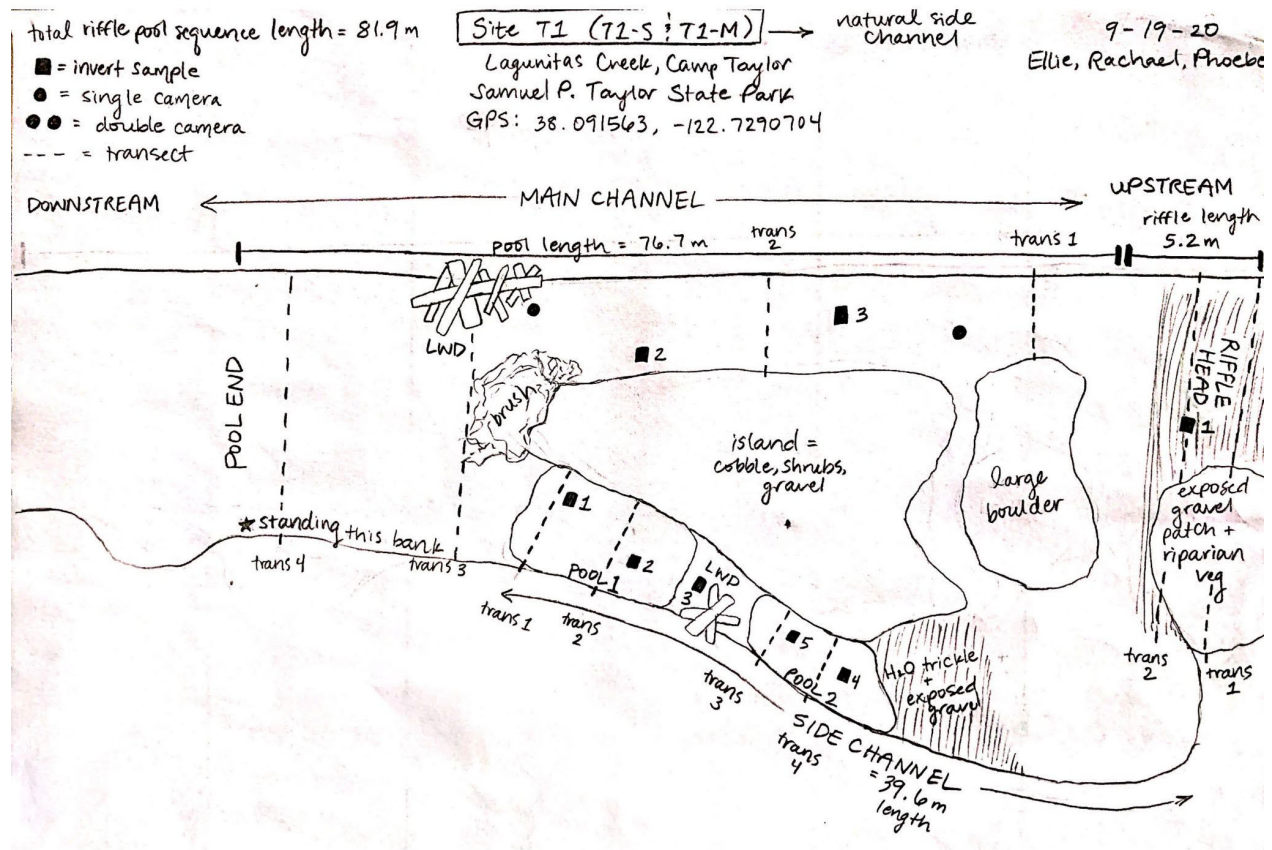


Figure A1. T1 site map. In the field I sketched an aerial view map of each study site showing stream morphology and habitat features, including pool and riffle segments, main channel, side channel or side pool, large boulders, vegetation, large woody debris clusters, and streambed substrate. I also marked the placement of microhabitats sampled for invertebrates, underwater cameras, and transects along which habitat data was collected. This figure displays site T1, though other site maps mimic this archetypal layout.

APPENDIX B: Site Geography and Photos

Table B1. Sampling location descriptions. I collected data from four sampling areas within Lagunitas Creek, each containing a treatment (T) and control (C) site. Within each treatment site is one main channel (M) and one side channel (S), with the exception of T3 which has both a small (SM) and large (LG) side channel. Side habitat at treatment sites is naturally occurring or artificially constructed.

Channel	Side Channel Type	GPS Coordinates	Sampling Area Description
C1		38.018656, -122.730336	
T1-S	Natural	38.019563, -122.7290704	Lagunitas Creek, Camp Taylor, Samuel P. Taylor State Park
T1-M			
C2		38.011276, -122.712409	
T2-S	Natural	38.013796, -122.715625	Lagunitas Creek, between Shafter Bridge and Irving Creek confluences
T2-M			
C3		38.034511, -122.743798	
T3-S-SM	Constructed	38.035473, -122.745220	Lagunitas Creek, between Cheda Creek and Devil's Gulch confluences
T3-S-LG			
T3-M			
C4		38.043378, -122.747276	
T4-S	Constructed	38.043944, -122.749089	Lagunitas Creek, Turtle Island Restoration Network / SPAWN office
T4-M			



Figure B1. Map of study sites. I collected data from each of the four sampling areas in Lagunitas Creek indicated by this figure. Red pins represent treatment sites and blue pins represent control channels within each sampling area.

(a)



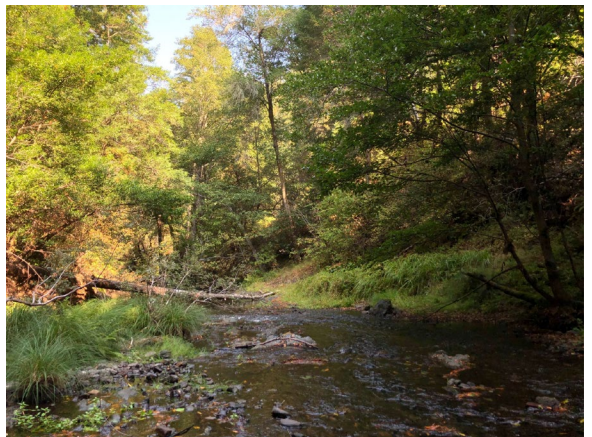
(b)



(c)



(d)



(e)



(f)



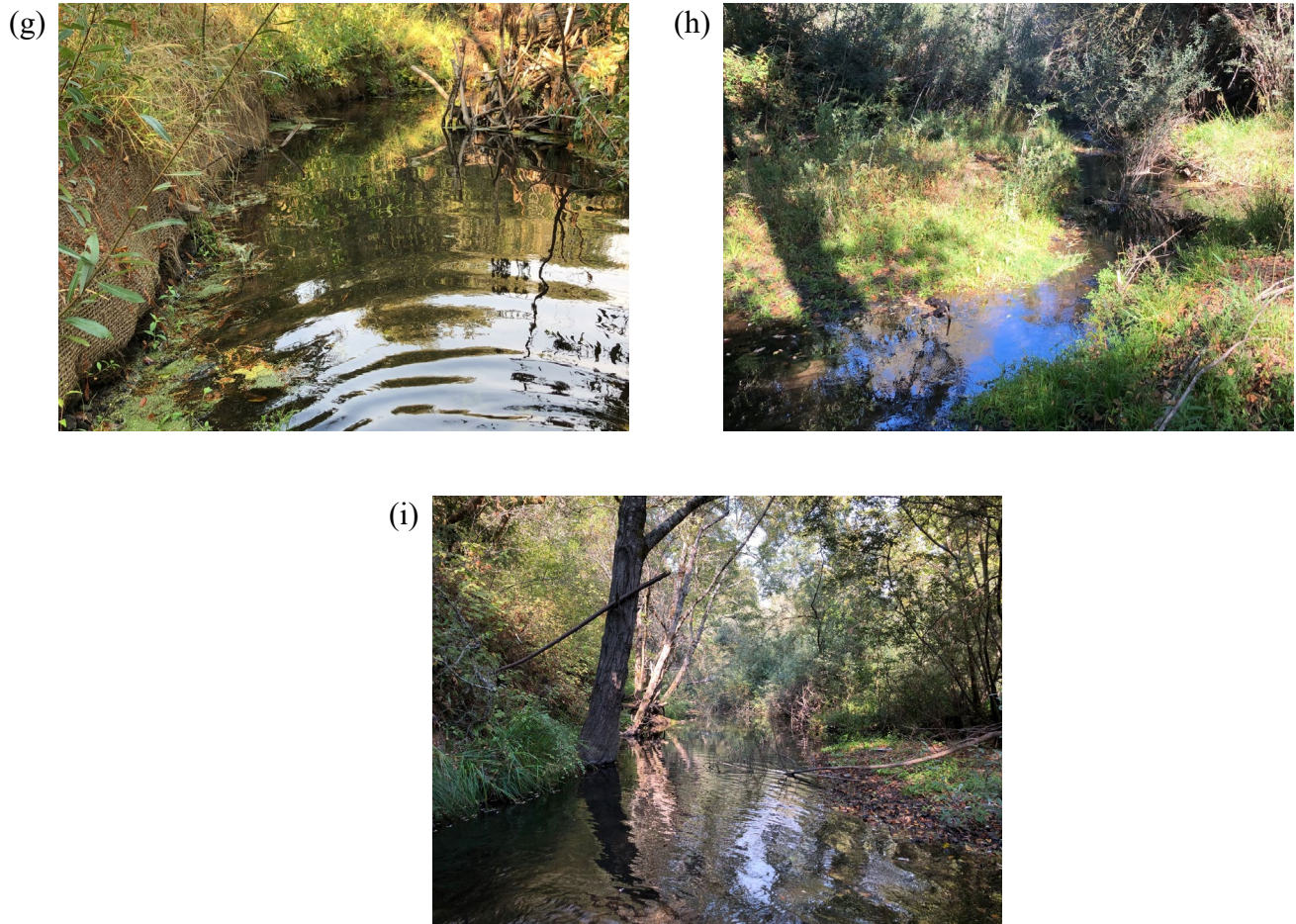


Figure B2. Treatment site photos. Images to distinguish main and side channels within the four treatment sites: (a) T1-S, (b) T1-M, (c) T2-S, (d) T2-M, (e) T3-S-SM, (f) T3-S-LG, (g) T3-M, (h) T4-S, (i) T4-M.



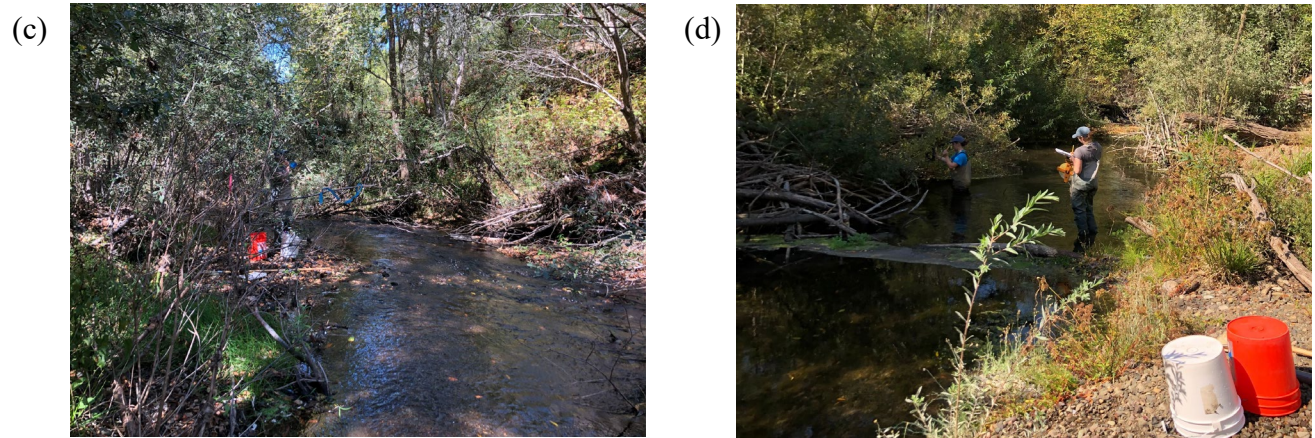


Figure B3. Control site photos. Images to distinguish main and side channels within the four treatment sites: (a) C1, (b) C2, (c) C3, (d) C4.

APPENDIX C: Microhabitats**Table C1. Microhabitat descriptions by channel.** Composite samples included macroinvertebrates that I collected from several distinguishable microhabitats within each channel.

Channel	Microhabitat Descriptions	Total Invert Count for Composite Sample
C1	(1) Cobble, leaf litter (2) Gravel along bank edge (3) Riffle	263
T1-S	(1) Cobble mixed with larger rocks (2) Leaf litter, silt (3) Larger rocks under woody debris cover (4) Cobble (5) Sand, silt	57
T1-M	(1) Riffle (algae, cobble, fast flowing) (2) Leaf litter, algae (3) Cobble, leaf litter	178
C2	(1) Sand, leaf litter, silt (2) Macrophytes near bank edge (3) Cobble (4) Riffle	169
T2-S	(1) Cobble (2) Sand, silt, larger rocks (3) Leaf litter	104
T2-M	(1) Shallow water gravel (2) Bed rock, algae (3) Leaf litter, larger gravel (4) Sand at bank edge (5) Riffle	246

APPENDIX D - Macroinvertebrate Sample Processing

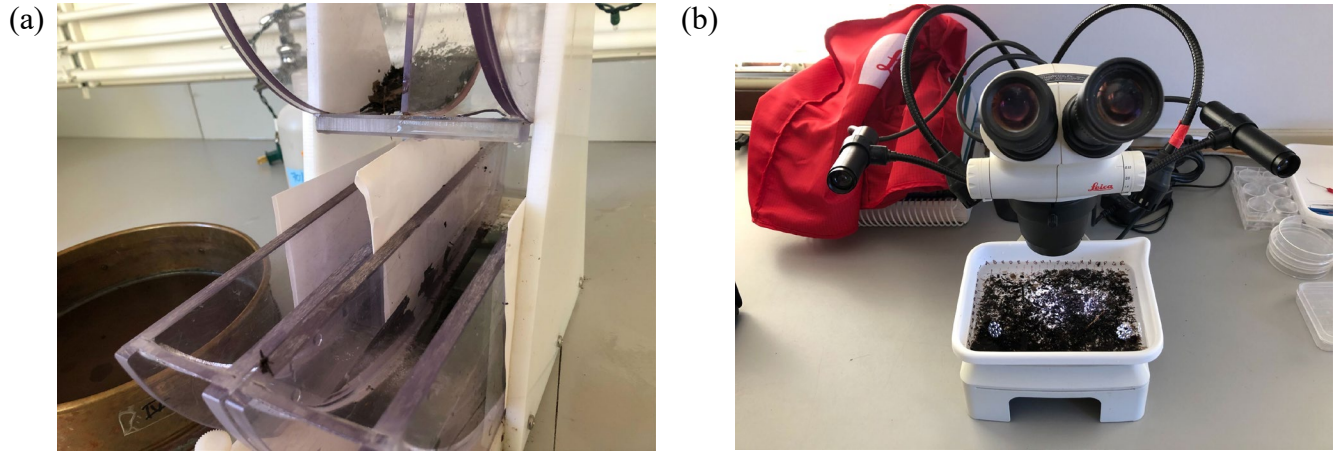


Figure D1. Lab equipment. To process macroinvertebrate composite samples from each channel, I used (a) a plankton splitter to subset samples into halves and (b) a Leica S6 Stereo Zoom dissecting microscope to sort and identify individuals.