Macroinvertebrate Production and Aquatic Food Web Response to Stage 0 Restoration

Jeremy Jennings, J. Ryan Bellmore, Jonathan Armstrong

Abstract

Contemporary stream restoration efforts increasingly prioritize restoring natural stream processes to regain lost ecosystem functions. Stage 0 stream restoration resets disturbed, channelized streams to a theoretical pre-disturbance state (“Stage 0”). It is assumed that this valley-scale restoration/disturbance will restore natural abiotic and biotic processes, leading to greater primary and secondary biological productivity, maximizing potential ecosystem services such as the abundance of desirable fish species. As Stage 0 restoration projects have been implemented in Oregon and across North America, post-restoration studies have not fully assessed this assumption. In this study, we seasonally sampled aquatic macroinvertebrate communities and fish diets on the South Fork McKenzie River, OR in a reach that underwent stage 0 restoration in 2018, as well as two upstream, unrestored reference reaches. We estimated total annual secondary macroinvertebrate production on the benthos and submerged wood surfaces, and constructed food webs from the dominant taxa found in fish diets. Contrary to expectations, annual production estimates were ~3x *lower* on a per-meter-squared basis in the restored reach than in an unrestored reference reach directly upstream. However, because there was ~4.5-times greater wetted area available in the restored reach. Fish diet assemblages also appeared more complex in the restored reach relative two upstream reference reaches. Additionally, the distinct aquatic habitat patches created by stage 0 restoration hosted a greater diversity of macroinvertebrate community assemblages in the restored reach relative to the unrestored reference reaches. These findings suggest that Stage 0 restoration may increase overall macroinvertebrate productivity as well as create a more diverse assembly of prey items with the potential for more consistent prey availability and greater overall habitat and foraging opportunities for mobile consumers such as salmonid fishes.

Introduction

At multiple sites throughout Oregon, the U.S. Forest Service and partner agencies have developed a method of floodplain restoration known as *Stage 0* restoration (Powers et al. 2019) that aims to transform incised, and disconnected single-channel river systems into spatially complex, multi-thread systems that support fluvial and biotic processes at the valley scale (Behan et al. 2021). Stage 0 restoration of the South Fork McKenzie River (SFMR), OR, was carried out during the summer of 2018, and increasing the capacity of the SFMR to support endangered & threatened species of salmonids including chinook, steelhead, and bull trout was a major objective of the project. Stage 0 stream restoration can be viewed as a large-scale disturbance event that could have negative impacts on the aquatic and riparian ecosystems. To date, no published studies have empirically evaluated how restoring channels to a Stage 0 state affects the capacity for restored river segments to support fishes, or how it impacts ecological productivity. Advocates and practitioners of the approach assume that any negative responses will be short term and insignificant relative to the longer-term ecological recovery initiated by the restoration (Behan et al. 2021). As the practice of stage 0 restoration gains momentum, there is a need for empirical studies testing the assumptions surrounding the ecological responses to this restoration approach.

In this study, we examined the impact of stage 0 restoration on the productivity of aquatic macroinvertebrates, a primary food resource supporting stream salmonids such as Pacific salmon and trout (Zaroban et al. 1999). We compared seasonal and annual estimates of benthic macroinvertebrate biomass and secondary production in the restored segment with two unrestored, upstream reaches. Invertebrate biomass estimates provide ‘snap-shots’ of food availability per unit of area (grams/m2), while estimates of secondary production, defined as the formation of invertebrate biomass over a given period of time (Benke and Huryn 2017), provide a temporally integrated estimate of food availability. Estimates of seasonal or annual secondary production (grams/m2/time) provide an estimate of the total amount of aquatic prey available to support fishes. Estimates of macroinvertebrate secondary production also provide important mechanistic details on the linked physical-biological processes that control the direction and magnitude of the ecological response to stage 0 restoration, and the affects on aquatic invertebrate food production and community composition. We also compared fish diets between the restored and unrestored sites, quantifying the proportions of total diet biomass for each fish species, to provide insight into the food web supporting that fish’s production (sensu Cross et al. 2011). We expected to see: 1) greater annual biomass and secondary production of benthic macroinvertebrates in the restored reach, and 2) the composition of the macroinvertebrate assemblage, and associated fish diets, to be different in the restored reach, relative to the upstream reference reaches.

Methods

Study Site

The South Fork McKenzie River is a fourth-order tributary of the Willamette River in west-central Oregon, and joins the mainstem McKenzie River ~70 km east of Springfield, OR in the Cascade Mountains (Figure 1). Its watershed encompasses an area of 539 km2, with spring-dominated, year-round flows of cool water originating in the porous, volcanic mountains of the High Cascades. Mean annual discharge at the study site for the period of record (1948-2020) was 24 m3/s (USGS Discharge Data). A peak flow as high as 700 m3/s was recorded prior to the period of record, with much lower peaks (< 255 m3) recorded after 1963, when Cougar Dam was constructed ~7 km upstream from the confluence of the South Fork and the mainstem McKenzie Rivers (USGS Water Year Summary). Dam operation disrupted fish passage, seasonal flow patterns, and altered the thermal regime in the downstream reach, negatively affecting the habitat, migration and emergence timing of threatened juvenile spring chinook salmon (*Onchoryhnchus tshawytscha*), bull trout (*Salvelinus confluentus*), and steelhead (*Onchoryhnchus mykiss*), as well as the pacific lamprey (*Entosphenus tridentatus*) (USACE et al. 2007). A temperature control tower began regulating the temperature of water released from the reservoir in 2005, bringing the thermal regime closer to historic patterns and improving chinook salmon survival rates in the South Fork below the dam and mainstem McKenzie (USACE et al. 2007). However, the temperature control tower also exported new subsidies of lentic organisms and material from surface waters of the reservoir into the downstream reach, reducing macroinvertebrate density and altering aquatic macroinvertebrate food webs that support fish production (Murphy et al. 2021). To date there is no upstream fish passage at Cougar Dam, and spring chinook production remains supplemented by Leaburg fish hatchery on the mainstem McKenzie River (USACE et al. 2007).

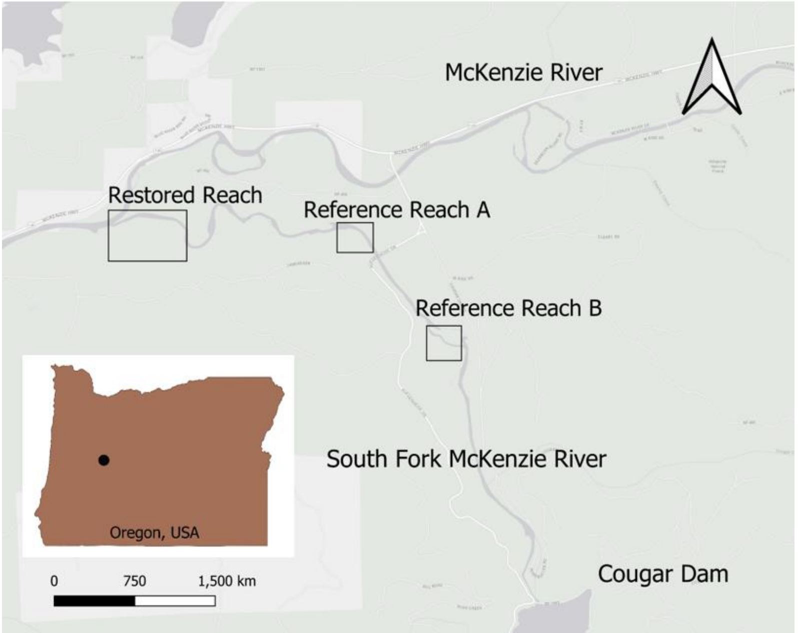

Figure 1. Benthic macroinvertebrate and fish diet sampling sites. Direction of flow is from East to West and South to North.

Study Design

To determine how stage 0 restoration affects macroinvertebrate production and assemblage composition, We compared secondary production estimates and fish diet compositions between the stage 0 restored reach (impacted reach) and two upstream unrestored reaches (control reaches) on the SFMR. In using an impact-control study design, We assumed that the restored reach was similar to the unrestored sites prior to restoration, and that the magnitude of any differences between these sites prior to restoration was small, relative to the ecological response to the stage 0 stream restoration.

Sampling Design

The patchy spatial distribution of aquatic macroinvertebrates across the benthos can be a significant source of innacuracy and uncertainty in community biomass and production estimates. Collecting accurate biomass samples requires both sampling an adequate total surface area, and capturing the heterogeneity of the benthic habitat patches in the sample set. To increase the sample area and reduce sample error, We used a Surber sampler with a larger sampling area (0.25 m2) than standard (0.096 m2), and a stratified random sampling approach. Benthic macroinvertebrate sampling in the restored reach was stratified into the three distinct reach-scale habitat patches created by the restoration, that we called “Main Channel”, “Side Channel”, and “Wetted Forest” (Figure 2). The Main Channel habitat features interbraided channels with gravel and small to medium cobbles, small islands, pools, slow water areas with sand and unconsolidated sediments, and a high density of large wood. The Wetted Forest habitat consists of inundated stands of maples, alders, cottonwoods, and cedars on the intact valley bottom, with networks of channels and pools. The Side channel habitat is a complex of relict channels that were restored to stream flow, with an abundance of large wood and a substrate dominated by mud, aquatic macrophytes, and small gravels. Samples were also collected from the submerged surfaces of large wood in the Main and Side Channel, using a small D-frame kick-net.

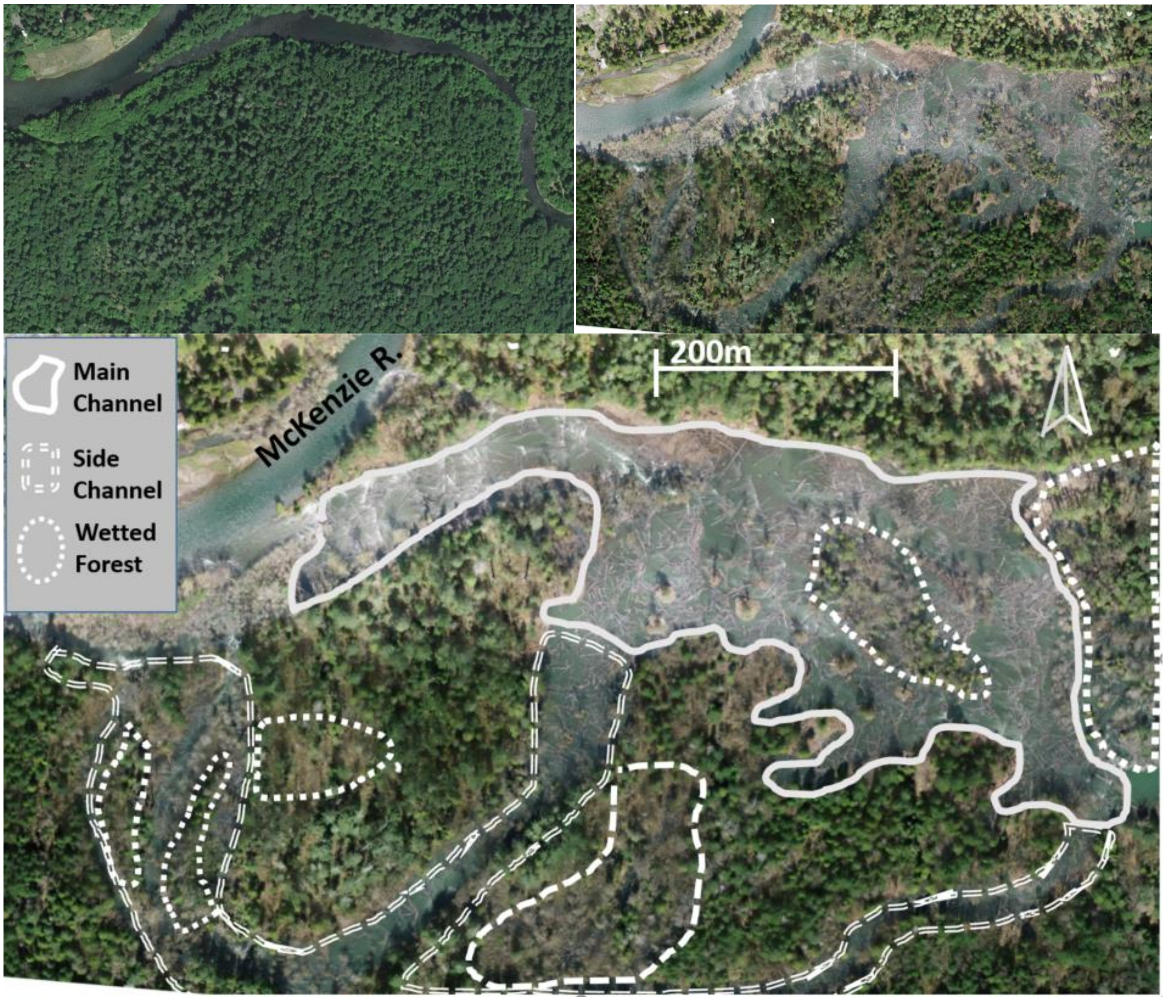

Figure 2. Stratified habitat patches where macroinvertebrate samples were taken in the restored reach of S.Fk. McKenzie River, OR. Top left image, before restoration. Top right image, after restoration.

Sampling was conducted seasonally, with sampling events occurring in July and October of 2019, and February and April of 2020. Samples were collected by holding the Surber sampler in flowing water against the benthos, hand-scrubbing the surface of all large cobbles within the area of the sample quadrat, and disturbing the substrate to a depth of ~10 cm with a short length of rounded steel rod. In low-flow areas, the substrate was alternately disturbed and waved by hand into the sampling net. Submerged wood surface samples were collected by holding the frame of the kick-net against the surface of the wood and hand-scrubbing an area equal to the area of the opening of the kick-net. Sample placement was randomized by visually defining the bounds of a sampling frame using landmarks at each site, and using a pair of random numbers between 0 and 100 to serve as X and Y coordinates for the proportion of the total length and width of the sample frame to travel before placing the sampler. All seasonal samples were elutriated with a ~500 µm sieve bucket to remove as much organic material as possible, placed in sample jars, and preserved with 95% EtOH.

Five total benthic macroinvertebrate biomass samples were collected each season from each habitat patch in the restored area, and from each reference reach, for a total of 20 samples (n

= 20) from each patch/reach. Three submerged wood surface samples were also collected each season in the Main and Side channel patches of the restored reach,. Each wood surface sample consisted of 4 kick-net sub-samples, for a total area of 0.6 m2 per sample. Each benthic sample also consisted of several sub-samples, collected in proportion to the occurrence of the dominant hydraulic habitat types within each patch. In the Main Channel, each benthic sample consisted of 5 sub-samples collected with the large (0.25 m^2) Surber sampler: 2 from riffles, 2 from runs, and 1 from semi-stagnant water, for a total area of 1.25 m^2 per sample. Each sample in Reference reaches A and B also consisted of 5 sub-samples collected with the large Surber sampler: 2 from riffles, 3 from runs, for a total area of 1.25 m^2 per sample. In the Side Channel, each sample consisted of only 4 sub-samples collected with the large Surber sampler: 3 from non-vegetated substrate, 1 from vegetated, for a total area of 1 m^2 per sample. Each sample in the Wetted Forest also consisted of 4 sub-samples, randomly placed with no stratification, and collected with a standard Surber sampler (0.09 m^2), for a total area of 0.36 m^2 sampled. Fewer sub-samples were taken in the Side channel and Wetted Forest, and a smaller sampler used in the Wetted Forest, in order to minimize the amount of organic detritus in the samples, and to keep samples to a manageable volume for preservation and processing.

To calculate the growth rates of common aquatic invertebrate taxa, a separate set of benthic samples was collected on an approximately monthly-basis (Jul., Aug., Sep., Nov., Dec. 2019 & Feb. 2020) from Reference reach A. Each monthly sample consisted of 3 sub-samples taken from riffles, for a total area of 0.75 m^2 per sample. These samples were elutriated with a ~250 micron sieve and preserved in jars with 95% EtOH.

Preserved invertebrates were picked from each sample in the lab, removing the largest (>10mm) individuals first, and subsampling with Caton tray or gridded sieve until 500 total individuals were picked. All invertebrates were identified to family, genus, or species/group level according to the Pacific Northwest Aquatic Monitoring Partnership standard taxonomic level 2, measured to nearest 0.5mm length, sorted by size-class, and counted. Seasonal biomass estimates of ash-free dry mass (DM) per taxon were calculated from the seasonal samples using the abundances and published length-weight regressions for each taxon (Benke et al. 1999), and standardized to 1m^2 sample area.

Macroinvertebrate Data Analysis

The mean seasonal biomass for each invertebrate taxon was calculated and summed to derive total seasonal biomass estimates for the entire assemblage. In turn, annual mean biomass estimates and 95% Confidence Intervals (CI) were calculated for each site by bootstrap resampling from the seasonal biomass data with a custom script written in R using the tidyr package (Wickham 2020). Biomass values for each taxon were randomly resampled, with replacement, from the original seasonal sample sets and the means calculated, and the process repeated for 10,000 iterations to generate a bootstrap distribution of means for each taxon in each sample reach. The percentile method was used to obtain the upper and lower bounds of the 95% confidence interval from the bootstrap distributions, and taxa with confidence intervals that overlapped with 0 were removed from the dataset. The annual mean biomass estimates of all remaining taxa were summed to get a bootstrap distribution of total annual biomass for each reach.

Annual secondary production (P) (g DM * m-2 * yr-1) estimates were calculated from the samples taken monthly in Reference site A using the size-frequency method (Benke & Huryn

2017), where differences between the abundances of size-classes through time were used to account for the total biomass produced by an average cohort over that time. Plots of size-frequency distributions over the sample period were used to estimate cohort production intervals (CPI), or the time for a generation to complete development, to correct the annual production estimates for each taxon. The corrected annual production estimates were then divided by the total annual biomass (B) from the monthly samples to obtain taxon-specific P:B estimates:

$$\frac{P \times CPI}{B} = \frac{P}{B}$$

Annual secondary production for each taxa in the restored and reference sites was then calculated by multiplying average annual mean biomass estimates by the taxon-specific P/B ratio, using either P/B estimates that were calculated from the monthly data or those from the published literature (Appendix A), as follows:

$$bootstrap\ annual\ B \times monthly\ \frac{P}{B} = annual\ P$$

Annual production totals for each reach were then obtained by summing the taxon-specific production estimates. 95% confidence intervals for production were obtained by scaling the upper and lower bounds of the bootstrap biomass 95% CI's by the total reach P/B ratios. Finally, the annual production estimates and 95% CI's were scaled to the total wetted area of each reach; for the restored reach, this was achieved by summing the scaled estimates from each habitat patch. Total reach production estimates were standardized to 100m of valley length by dividing the total esimate by valley length and then multiplying by 100.

To examine compositional differences between patches and reaches, we conducted an Nonmetric MultiDimensional Scaling (NMDS) analysis. The mean biomass estimates for each taxon and sample reach were standardized as a proportion of the total assemblage biomass and log transformed to correct for bias caused by the large spread between maximum and minimum values, and the large number of zeroes in the data set. The standaradized mean biomass estimates were then plotted via NMDS ordination, and groups (treatment & season) analyzed for statistically significant differences via Analysis of Similarity (ANOSIM) using the Vegan (Oksanen et al. 2020) and Ecodist (Goslee & Urban 2007) packages in the R statistical programming environment version 3.6.3 (R Core Team 2020) in RStudio version 1.2.5033 (RStudio Team 2019).

Fish Diets and Food Webs

Fish sampling was conducted in the summer and fall of 2019, and early winter of 2020. Fish sampling in the spring of 2020 was not conducted due to Covid-19 pandemic restrictions. Several methods of fish capture were attempted, but electrofishing and angling proved most successful. Electrofishing by boat was not possible, as the sample reaches were not navigable, but backpack electrofishing was moderately successful at capturing sculpin (*Cottus* spp.), dace (*Rhinichthys* spp.), and juvenile trout, but not as successful at capturing adult trout. The majority of the adult rainbow (*O. mykiss*) and cutthroat (*O. clarkii*) trout were captured via angling. All of the juvenile chinook (*O. tshawytscha*) were also captured via angling. Bull trout (Salvelinus confluentis) and mountain whitefish (Prosopium williamsoni) were present in the sample reaches, but no whitefish were captured, and only a single bull trout with an empty stomach was captured. The overall low number of fish captured across all reaches (Appendix B) required lumping the adult rainbow and cutthroat into an "adult trout" group for comparisons between restored and unrestored reaches, and lumping sculpin and dace at generic level.

Fish captured by electrofishing and hook-and-line were anaesthetitized with a solution of 0.25 mL Aqui-S 20E to 1L water. Wet weight and total length were recorded for every fish, and gut contents extracted with gastric lavage and preserved in 95% EtOH. Dace and the smallest sculpin were euthanized and preserved in 95% EtOH, and gut constents extracted via dissection of the foregut in the lab. All prey items were identified to species or genus, and head width or body length measured. Dry mass estimates of all prey items were made using head width and body length measurements and published regressions from the literature. Mean proportions of total diet biomass for each taxon and species of fish were calculated and used to construct food web diagrams of the prey and fish communities in the restored and unrestored reaches.

Results

Seasonal Macroinvertebrate Biomass

Seasonal macroinvertebrate biomass estimates were higher overall in the unrestored reference reaches, with especially high estimates in Reference A (Figure 3). However, there were no consistent differences in seasonality in the patterns of macroinvertebrate biomass between the reference reaches and the habitat patches in the restored reach. Additionally, there were only slight differences in seasonal biomass dynamics between the habitat patches in the restored reach: the Main Channel and Wetted Forest had the highest macroinvertebrate biomass in the fall and lowest biomass in spring, while the Side Channel had the highest biomass in the summer and lowest in the winter. Overall, the differences between seasons in the restored patches tended to be small and within error bounds.

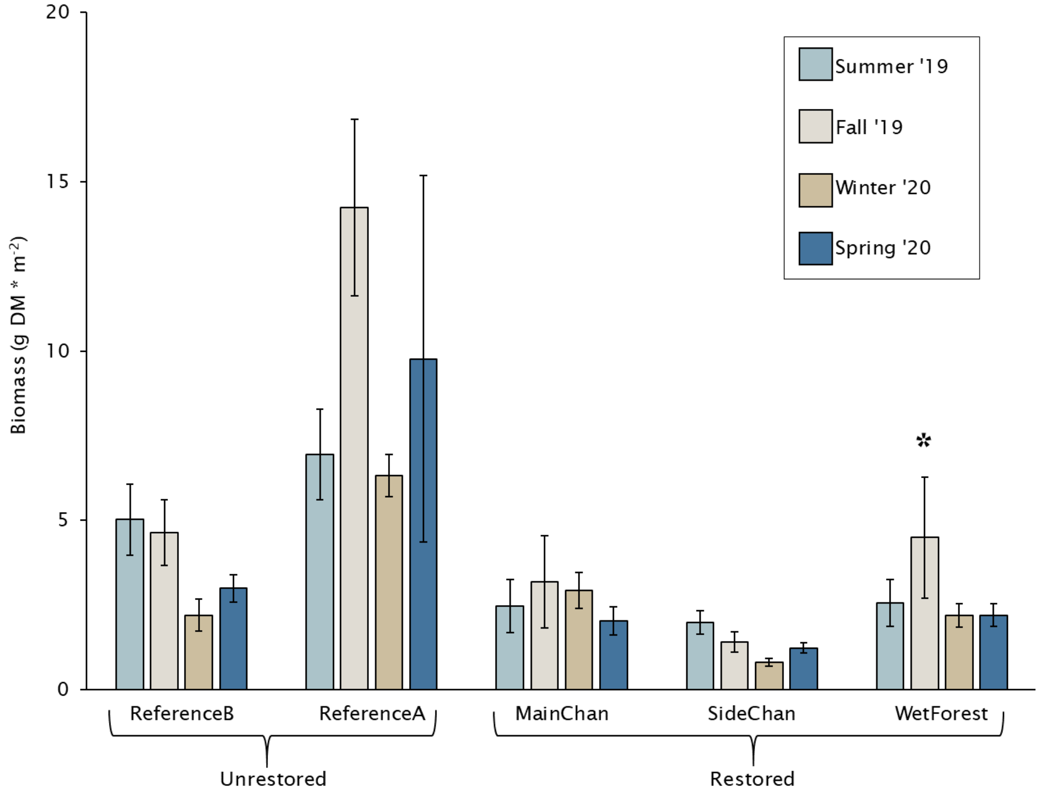

Figure 3. Seasonal average benthic macroinvertebrate biomass per-area (mean ± SE) in the unrestored (Reference A & B) reaches and stage 0 restored habitat patches in the restored reach of the S.Fk. McKenzie River. n=5, except as indicated by asterisk (n=2).

Total Annual Macroinvertebrate Biomass and Secondary Production

Contrary to expectations, average annual biomass and production of aquatic macroinvertebrates was higher on a per meter squared basis in the unrestored reaches, relative to the habitat patches sampled in the restored reach (Figure 4). Reference A had the highest overall annual biomass and production (8.7 and 43.3 g DM * m^{-2} * yr^{-1}), which is ~3x greater than the highest estimate from the distinct aquatic habitat patches within the restored reach (Table 1), the Main Channel patch (2.4 and 13.3 g DM * m^{-2} * yr^{-1}). However, there was about 4.5x greater aquatic habitat area in the restored reach than in the unrestored reaches, and when scaled to the total amount of aquatic habitat area and the distinct aquatic habitat patches are considered in aggregate, the restored reach had at least 2x as much macroinvertebrate biomass (24.2 kg DM * yr $^{-1}$ in Reference A and 8.6 kg DM * yr $^{-1}$ in Reference B vs. 50.3 kg DM * yr $^{-1}$ in the restored reach) and production (120.4 kg DM * yr $^{-1}$ in Reference A and 40.0 kg DM * yr $^{-1}$ in Reference B vs. 274.4 kg DM * yr $^{-1}$ in the restored reach) per 100 meters of valley length than the reference reaches (Figure 5).

Additionally, these benthic estimates do not account for macroinvertebrates production supported by the substantial amount of submerged wood surfaces in the restored reach. On a per meter squared basis, submerged wood surfaces supported 218 mg * m^{-2} of biomass and 1.3 g * m^{-2} * yr $^{-1}$ of production in the Main Channel, and 317 mg of biomass * m^{-2} and 1.9 g * m^{-2} * yr $^{-1}$ of production in the Side Channel. If we assume there is an amount of submerged wood surface habitat available equivalent to 20% of the benthic habitat area, this would contribute an additional 8.8 kg of biomass and 53.4 kg of production to the annual totals in the restored reach, equal to about 2% of the benthic total.

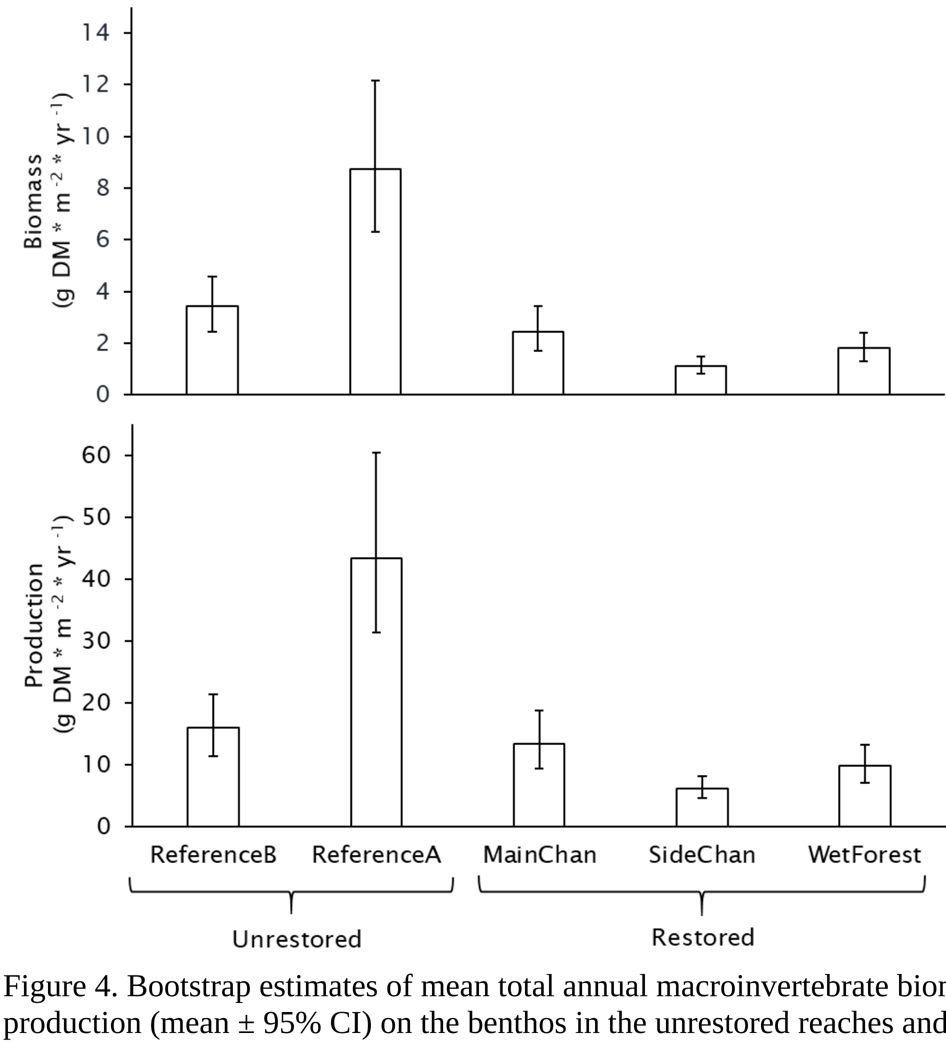

Figure 4. Bootstrap estimates of mean total annual macroinvertebrate biomass and secondary production (mean ± 95% CI) on the benthos in the unrestored reaches and the habitat patches in the stage 0 restored reach of the S.Fk. McKenzie River, OR.

Table 1. Average annual macroinvertebrate biomass and annual production estimates, with 95% confidence intervals in the unrestored reaches and the habitat patches in the stage 0 restored reach of the S.Fk. McKenzie River, OR.

Site	Avg. Annual B (g DM)	0.975	0.025	Avg. Annual P (g DM)	0.975	0.025
ReferenceB	3.436	1.147	0.994	15.950	5.322	4.613
ReferenceA	8.719	3.433	2.411	43.322	17.058	11.979
MainChan	2.437	0.981	0.719	13.319	5.360	3.927
SideChan	1.126	0.358	0.291	6.118	1.947	1.579
WetForest	1.812	0.601	0.527	9.856	3.267	2.866

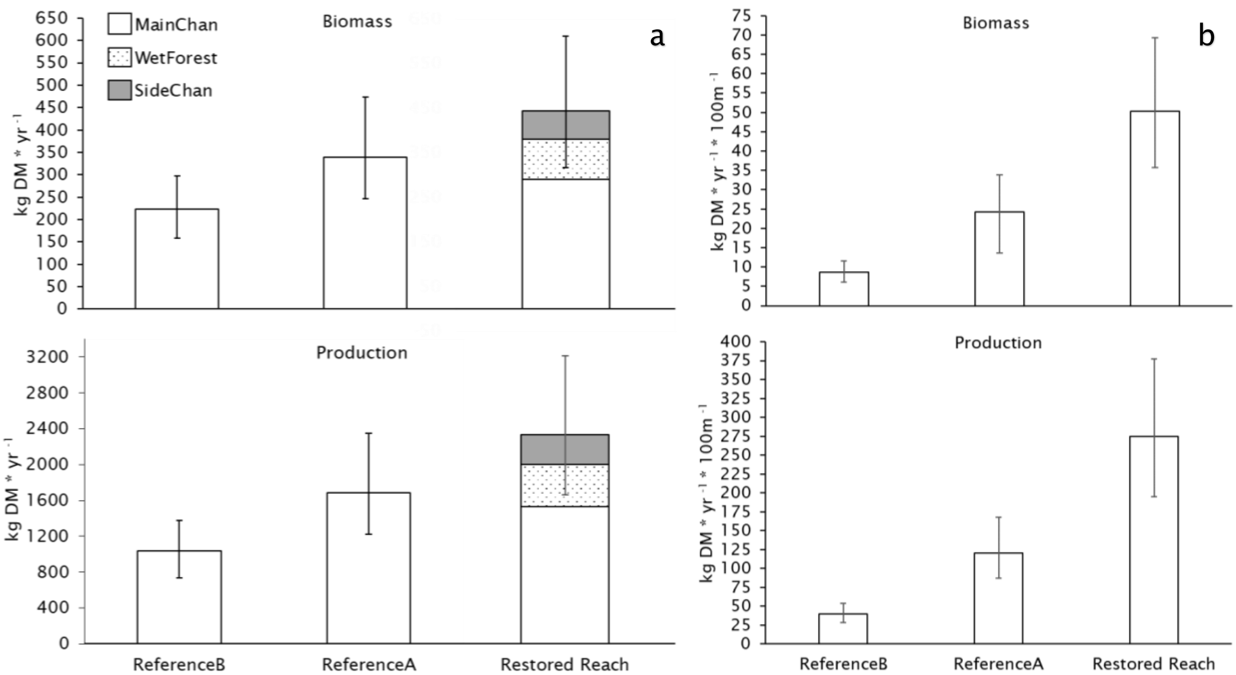

Figure 5. Total annual biomass and production scaled to (a) total wetted area and (b) per 100 m of valley length for the unrestored reference reaches and stage restored reach of the S.Fk. McKenzie River, OR.

Assemblage Composition of Annual Production

The assemblage of macroinvertebrates accounting for the majority of production was different between the reference reaches and the restored reach. While mayflies, stoneflies, and caddisflies (EPT taxa) accounted for the majority of production across all reaches, the Wetted Forest was an exception, where mayflies, caddisflies and true flies (Diptera) dominated (Table 2). Indeed, the most pronounced compositional differences were between the more lentic habitats of the Side Channel and Wetted Forest in the restored reach, and the reference reaches (Figure 6). Annual production in the reference reaches was dominated by Hydropschidae, Baetidae, and Ephemerellidae, which made up ~60% of the total production. Annual production in the more lentic Side Channel and Wetted Forest aquatic habitat patches in the restored reach was dominated by Baetidae and Chrinomidae, accounting for ~50% of total production. Annual production in the Main Channel habitat patch was distributed more evenly across a larger assemblage of taxa that resembled both the reference reaches, and the more lentic habitat patches in the restored reach: Baetidae and Hydropsychidae accounted for ~25% of the total production, similar to the reference reaches, while Chironomidae, Perlidae, Perlodidae, and Heptageniidea contributed about equally to the production totals. Limnephilida, Heptageniidae, Leptophlebiiadae and Oligochaeta were also significant contributors (>5%) to the total annual production in the restored reach, but insignificant in the both reference reaches. Similar overall patterns were observed in the composition of macroinvertebrates contributing to average annual biomass (Appendix C).

The relative contributions and the overall assemblages of macroinvertebrates contributing to annual production on submerged wood surfaces were similar to the benthic average annual production totals in the same habitat patches (Figure 7). Both Baetidae and Chironomidae contributed to a large proportion of the total production on wood surfaces, similar to their benthic contributions. Together with Heptageniidae and Perlidae, they accounted for ~60% of the total production on wood surfaces.

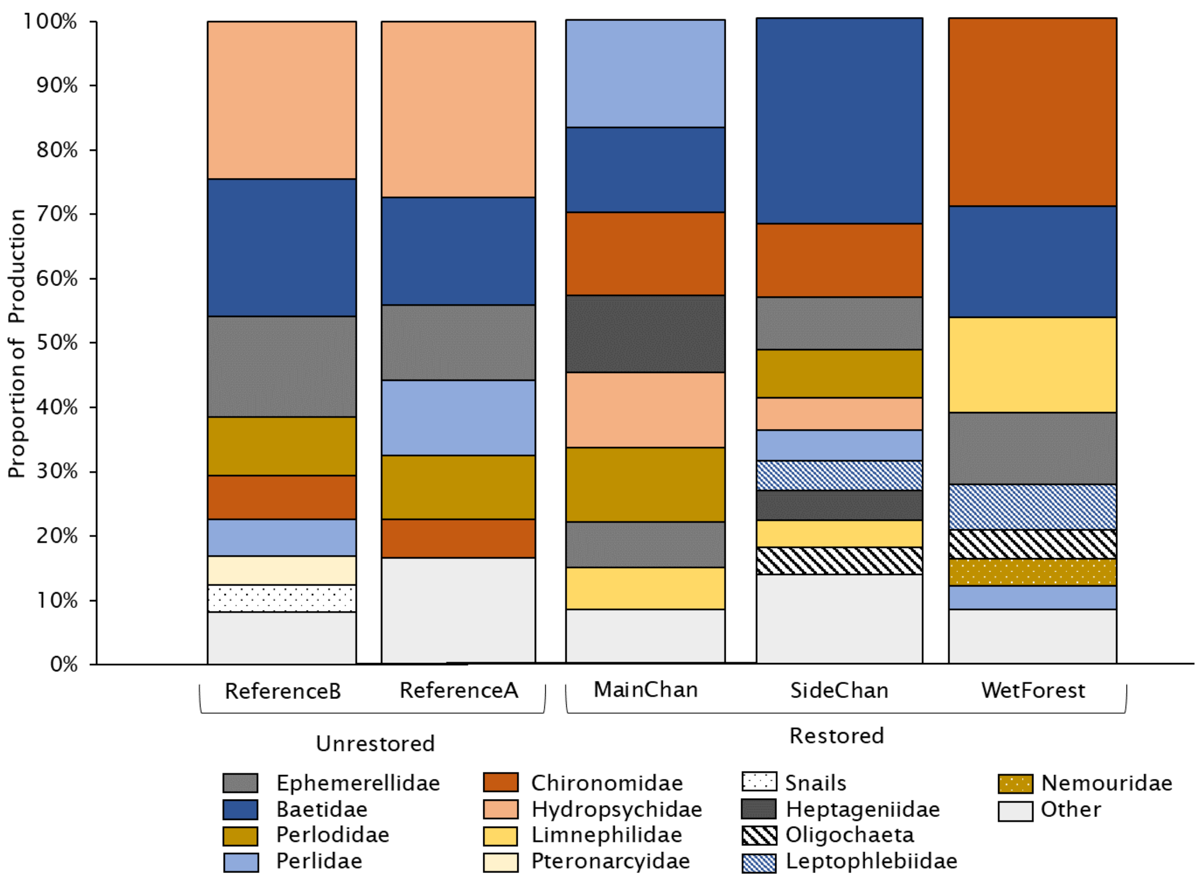

Figure 6. Proportions, by dominant taxa, of the total mean annual benthic macroinvertebrate production for each unrestored reach and each habitat patch in the stage 0 restored reach of the S.Fk. McKenzie River, OR.

Table 2. Relative contributions of major taxonomic groups to total annual production in each unrestored reach and each habitat patch in the stage 0 restored reach of the S.Fk. McKenzie River, OR. (Ephem = Ephemeroptera, Pleco = Plecoptera, Tricho = Trichoptera, EPT = Sum of Ephem, Pleco, Tricho)

% Total Prod.	Ephem	Pleco	Tricho	EPT	Diptera	Non-insect	Coleoptera
Reference B	39.1	19.9	28.0	87.0	7.8	5.2	0.0
Reference A	31.4	26.8	31.8	90.0	6.6	1.2	2.2
Main Channel	32.8	29.5	20.8	83.0	14.3	2.0	0.7
Side Channel	49.0	14.1	14.4	77.5	14.4	7.6	0.5
Wetted Forest	38.3	7.8	20.1	66.2	29.8	5.8	1.2

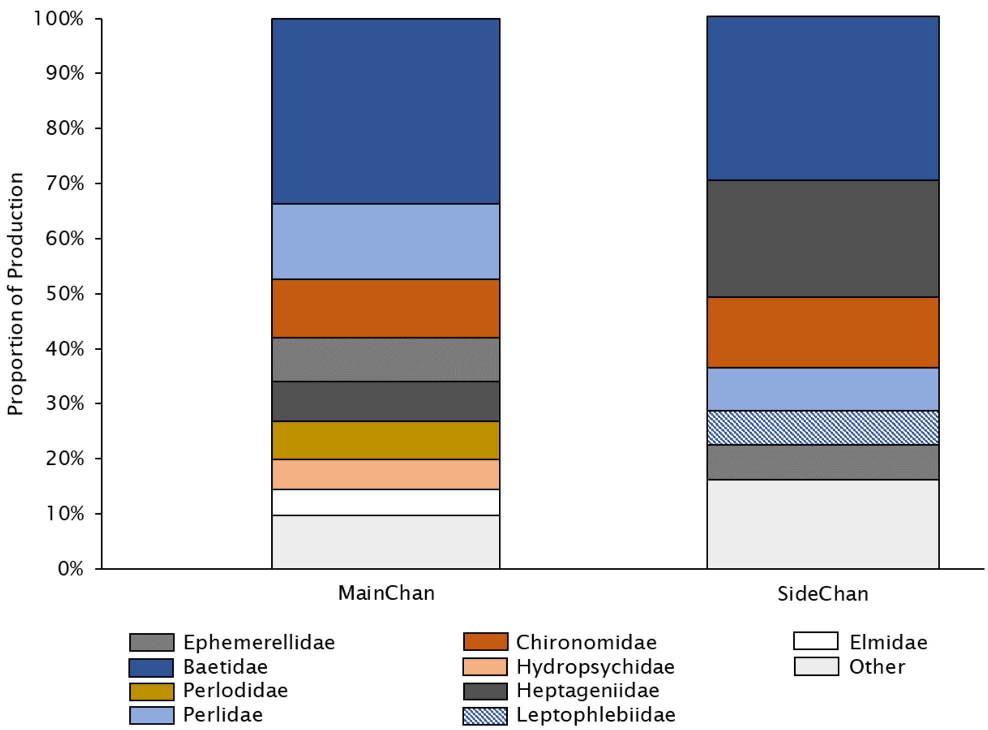

Figure 7. Proportion of total annual wood surface macroinvertebrate production by family, in the Main and Side Channel habitat patches in the stage 0 restored reach of the S.Fk. McKenzie River, OR.

Nonmetric Multidimensional Scaling (NMDS) and Analysis of Similarity (ANOSIM) of Seasonal Community Biomass

There were statistically significant differences in community composition amongst reaches/treatments (Figure 8, ANOSIM R = 0.4235, $p < 0.5$), with the strongest differences seen between the reference reaches and the wetted forest habitat patch in the restored reach. Statistical differences were most strongly driven by a greater prevalence of Hydropsychidae in the reference reaches, while the wetted forest patch had a greater prevalence of Chironomidae. Additionally, seasonal variation in the macroinvertebrate composition was strong and statistically significant (ANOSIM R = 0.5963, $p < 0.5$) Seasonality was similar across all of the reaches, as well as amongst aquatic habitat patches in the reference reach (Figure 8), and was driven by the prevalence of Chironomidae and Ephemerellidae in the Summer, and Hydropsychidae and Heptageniidae in the Winter.

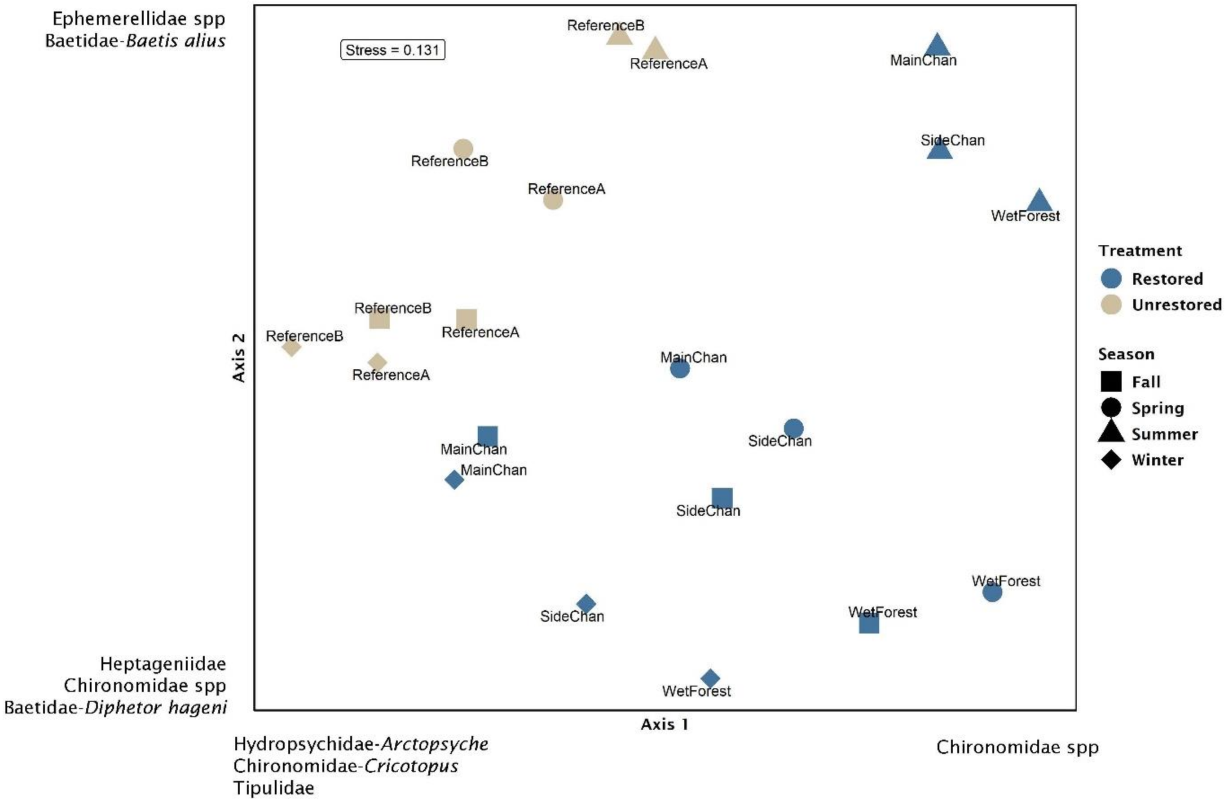

Figure 8. Nonmetric Multidimensional Scaling (NMDS) ordination plot of average seasonal benthic macroinvertebrate biomass, for each taxon, in each sample reach (stress = 0.131). Taxon names next to each axis account for the majority of variation along that axis.

Fish Diet Assemblage Composition

The primary prey items found in fish diets were similar between the restored and reference reaches, with Baetidae, Perlodidae, Nemouridae, and Chironomidae common across all reaches and fish species (Figure 9). Although the dominant contributors to adult trout diets were similar between the reference reaches and the restored reach, terrestrial invertebrates and Hydropsychidae were a significant proportion of diets only in the reference reaches, while Ephemerellidae, Limnephilidae, and Oligochaet worms contributed an equivalent proportion to adult trout diets in the restored reach. There were also more nuanced differences between the adult trout diets, with diets in the restored reach consisting of more non-EPT taxa such as snails, beetle larvae, and oligochaet worms. Sculpin diets were also quite similar across reaches, with ~60% of the diet consisting of Baetidae, Perlodidae, and Chironomidae in the reference reaches, and Baetidae, Perlodidae, and Nemouridae in the restored reach. Adult trout and sculpin diets were also less similar in the reference reaches than in the restored reach. While both adult trout and sculpin had a large proportion of diet attributed to Baetidae across all reaches, Nemouridae and terrestrial invertebrates were the next largest contributors to adult trout diets in the reference reaches, while Chironomidae and Perlodidae were the next largest contributors in the restored reach. Adult trout and sculpin diets in the restored reach were more similar, both with large contributions by Nemouridae and Perlodidae.

Although there are overall similiarities between the reaches, the differences in diet content reflect differences in the pathways of energy flow supporting fish production. Food web diagrams illustrate the different structures of these pathways in the reference reaches (Figure 10) and the restored reach (Figure 11). The major difference between structures is the absence of juvenile chinook and dace in the reference reaches. Though they are certainly present in the reference reaches, none were captured using the same sampling effort as in the aquatic habitat patches in the restore reach, suggesting they may play a much smaller role in the aquatic food web in the upstream reference reaches.

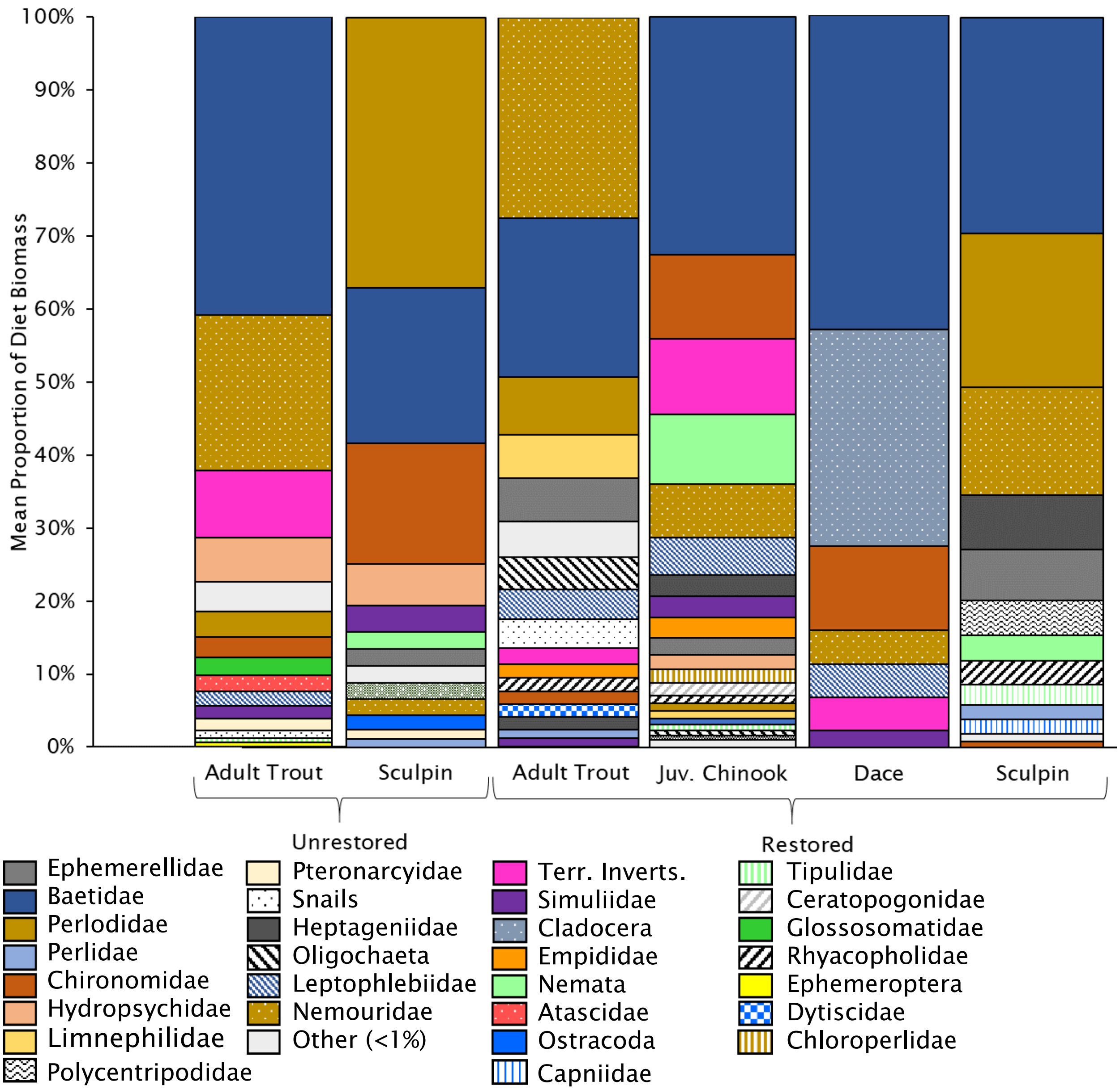

Figure 9. Fish Diet compositions, by macroinvertebrate taxonomic group.

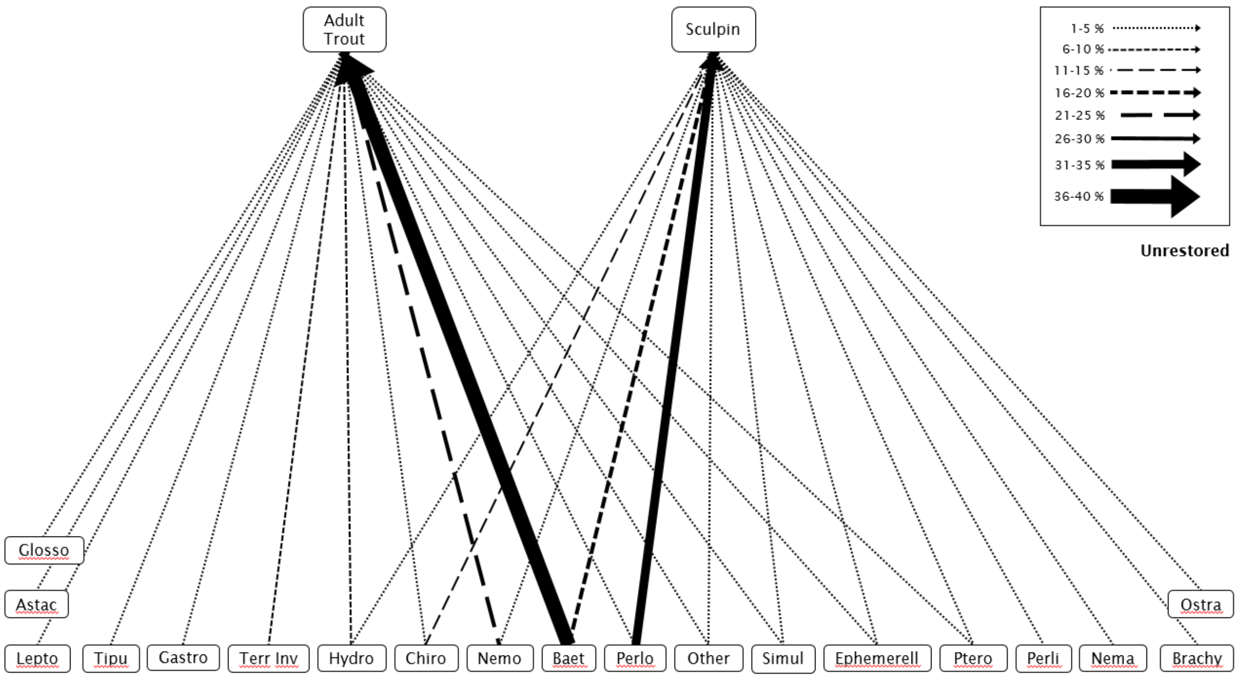

Figure 10. Food web diagram of the average contributions of the major taxonomic groups to the total biomass of fish diets for adult trout and sculpin in the unrestored reference reaches of the S.Fk. McKenzie River, OR.

.

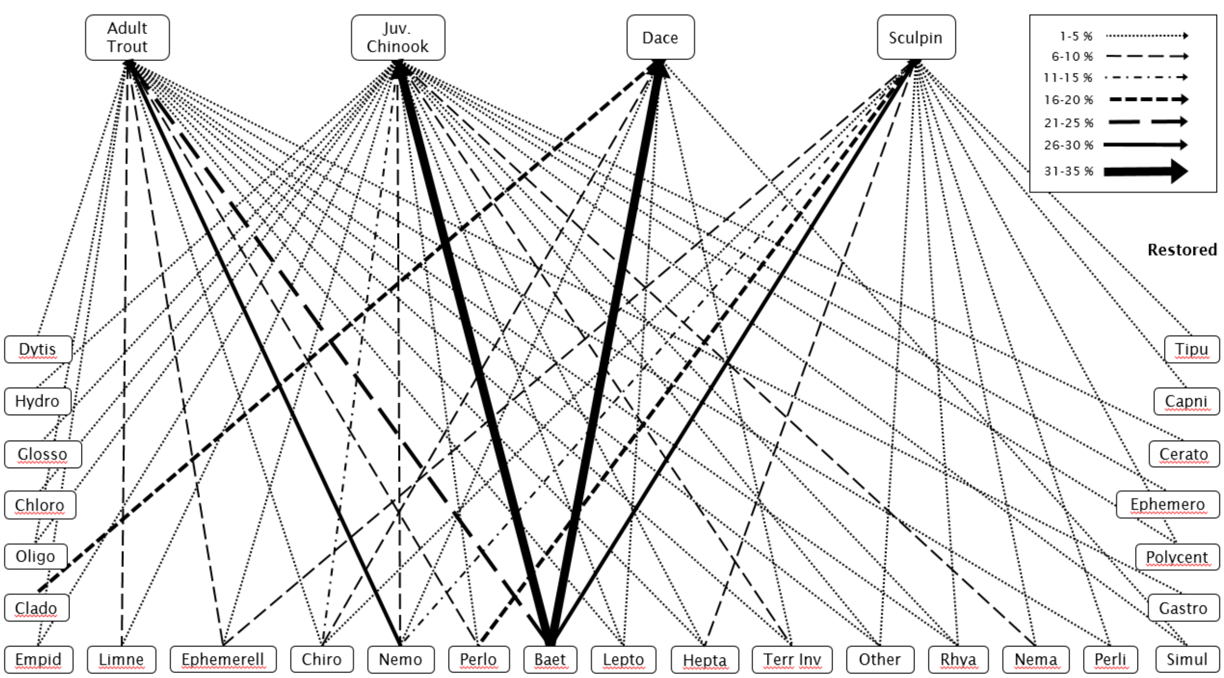

Figure 11. Food web diagram of the average contributions of the major macroinvertebrate taxonomic groups to the total biomass of fish diets for adult trout, sculpin, dace, and juvenile chinook in the stage 0 restored reach of the S.Fk. McKenzie River.

Discussion

The findings from our study suggest that stage 0 restored sites may support greater biological productivity, as well as a diversity of macroinvertebrate community assemblages shortly after project implementation. One year after restoration in the South Fork McKenzie River, total aquatic macroinvertebrate production was 2x higher in the stage 0 restored reach than in either of the unrestored reaches, which can be attributed to the dramatic expansion of wetted area across the floodplain following restoration. However, on a per unit area basis, macroinvertebrate production in the restored reach was equal to or lower than in the unrestored reaches, consistent with observed macroinvertebrate responses to disturbance events that aggrade channels, such as landslides (Lamberti et al. 1991, Kobayashi et al. 2010) and dam removal (Thomson et al. 2005, Orr et al. 2008). These findings suggest that while stage 0 restoration may increase the energetic capacity to support fish populations by increasing the wetted area available for prey production, stage 0 restoration may reduce the growth potential for individual fishes, at least in the near-term.

These findings also illustrate how the diversity of aquatic habitats created by stage 0 restoration (Side Channel vs. Main Channel vs. Wetted Forest) may provide a template for unique communities of macroinvertebrates and unique food web compartments that support higher consumers like fish. These distinct meta-food webs could enhance ecological stability (Rooney & McCann 2012, Bellmore et al. 2015), particularly for mobile consumers such as salmon and trout, that can move amongst habitat types (Armstrong et al. 2013, Armstrong et al. 2016).

Production and Disturbance

Contrary to expectation, average annual biomass and production was found to be highest on a per meter squared basis in the reference reaches, rather than in the restored reach. However, the production estimates were quite different between the two reference reaches. Reference reach A had the greatest production, with an average 43.3 g DM * m^{-2} * yr^{-1}, a value 2.5x larger than the next highest production estimate of 15.9 g DM * m^{-2} * yr^{-1} in Reference B. The construction and operation of Cougar Dam led to altered flow patterns, channel simplification, the reduction of smaller gravels, and the dominance of large cobbles in the channel downstream (Ligon et al. 1995), and these downstream effects may account for some of the differences in productivity observed between Reference reaches A and B. For example, in Reference reach B, the reference reach closest to Cougar Dam (~1.6 km downstream), the substrate is dominated by large embedded cobbles, with few smaller gravels which may offer less interstitial habitat between cobbles for net-spinning caddisflies relative to Reference A. Reference reach A is also about twice as far downstream (~3.4 km) from the dam as Reference B, and features less embeddedness and a higher density of mid-sized cobbles with potentially more surface and interstitial area for colonization by net-spinning caddisflies and other macroinvertebrates. Furthermore, export of lentic surface water materials and biota from Cougar Dam have been shown to reduce macroinvertebrate density and alter downstream food webs (Murphy et al. 2021). Cladocera and copepoda, invertebrates normally associated with lakes and reservoirs, were observed in high densities in some of the benthic samples collected in Reference B during the summer of 2019. These invertebrates were not observed in samples from Reference A, which suggests that Reference B may be more strongly influenced by exports from the upstream reservoir than Reference A. As a result of the combined direct and indirect influences of both the dam and reservoir, Reference reach B may not be as appropriate a “reference condition” for comparison with the restored reach, relative to Reference A, which is both farther from the dam and closer (~1.7 km upstream) to the restored reach.

It is also possible that the disturbance caused by the restoration depressed production in the restored reach. The aquatic habitat patches in the restored reach had much lower average annual biomass and secondary production estimates than the closest reference reach (Reference A). These samples were collected only a year after restoration implementation, and the macroinvertebrate community may still be in a post-disturbance, successional recovery state with an unknown time to full recruitment and fulfillment of production potential. However, when considered in aggregate, the restored reach patches add up to as much or more total production as in Reference reach A.

Total annual production in Reference reach B and the aquatic habitat patches in the restored reach fell within a similar range of values observed in other floodplain rivers. Values ranged from 15.9 g DM * m^{-2} * yr^{-1} in Reference B, to 6.1 g DM * m^{-2} * yr^{-1} in the Side Channel habitat, similar to values found in the Methow River, WA (4.7 g DM * m^{-2} * yr^{-1} to 18.8 g DM * m^{-2} * yr^{-1}) (Bellmore et al. 2013), and the River Welland, UK (3.2 g DM * m^{-2} * yr^{-1} to 11.6 g DM * m^{-2} * yr^{-1}) (Al-Zankana et al. 2020). However, production in Reference reach A was exceptionally high (43.3 g DM * m^{-2} * yr^{-1}), exceeding the highest estimates from both the Methow River, WA and River Welland, UK, but similar to the low end of the range of estimates from a highly productive lake outflow in Iceland (~40 g DM * m^{-2} * yr^{-1} to 880 g DM * m^{-2} * yr^{-1}) (Huryn & Wallace 2000). While Reference A exhibited an exceptionally large production estimate, it is still well below the most productive streams in southeast N. America which range from169 g DM * m^{-2} * yr^{-1} in a North Carolina to 612 g DM * m^{-2} * yr^{-1} in West Virginia (Huryn & Wallace 2000). Production in Reference reach A may have been so much higher due to a combination of factors, such as lower turbidity, higher in-stream primary productivity, muted flow regime, greater bed stability, higher quality and availability of benthic habitat, and differences in autochthonous and detrital resources.

Macroinvertebrate Community Assemblages

Although the restoration does not appear to have increased production on a per meter squared basis, the restoration may have resulted in important shifts in both the assembly of taxa, and the dominant contributors to total production. There were statistically significant differences in the macroinvertebrate communities observed both between the reference and restored reaches, as well as amongst the habitat patches in the restored reach. The assemblages in the restored patches were dominated by small collector/gatherers such as Baetidae, Chironomidae, and Ephemerellidae which tend to have high P/B rates and multivoltine life histories (Huryn & Wallace 2000, Merritt et al. 2019), and clinging scraper/collectors like Leptophlebiidae, Limnephilidae, and Perlodidae, which are non-seasonal and slow-maturing taxa (Stewart & Stark 2002, Wiggins 2018). When compared to the assemblage of taxa in the reference reaches, a more diverse assembly of taxa with greater diversity of life histories and trophic strategies in the restored reach could contribute to a more consistent availability of prey items for foraging fish. When considered together with the more diverse assemblage of fine-scale habitat patches and slow-water, off channel refugia and the steady-state press of continuous small scale disturbance driven by alluvial processes in the restored reach, the restoration may have created a dynamic mosaic of prey items and fine-scale habitat patches across time and space (Townsend 1989, Stanford et al. 2005), such that there is a greater variety of foraging opportunities for fishes, and more consistent availability of prey throughout the year (Wipfli & Baxter 2010, Bellmore et al. 2013, Kaylor et al. 2021).

The fact that no juvenile chinook or dace were caught in the reference reaches with the same fishing effort as in the restored reach, might indicate that the food web in the upstream reference reaches is less complex, and that small minnows and juvenile fish are less important components of the food web. This also suggests that there may be more forage opportunities for juvenile salmonids and minnows in the restored reach, facilitated by a greater diversity of habitat patches and prey items across the riverscape. Consumers have been observed to favor places on the landscape that feature habitat that facilitates optimal foraging or prey availability, while minimizing foraging effort, competition, and exposure to predation (Kaufmann et al. 2007, Hopcraft et al. 2007). The initial disturbance caused by the restoration may have facilitated a process of recolonization, competition and succession, and a continuous press of small scale disturbances throughout the distinct habitat patches in the restored reach as sediment and wood moves, riparian plants colonize, and macroinvertebrate communities assemble at different scales. It is unclear what the trajectory of the macroinvertebrate community in the restored reach may be, but theoretical and empirical research would suggest that these factors contribute to a stream system capable of hosting a dynamic assemblage of adaptive alternative stable states, as fundamental ecological parameters shift and respond to changes over time (Beisner et al. 2003, Catford et al.2013, Palmer & Ruhi 2019, Castro & Thorne 2019). For example, macroinvertebrate assemblages dominated by macroinvertebrate scrapers and clingers supported by diatoms, algae and periphyton could shift to assemblages dominated by shredders and collectors as riparian vegetation becomes established and shades out in-stream primary producers and increases allochthonous subsidies. Increased riparian vegetation could in-turn, attract herbivores such as deer, elk, and beavers, whose browsing might reduce plant density, reducing shading and subsidies of allochthnous organic matter, shifting the macroinvertebrate community back towards domination by macroinvertebrates that rely on in-stream primary production (Beschta & Ripple 2012).

The abundance of large wood in the restored reach also augments available habitat for fish, macroinvertebrates, and periphyton, and while the invertebrate assemblage observed on large wood strongly resembled the benthic community and was much less productive, over time, the large wood surface component may provide increased detrital and primary resources, along with a distinct macroinvertebrate assemblage (Coe et al. 2006), contributing to the diversity of the mosaic of habitat patches in the restored reach.

Plans For Continued Monitoring

There are no plans for continued monitoring of macroinvertebrate production in the first restored reach of the S. Fk. McKenzie that was the focus of this study. However, an additional year of seasonal benthic macroinvretebrate samples (May, Aug, Nov 2021, and Jun 2022) were collected from the reference reaches used in this study, following the same sampling protocols of this study. These samples can provide additional baseline data on production dynamics in the unrestored reaches, and can be used for a post-restoration BACI study if/when stage 0 restoration of the remaining reaches of the S. Fk. McKenzie River below Cougar Dam is completed.

Lessons Learned & Recommendations

It is difficult to place these findings in the context of other river restoration projects, as emphasis has historically been on restoring habitat structure and monitoring post-restoration geomorphic effects, rather than the ecological responses of the aquatic food webs (Naiman et al. 2012). A lack of pre-restoration macroinvertebrate community data also makes assessing the food web response to restoration a challenge. Longer-term studies examining ecological conditions before and after stage 0 restoration are needed in order to examine the trajectories of disturbance, recovery, and community and food-web assembly. Additionally, few studies have attempted to quantify production on submerged wood surfaces, and there are no standardized methods for sampling these surfaces or quantifying the total wood surface available to macroinvertebrates (Coe et al. 2006, Wallace & Benke 1984). While significant gaps in knowledge concerning food web response to stream restoration and the addition of large wood debris remain, this study is an important addition to the current body of knowledge and can serve as a useful reference for future studies.

Stage 0 restoration also creates novel challenges for sampling and study design. Traditional systems of channel and hydraulic classifications (Rosgen 1985, Thomson et al. 2004, Simon et al. 2007) are not easily applied to a stream in a stage 0 state on the valley bottom that lacks a dominant channel or other features commonly used to classify instream habitat (e.g. riffle-pool complexes). The abundance of large woody debris, unconsolidated sediments, pools, and slackwater features also make field-sampling approaches (e.g. transect sampling) extraordinarily difficult, impeding transit across the site, and rendering standard methods of fish capture less useful. Stage 0 sites are generally non-navigable, making the use of boats or kayaks impossible. While backpack electroshock fishing and angling was possible, efficient sampling is negatively impacted by the constant presence of woody snags, channel structure, and fish responses to capture effort (Bayley & Dowling 1993, Peterson et al. 2004).

Food web studies and secondary production estimates can offer greater insight into the effects of stream restoration and how well they have achieved desired goals, but a there is a lack of macroinvertebrate food web studies from the Pacific Northwest that creates additional challenges to generating reliable estimates of production. The majority of published taxon-specific production estimates are from the eastern US and inter-mountain west. These studies provide a useful base of knowledge about turnover rates for small-bodied, fast generation time taxa such as Chironomidae and Baetidae that are often dominant contributors to total community production. However, invertebrate growth rates in the Pacific Northwest are likely different from those found in warm water systems, or mountain streams in the Midwest or Appalachians, and may not be typical of the patterns of production these taxa exhibit in the Pacific Northwest. Furthermore, estimating production for small, fast growing taxa, such as as Chironmidae and Baetidae is logistically challenging, (Stites & Benke 1989). We used P/B values from the literature for estimating production of these taxon in this study, and this may have biased production totals. There remains a need for a comprehensive dataset of cohort production intervals and turnover rates for both insect and non-insect taxa specific to gravel bottom streams of the Pacific Northwest, so that community production estimates more reliably reflect the range of stream conditions and taxa typical in this region.

Conclusion

Stage 0 restoration holds promise for increasing both the complexity and overall productivity of aquatic ecosystems, and these increases may in fact benefit fish populations. However, additional studies are needed to evaluate the near and far-term ecosystem responses to stage 0 restoration, and how these responses vary across different geographic, hydrologic, and ecological contexts. As stage 0 restoration is implemented in different ecoregions and hydrologic regimes across North America and the Pacific Northwest, more research is needed to understand the context dependent responses to stage 0 restoration in these different systems. Secondary production studies may prove especially useful in examining these responses, as production estimates integrate many of the physical and biological changes wrought by stream restoration, reducing them to a manageable number of relevant functional metrics. Secondary production, complemented by estimates of primary production, community respiration, and stable isotope analysis, could provide the long-term, high resolution temporal responses needed for improving our understanding of how stage 0 restoration affects the aquatic ecosystem.

Acknowledgements

The authors express sincere appreciation for the financial and material support of the Oregon Watershed Enhancement Board, McKenzie Watershed Council, Oregon Department of Fish & Wildlife, USFS Pacific North West Research Station, USFS McKenzie River Ranger Station.

Additional thanks to:

Kate Meyer, Matt Helstab, Carla Rothenbeucher, Mickey Means-Brous, and Logan Bodiford from the McKenzie River Ranger Station for help with fish and macroinvertebrate sampling.

Aquatic ecologist Bruce Hansen from the USFS PNW Research Station, Corvallis, for assistance with fish permitting, fish sampling equipment, and field sampling.

Jared Weybright and Chase Antonovich from the McKenzie Watershed Council for help with invoicing, reporting, and field sampling.

Robert Wisseman and Aquatic Biology Associates, Inc. for support with macroinvertebrate sampling, processing, preservation, and identification.

Brian Staab, Steve Wondzell, Kate Meyers, Becky Flitcroft, Paul Powers, Matt Helstab**,** and Johan Hogervorst for coordination of research porjects on the South Fork Mckenzie River.

References

Al-Zankana, A.F.A., Matheson, T., Harper, D.M. 2021. Secondary production of macroinvertebrates as indicators of success in stream rehabilitation. River Research and Applications 37(3): 408-422.

Armstrong, J.B., Schindler, D.E., Ruff, C.P., Brooks, G.T., Bentley, K.E., Torgersen, C.E. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94(9): 2066-2075.

Armstrong, J.B., Takimoto, G., Schindler, D.E., Hayes, M.M., Kauffman, M.J. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97(5): 1099-1112.

Atkinson, C.L., Allen, D.C., Davis, L., Nickerson, Z.L. 2018. Incorporating ecogeomorphic feedbacks to better understand resiliency in streams: a review and directions forward. Geomorphology 305: 123-140.

Bayley, P.B., Dowling, D.C. 1993. The effect of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. Polskie Archiwum Hydrobiologii 40: 5-5.

Beechie, T.J., Liermann, M., Pollock, M.M., Baker, S., Davies, J. 2006. Channel pattern and river-floodplain dynamics in forested mountain river systems. Geomorphology 78(1-2): 124-141.

Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., Pollock, M.M. 2010. Process-based principles for restoring river ecosystems. BioScience 60(3): 209+.

Behan, J., Fetcho, K., Davis, R., Gaines, L. 2021. River Restoration to Achieve a Stage 0 Condition: Summary of a Workshop Held November 5-6, 202. Report to the Oregon Watershed Enhancement Board (Salem, Oregon) and the Institute for Natural Resources (Corvallis, Oregon).

Beisner, B.E., Haydon, D.T., Cuddington, K. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1(7): 376-382.

Bellmore, J.R., Baxter, C.V., Connolly, P.J. 2015. Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. Ecology 96(1): 274-283.

Bellmore, J.R., Baxter, C.V., Martens, K., Connolly, P.J. 2013. The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecological Applications 23(1): 189-207.

Benke, A.C. 1984. Secondary production of aquatic insects. The Ecology of Aquatic Insects 10: 289-322.

Benke, A.C., Huryn, A.D. 2017. Secondary production and quantitative food webs. In Methods in Stream Ecology, 3rd Edition (pp. 235-254). Academic Press.

Benke, A.C., Huryn, A.D., Smock, L.A., Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18(3): 308-343.

Beschta, R.L., Ripple, W.J. 2012. The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology*, *157*, 88-98.

Catford, J.A., Naiman, R.J., Chambers, L.E., Roberts, J., Douglas, M., Davies, P. 2013. Predicting novel riparian ecosystems in a changing climate. Ecosystems 16(3): 382-400.

Castro, J.M., Thorne, C.R. 2019. The stream evolution triangle: Integrating geology, hydrology, and biology. River Research and Applications 35(4): 315-326.

Cluer, B., Thorne, C. 2014. A Stream evolution model integrating habitat and ecosystem benefits. River Research and Applications 30(2): 135–54.

Coe, H.J., Kiffney, P.M., Pess, G.R. 2006. A comparison of methods to evaluate the response of periphyton and invertebrates to wood placement in large Pacific coastal rivers. Northwest Science 80(4): 298.

Cross, W.F., Baxter, C.V., Donner, K.C., Rosi-Marshall, E.J., Kennedy, T.A., Hall Jr, R.O., Kelly, H.A.W, Rogers, R.S. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecological Applications 21(6): 2016-2033.

Cross, W.F., Baxter, C.V., Rosi-Marshall, E.J., Hall Jr, R.O., Kennedy, T.A., Donner, K.C., Yard, M.D. 2013. Food-web dynamics in a large river discontinuum. Ecological Monographs 83(3): 311-337.

Goslee, S.C., Urban, D.L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22(7):1-19.

Guan, R.Z. 2000. Abundance and production of the introduced signal crayfish in a British lowland river. Aquaculture International 8(1): 59-76.

Hamill, S.E., Qadri, S.U., Mackie, G.L. 1979. Production and turnover ratio of *Pisidium casertanum* (Pelecypoda: Sphaeriidae) in the Ottawa River near Ottawa-Hull, Canada. Hydrobiologia 62(3): 225-230.

Höckendorff, S., Tonkin, J.D., Haase, P., Bunzel-Drüke, M., Zimball, O., Scharf, M., Stoll, S. 2017. Characterizing fish responses to a river restoration over 21 years based on species' traits. Conservation Biology 31(5): 1098-1108.

Hopcraft, J.G.C., Sinclair, A.R.E., Packer, C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74(3): 559-566.

Huryn, A.D. 1990. Growth and voltinism of lotic midge larvae: patterns across an Appalachian Mountain basin. Limnology and Oceanography 35(2): 339-351.

Huryn, A.D., Wallace, J.B. 1987. Production and litter processing by crayfish in an Appalachian mountain stream. Freshwater Biology 18(2): 277-286.

Huryn, A.D., Wallace, J.B. 2000. Life history and production of stream insects. Annual Review of Entomology 45(1): 83-110.

Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R., Boyce, M.S. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. Ecology Letters 10(8): 690-700.

Kaylor, M.J., Justice, C., Armstrong, J.B., Staton, B.A., Burns, L.A., Sedell, E., White, S.M. 2021. Temperature, emergence phenology and consumption drive seasonal shifts in fish growth and production across riverscapes. Journal of Animal Ecology.

Kobayashi, S., Gomi, T., Sidle, R.C., Takemon, Y. 2010. Disturbances structuring macroinvertebrate communities in steep headwater streams: relative importance of forest clearcutting and debris flow occurrence. Canadian Journal of Fisheries and Aquatic Sciences 67(2): 427-444.

Lamberti, G.A., Gregory, S.V., Ashkenas, L.R., Wildman, R.C., Moore, K.M. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48(2): 196-208.

Ligon, F.K., Dietrich, W.E., Trush, W.J. 1995. Downstream ecological effects of dams. BioScience 45(3): 183-192.

Lugthart, G.J., Wallace, J.B., Huryn, A.D. 1990. Secondary production of chironomid communities in insecticide-treated and untreated headwater streams. Freshwater Biology 24(3): 417-427.

Merritt, R.W., Cummins, K.W., Berg, M.B. 2019. Aquatic insects of North America. Kendall Hunt, Dubuque.

Murphy, C.A., Johnson, S.L., Gerth, W., Pierce, T., Taylor, G. 2021. Unintended consequences of selective water withdrawals from reservoirs alter downstream macroinvertebrate communities. Water Resources Research 57(6): e2020WR029169.

Naiman, R.J., Alldredge, J.R., Beauchamp, D.A., Bisson, P.A., Congleton, J., Henny, C.J., Huntly, N., Lamberson, R., Levings, C., Merrill, E.N., Pearcy, W.G., Rieman, B.E., Ruggerone, G.T., Scarnecchia, D., Smouse, P.E., Wood, C.C. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences 109(52): 21201-21207.

O'Doherty, E.C. 1985. Stream-dwelling copepods: Their life history and ecological significance. Limnology and Oceanography 30(3): 554-564.

Oksanen, J., Blanchet, F.G., Friendly, M. , Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L. Solymos, P.R., Henry, M., Stevens, H., Szoecs, E., Wagner, H. 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Orr, C.H., Kroiss, S.J., Rogers, K.L., Stanley, E.H. 2008. Downstream benthic responses to small dam removal in a coldwater stream. River Research and Applications 24(6): 804-822.

Paillex, A., Dolédec, S., Castella, E., Mérigoux, S. 2009. Large river floodplain restoration: Predicting species richness and trait responses to the restoration of hydrological connectivity. Journal of Applied Ecology 46(1): 250–58.

Palmer, M., Ruhi, A. 2019. Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration. Science, 365(6459).

Peterson, J.T., Thurow, R.F., Guzevich, J.W. 2004. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. Transactions of the American Fisheries Society 133(2): 462-475.

Powers, P.D., Helstab, M., Niezgoda, S.L. 2019. A process-based approach to restoring depositional river valleys to Stage 0, an anastomosing channel network. River Research and Applications 35(1): 3-13.

Ramírez, A., Pringle, C.M. 1998. Structure and production of a benthic insect assemblage in a neotropical stream. Journal of the North American Benthological Society 17(4): 443-463.

Rooney, N., McCann, K.S. 2012. Integrating food web diversity, structure and stability. Trends in Ecology & Evolution 27(1): 40-46.

Rosgen, D.L. 1985. A stream classification system. In Riparian Ecosystems and Their Management. First North American Riparian Conference. Rocky Mountain Forest and Range Experiment Station RM-120: pp. 91-95.

RStudio Team 2019. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Simon, A., Doyle, M., Kondolf, M., Shields Jr, F.D., Rhoads, B., McPhillips, M. 2007. Critical evaluation of how the Rosgen classification and associated "natural channel design" methods fail to integrate and quantify fluvial processes and channel response. Journal of the American Water Resources Association 43(5): 1117-1131.

Stanford, J.A., Lorang, M.S., Hauer, F.R. 2005. The shifting habitat mosaic of river ecosystems. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 29(1): 123-136.

Stewart, K.W., Stark, B.P. 2002. Nymphs of North American stonefly genera (Plecoptera). Caddis Press, Columbus.

Stites, D.L., Benke, A.C. 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for P: B ratios. Limnology and Oceanography 34(7): 1278-1289.

Thomson, J.R., Taylor, M.P., Brierley, G.J. 2004. Are River Styles ecologically meaningful? A test of the ecological significance of a geomorphic river characterization scheme. Aquatic Conservation: Marine and Freshwater Ecosystems 14(1): 25-48.

Thomson, J.R., Hart, D.D., Charles, D.F., Nightengale, T.L., Winter, D.M. 2005. Effects of removal of a small dam on downstream macroinvertebrate and algal assemblages in a Pennsylvania stream. Journal of the North American Benthological Society 24(1): 192-207.

Thorp, J.H., Thoms, M.C., Delong, M.D. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Research and Applications 22(2): 123-147.

Tockner, K., Malard, F., Ward, J.V. 2000. An extension of the flood pulse concept. Hydrological Processes 14(16-17): 2861-2883.

Tockner, K., Stanford, J.A. 2002. Riverine flood plains: Present state and future trends. Environmental Conservation 29(3): 308–30.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8(1): 36-50.

USACE, BPA, & USBR. 2007. Supplemental biological assessment of the effects of the Willamette River Basin flood control project on species listed under the Endangered Species Act (Submitted to National Marine Fisheries Service and U.S. Fish and Wildlife Service) (p. 362). Retrieved from https://usace-contentdm-oclc-org.ezproxy.proxy.library.oregonstate.edu/digital/collection/p16021coll7/id/8226/

Wallace, J.B., Benke, A.C. 1984. Quantification of wood habitat in subtropical coastal plain streams. Canadian Journal of Fisheries and Aquatic Sciences 41(11): 1643-1652.

Wickham, H. 2020. tidyr: Tidy Messy Data. R package version 1.1.2. https://CRAN.R-project.org/package=tidyr

Wiggins, G. 2018. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press.

Wipfli, M.S., Baxter, C.V. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries, 35(8), 373-387.

Wohl, E., Lane, S.N., Wilcox, A.C. 2015. The science and practice of river restoration. Water Resources Research 51(8): 5974–97.

Zaroban, D.W., Mulvey, M.P., Merritt, G.D., Hughes, R.M., Maret, T.R. 1999. Classification of species attributes for Pacific Northwest freshwater fishes. Northwest Science 73(2): 81-93.

Outreach

Presentations

These findings were presented in a thesis defense at Oregon State University in Dec. 2021 to an audience of ~50 people consisting of OSU faculty, students, and members of the public. This study was also presented at a virtual meeting in Feb. 2022 to an audience of ~15 people consisting of OWEB and USFS personnel, and again in Mar. 2022 at the annual meeting of the Oregon Chapter of the American Fisheries Society to an audience of ~100 fisheries scientists and students.

Publications

Jennings, J. C. 2021. Effects of Stage 0 Stream Restoration on Aquatic Macroinvertebrate Production. Master's thesis. Oregon State University, Corvallis OR. https://ir-library-oregonstate-edu.ezproxy.proxy.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/0r967b66n

Flitcroft, R., W. R. Brignon, B. Staab, R. Bellmore, J. Burnett, P. Burns, B. Cluer, G. Giannico, M. Helstab, J. Jennings, C. Mayes, C. Mazzacano, L. Mork, K. Meyer, J. Munyon, B. Penaluna, P. Powers, D. N. Scott, and S. Wondzell. 2022. Rehabilitating Valley Floors to a Stage 0 Condition: A Synthesis of Opening Outcomes. Accepted to *Frontiers*.

Funding

Cash Contributions: $150,000 of OWEB funding; $100,000 of Forest Service, Region 6

In-Kind Contributions: Total = $25,000
Materials: We used existing USFS field sampling equipment representing a purchase cost of $5,000.
Labor: Time commitments needed from various personnel to complete field sampling, and obtain and do reporting for sampling permits. Field sampling required approximately 30 days of USFS people time, and permitting required another 25 days of time, representing an in-kind salary contribution of $25,000.

Appendices

Appendix A: Tables of P/B values used in secondary production calculations.

Table A1. P/B ratios calculated from S.Fk. McKenzie River monthly benthic samples.

Taxon	Family	Order	P/B
Antocha	Tipulidae	Diptera	6.6
Arctopsyche	Hydropsychidae	Trichoptera	8.8
Baetis alius	Baetidae	Ephemeroptera	10.9
Baetis tricaudatis complex	Baetidae	Ephemeroptera	10.4
Brachycentrus americanus	Brachycentridae	Trichoptera	3.1
Caudatella columbiella	Ephemerellidae	Ephemeroptera	8.3
Caudatella edmundsi	Ephemerellidae	Ephemeroptera	8.8
Caudatella hystrix	Ephemerellidae	Ephemeroptera	7.9
Cinygmula	Heptageniidae	Ephemeroptera	7.4
Diphetor hageni	Baetidae	Ephemeroptera	7.3
Drunella flavilinea	Ephemerellidae	Ephemeroptera	4.6
Epeorus	Heptageniidae	Ephemeroptera	10.5
Ephemerella excrucians group	Ephemerellidae	Ephemeroptera	7.7
Glossosoma	Glossosomatidae	Trichoptera	3.8
Hesperoperla pacifica	Perlidae	Plecoptera	5.2
Hydropsyche	Hydropsychidae	Trichoptera	6.0
Ironodes	Heptageniidae	Ephemeroptera	9.2
Isoperla	Perlodidae	Plecoptera	5.2
Lepidostoma (Neodinarthrum)	Lepidostomatidae	Trichoptera	2.7
Malenka	Nemouridae	Plecoptera	5.0
Micrasema	Brachycentridae	Trichoptera	3.7
Neoleptophlebia/Paraleptophlebia	Leptophlebiidae	Ephemeroptera	7.2
Neoplasta	Empididae	Diptera	5.2
Perlodidae	Perlodidae	Plectoptera	2.6
Rhyacophila brunnea/vemna group	Rhyacophilidae	Trichoptera	3.5
Simulium	Simuliidae	Diptera	8.1
Sweltsa	Chloroperlidae	Plecoptera	1.0
Thienemannimyia complex	Chironomidae: Tanypodinae	Diptera	9.9
Wiedemannia	Empididae	Diptera	4.9

Table A2. P/B ratios from literature used for calculating annual production estimates.

Source	Family	P/B
Bellmore et al. 2013	Chironomidae	22.3
" "	Brachycentridae	4.1
" "	Lepidostomatidae	9.1
" "	Hydropsychidae	8.8
" "	Ephemerellidae	7.1
" "	Tipulidae	5.5
" "	Baetidae	24
" "	Perlidae	5
" "	Heptageniidae	4.9
" "	Limnephilidae	5
" "	Perlodidae	4.1
" "	Uenoidae	5
" "	Glossosomatidae	8.4
" "	Leptophlebiidae	5.2
" "	Dytiscidae	5
" "	Chloroperlidae	5
" "	Empididae	6.3
" "	Ameletidae	4.5
" "	Pteronarcyidae	1.2
" "	Capniidae	4.2
" "	Elmidae	27.3
" "	Ceratopogonidae	5.8
" "	Sialidae	2.6
" "	Gastropoda	2.3
Ramirez & Pringle 1998	Hydroptila	12.9
Huryn & Wallace 1987	Cladocera	10
Benke 1984	Oligochaeta	5
Huryn & Wallace 1987	Ostracoda	10
Benke 1984	Nematoda	5
Benke 1984	Turbellaria	5
Huryn & Wallace 1987	Decapoda	0.58
O'Doherty 1985	Copepoda	18
Guan 2000	Astacidae	0.44
Hamill et al. 1979	Pisidium/Sphaeriidae	3.8
Huryn 1990, Lugthart et al. 1990 , Cross et al. 2013, Huryn & Wallace	Chironomidae	12

Appendix B: Counts of Total Fish Diets

Table B1. Fish diet samples, by species, sample reach, and habitat patch in the stage 0 restored reach, of the South Fork McKenzie River, OR.

	Chinook	**Cutthroat**	**Rainbow**	**Dace**	**Sculpin**	**Trout**
Wetted Forest Fall	0	0	0	18	0	0
Wettted Forest Summer	0	0	1	0	0	0
Wetted Forest Winter	4	0	1	0	0	0
Side Channel Fall	0	4	5	5	5	5
Side Channel Summer	0	0	0	0	0	0
Main Channel Fall	4	10	7	8	13	0
Main Channel Summer	38	0	3	0	0	0
Reference A Fall	0	5	19	0	20	0
Reference A Summer	0	0	1	0	0	0
Reference B Fall	0	3	18	2	37	0
Reference B Summer	0	0	0	0	0	0
Totals	46	22	55	33	75	5
Restored	46	14	17	31	18	5
Unrestored	0	8	38	2	57	0

Appendix C: Assemblage Composition of Annual Biomass

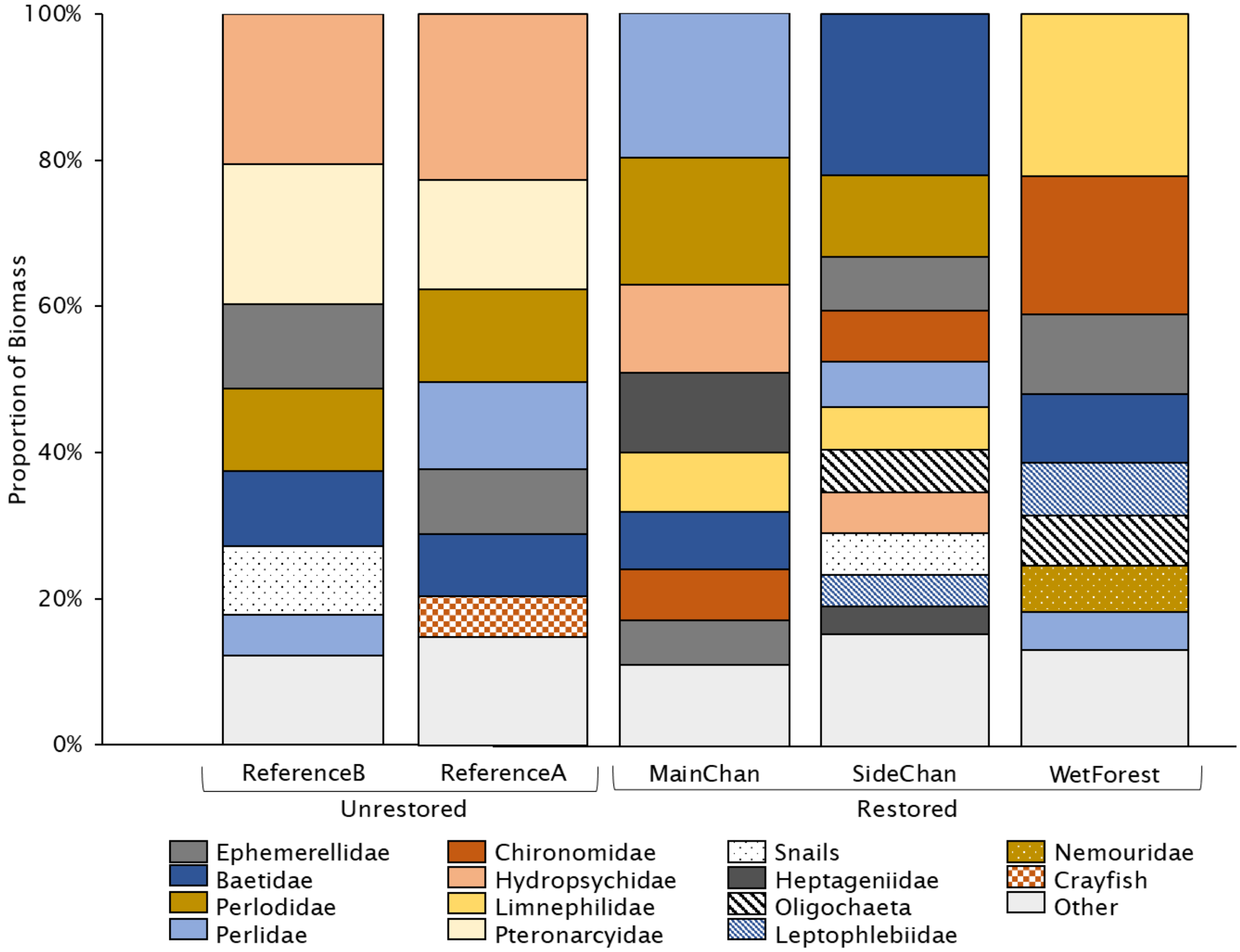

Figure C1. Proportions, by dominant taxa, of the total mean annual benthic macroinvertebrate biomass of each unrestored reach, and each habitat patch in the stage 0 restored reach, of the South Fork McKenzie River, OR.

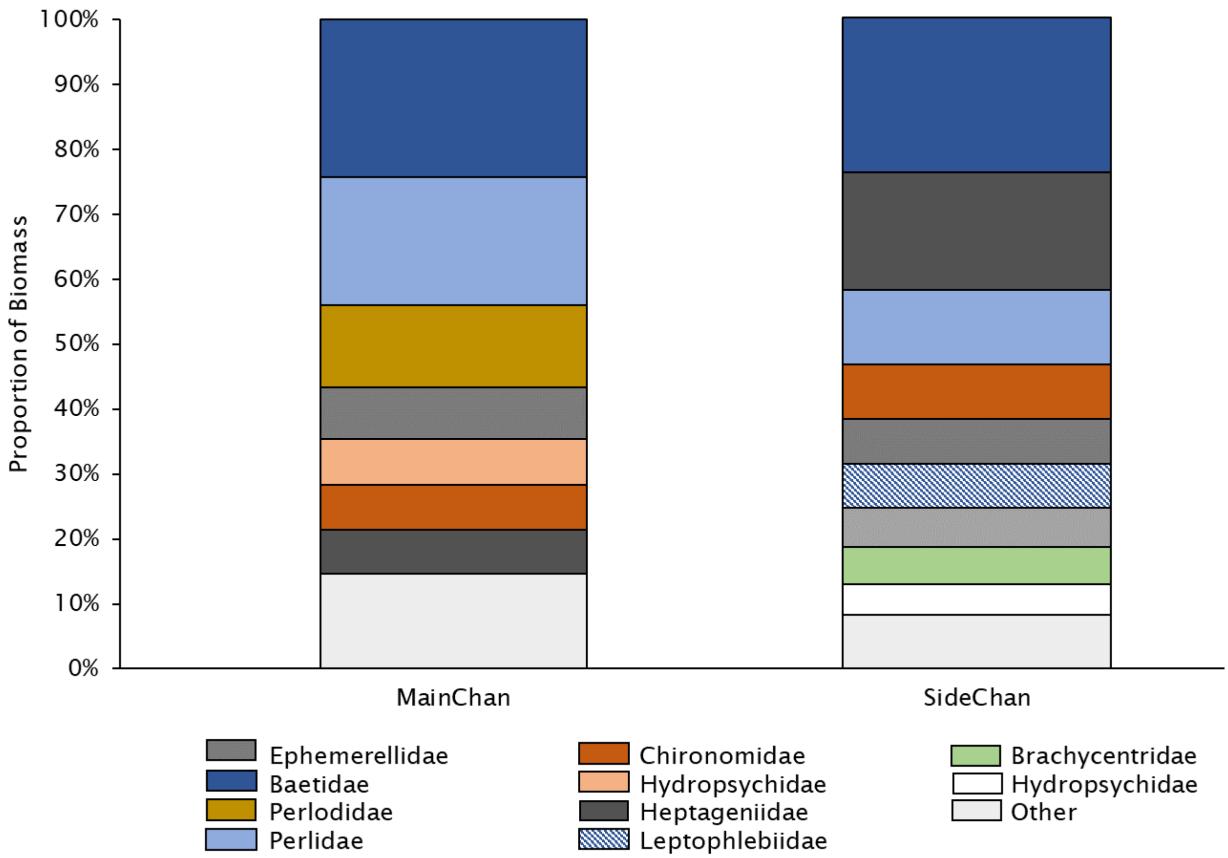

Figure C2. Proportions (by dominant taxa) of total annual macroinvertebrate biomass on submerged wood surfaces in the Main and Side Channel habitat patches in the stage 0 restored reach of the South Fork McKenzie River, OR.

Appendix D: Web links to relevant papers

- Jennings JC. (2021). Effects of Stage 0 Stream Restoration on Aquatic Macroinvertebrate Production. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/0r967b66n
- Flitcroft et al. (2022). Rehabilitating valley floors to a stage 0 condition: a synthesis of opening outcoming. https://www.frontiersin.org/articles/10.3389/fenvs.2022.892268/abstract

Appendix E: Raw macroinvertebrate data used to estimating invertebrate biomass, production, and composition. Provided as separate Excel spreadsheets.