Received: 16 December 2022 | Revised: 31 May 2023 | Accepted: 2 June 2023

DOI: 10.1002/rra.4174

RESEARCH ARTICLE

WILEY

Effects of process-based floodplain restoration on aquatic macroinvertebrate production and community structure

Jeremy C. Jennings[1] | J. Ryan Bellmore[2] | Jonathan B. Armstrong[1] | Robert W. Wisseman[3]

[1]Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[2]USDA Forest Service, Pacific Northwest Research Station, Juneau, Alaska, USA

[3]Aquatic Biology Associates Incorporated, Corvallis, Oregon, USA

Correspondence
Jeremy C. Jennings, Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97330, USA.
Email: jeremy.jennings@oregonstate.edu

Funding information
McKenzie Watershed Council; Oregon Watershed Enhancement Board; U.S. Forest Service

Abstract

Recent stream restoration approaches, such as Stage 0 restoration, aim to restore natural processes to regain lost ecosystem functions, but project implementation can also represent a reach-scale disturbance. Assumed outcomes of these restoration actions, like greater biological productivity, are rarely evaluated. In this study, we examined the short-term effects of Stage 0 floodplain restoration on the secondary production of aquatic macroinvertebrate communities in the South Fork McKenzie River, Oregon, 1–2 years following project implementation. We seasonally sampled macroinvertebrates from benthic and submerged wood surfaces in the restored reach, and two unrestored reference reaches located upstream, to estimate annual secondary production. Macroinvertebrate production estimates were 3× lower on a per-meter-squared basis in the restored reach than in the upstream unrestored reference reaches (9764 vs. 29,636 mg DM/m^2/yr). However, because there was 4.5-times greater wetted area available in the restored reach, overall macroinvertebrate production per unit of valley length was 3.4× higher in the restored reach than in unrestored reference reaches (2744 vs. 802 kg DM/km). Additionally, the mosaic of aquatic habitats created via restoration (main-channel, side-channel, and wetted forest habitats) supported a diversity of macroinvertebrate assemblages both within and among reaches. Our findings suggest Stage 0 project implementation, which can include dewatering and filling incised channels, may reduce aquatic macroinvertebrate production on a per-unit-area basis for at least 1 or 2 years following restoration. However, this short-term disturbance effect may be offset by channel aggradation and widening, which can provide a more wetted area for macroinvertebrate production and may support greater macroinvertebrate community diversity. Future studies are needed to examine the longer term (2–10 years) aquatic macroinvertebrate response to Stage 0 restoration, and the impacts of shifting resource availability on stream fishes.

KEYWORDS
aquatic macroinvertebrates, floodplains, river restoration, secondary production, Stage 0 restoration

1 | INTRODUCTION

River floodplains are considered to be amongst the most biologically productive ecosystems on the planet, supporting high rates of primary and secondary production and sustaining aquatic species that are culturally and economically important (Jeffres et al., 2020; Keddy et al., 2009; Tockner & Stanford, 2002). However, intact river floodplains have become exceedingly rare, as human activity and development in wetlands and along rivers have resulted in the loss and alteration of aquatic habitat, often resulting in reduced channel complexity and aquatic productivity (Abell et al., 2008; Beechie et al., 1994; Sparks, 1995). Consequently, enhancing aquatic ecosystem productivity is a common objective of river-floodplain restoration efforts. Although it is frequently assumed that restoring degraded river floodplains will indeed increase aquatic productivity (Castro & Thorne, 2019; Cluer & Thorne, 2014), primary or secondary production responses to restoration have rarely been quantitatively evaluated (Layman & Rypel, 2020). Given that floodplain restoration is a multi-million-dollar global industry, understanding primary and secondary production responses is imperative, especially as larger scale, process-based approaches to restoring river floodplains are employed.

One of the newest approaches to river-floodplain restoration is commonly referred to as "Stage 0" restoration (Flitcroft et al., 2022). "Stage 0" refers to the morpho-ecological state of a river-floodplain system prior to anthropogenic disturbances that promote transitions to less complex single-thread channels in the Stream Evolution Model proposed by Cluer and Thorne (2014). At Stage 0, there exists a dynamically stable and diverse mosaic of channels, backwaters, pools, wetlands, islands, and large wood across the valley bottom (Cluer & Thorne, 2014). In contrast to other river restoration approaches that employ only channel-scale physical structures, Stage 0 restoration is implemented at the valley scale, with the scope and intensity of the specific restoration actions tailored to the conditions and circumstances of the restoration site (Powers et al., 2019). With Stage 0 restoration, the focus is on actively filling and aggrading incised channels to "reestablish depositional environments to maximize longitudinal, lateral, and vertical connectivity at base flows, and facilitate development of dynamic, self-forming, and self-sustaining wetland-stream complexes" (Flitcroft et al., 2022). Dewatering the river is often required, using earth-moving equipment to aggrade the channel with local materials (cobble, gravel, large wood), reconnect historic channels, and restore pre-disturbance elevations and flows across the floodplain (Powers et al., 2019). Because Stage 0 restoration seeks to reestablish the alluvial processes (not just forms) that are believed to create biophysical complexity and biological productivity (Castro & Thorne, 2019; Cluer & Thorne, 2014; Flitcroft et al., 2022), "Stage 0 restoration" ultimately refers to a desired outcome, rather than to a precise method. Due to the scale and intensity of the manipulation employed during Stage 0 implementation, it remains a provocative approach to river-floodplain restoration, with concerns regarding counterproductive post-restoration outcomes (e.g., decreases in productivity and species abundance).

Although the Stage 0 approach differs from traditional floodplain restoration approaches, the biological objectives are similar to those of other methods—to increase biological productivity of freshwater habitats (primary and secondary production) and the capacity of restored areas to support desired organisms, such as fishes. In the Pacific Northwest, where this approach has been developed, one of the primary objectives has been to increase populations of Pacific salmon and trout, which are imperiled across much of the region (Flitcroft et al., 2022). The implicit assumption of Stage 0 restoration is that it will not only create more habitat for salmon spawning and rearing, but it will also stimulate greater productivity of the food base (e.g., aquatic macroinvertebrates) that supports these fishes (Katz et al., 2017; Rypel et al., 2012). Indeed, intact river floodplains have been shown to support high rates of aquatic primary production (Bellmore & Baxter, 2014; Davies Jr et al., 2008; Thorp et al., 1998), as well as high amounts of allochthonous organic matter inputs (Tank et al., 2010), supporting high rates of secondary production of aquatic invertebrates (Benke, 1984; Benke & Wallace, 2015; Walther & Whiles, 2011). River floodplains may support high rates of macroinvertebrate production for a number of reasons: they feature shallower depths and reduced stream power with more wetted edge and total wetted area relative to a confined channel, leading to increased light availability for aquatic primary producers, increased input rates of terrestrial organic matter (e.g., leaf litter and terrestrial invertebrates; Tank et al., 2010), increased retention rates and in-situ processing time of nutrient and organic matter (e.g., leaves, wood, etc.) (Bellmore & Baxter, 2014; Jeffres et al., 2020; Richardson et al., 2019), and increased total habitat area (Flitcroft et al., 2022). River floodplains are also known to support high aquatic macroinvertebrate diversity (Fernandes et al., 2014; Funk et al., 2013). Factors like habitat connectivity, channel network structure, residence time, depth, and flow select for different aquatic species based on trophic niche, propensity to drift, and other life-history traits, creating a spatial and temporal mosaic of macroinvertebrate communities (Arscott et al., 2005; Bellmore & Baxter, 2014; Corline et al., 2021). Given these observations, it is likely that Stage 0 restoration could increase both the quantity and diversity of foraging opportunities for stream fishes, such as juvenile salmon and trout (Beisner et al., 2003; Jeffres et al., 2020; Palmer & Ruhi, 2019).

While these predictions about Stage 0 restoration outcomes are based on sound research and experience, they have rarely been empirically evaluated. Furthermore, there is concern that the channel dewatering and mechanical disturbance associated with restoration may actually reduce aquatic productivity and the potential benefits to fishes. Additionally, the timescale for recovery and reassembly of aquatic communities and food webs is uncertain and could range from months to years or decades (Foster et al., 2020; Lamberti et al., 1991). To address these assumptions and concerns, we designed a control-impact study to examine the impact of Stage 0 restoration on aquatic macroinvertebrate secondary production in a ~1 km reach of the South Fork McKenzie River (SFMR), Oregon, that underwent Stage 0 restoration in 2018. One year after restoration, we compared secondary production in the Stage 0 restored reach with two upstream, unrestored reference sites that remained incised and disconnected from lateral floodplain habitats. We expected that the habitat diversity wrought by Stage 0 would result in greater annual secondary

production of aquatic macroinvertebrates relative to unrestored reference reaches. Furthermore, we expected that habitat heterogeneity created by restoration (braided gravel bed channels, floodplain side channels, and large sections of flooded forest) would create variation in aquatic macroinvertebrate assemblages across space, with distinct assemblages occurring in different patches of the floodplain mosaic.

2 | METHODS

2.1 | Study site

The South Fork McKenzie River (SFMR) is a fourth-order tributary of the Willamette River in west-central Oregon, and joins the main stem McKenzie River ~70 km east of Springfield, Oregon, in the Cascade Mountains (Figure 1). In 1963, Cougar Dam was constructed ~6 km upstream from the confluence of the SFMR and main stem McKenzie River, leading to loss of habitat access for threatened and endangered populations of spring Chinook Salmon (*Oncorhynchus tshawytscha*), Bull Trout (*Salvelinus confluentus*), Steelhead (*Oncorhynchus mykiss*), and the Pacific Lamprey (*Entosphenus tridentatus*) (USACE et al., 2007). Dam operation also resulted in the loss of peak flows, leading to channel simplification and reduction in floodplain habitat downstream of the dam (Meyer et al., 2018). To reverse some of these negative effects on fish habitat, a several-kilometer section of the South Fork McKenzie River below Cougar Dam before its confluence with the main stem McKenzie River has been prioritized for Stage 0 restoration.

2.2 | Restoration actions

Using the design method described by Powers et al. (2019), a ~ 1 km reach of the SFMR river, just above the confluence with the main stem McKenzie River, was first restored to a Stage 0 state in 2018 (Meyer et al., 2018), with upstream restoration scheduled for later phases of the project. Prior to restoration, the restored reach was an incised single-thread channel disconnected from adjacent floodplain habitats. Implementation began with construction of a temporary bypass channel and dewatering of the existing main channel. Excavators and bulldozers were then used to fill the incised channel and redistribute sediments across the valley bottom to reconnect relict floodplain channels and bring the river bottom closer to the historic valley gradient. Pieces of large wood with root wads were placed across the valley and the flow restored, allowing the wood and sediments to move with the flow and reestablish the islands, logjams,

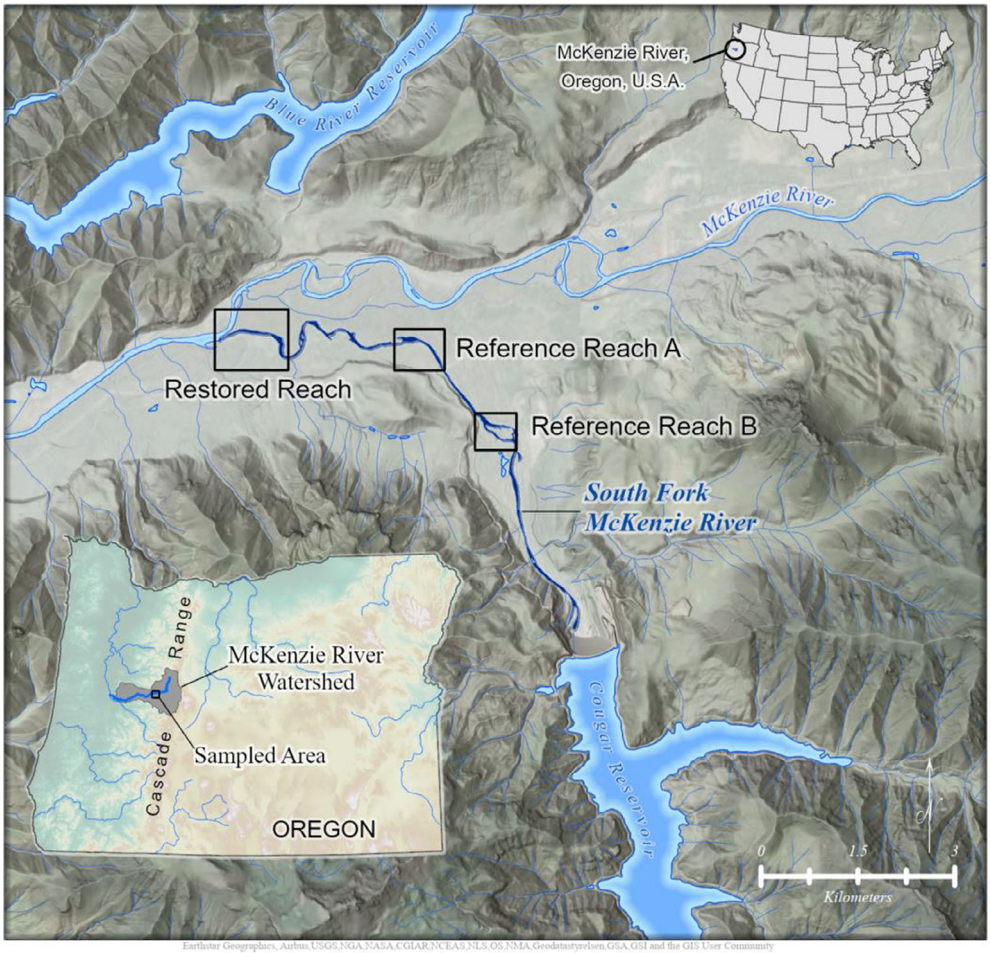

FIGURE 1 Benthic macroinvertebrate and fish diet sampling sites. Direction of flow is from east to west and south to north. Inset map shows the location of the South Fork McKenzie River in the western United States. [Color figure can be viewed at wileyonlinelibrary.com]

braided channels, pools, and slack waters assumed to be characteristic of a floodplain river in a pre-disturbance, Stage 0 state.

2.3 | Study and sampling design

We used a control-impact study design, comparing the annual secondary production of aquatic macroinvertebrates in the Stage 0 restored reach (impacted reach) with two incised and single-thread unrestored upstream reaches (control reaches). Secondary production is a measure of the generation of biomass over a given period of time (e.g., grams/m^2/year), and annual macroinvertebrate production estimates provide a temporally integrated estimate of food available to support insectivorous fishes such as salmon and trout. We sampled aquatic macroinvertebrates both seasonally and semi-monthly to attain per-unit-area average annual biomass estimates and local annual growth rate estimates for each taxon in order to calculate total secondary production for the entire assemblage.

Samples were collected by holding a 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 rebar (Hauer & Resh, 2017). In low-flow areas, the substrate was alternately disturbed and waved by hand into the sampling net. Samples were collected from submerged logs 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% ethanol.

The patchy spatial distribution of aquatic macroinvertebrates across the benthos can be a significant source of error in community biomass and production estimates (Lamberti & Hauer, 2017), and it can be easy to miss or underestimate the biomass and abundance of small-bodied taxa that occur in small, high-density patches across a sample area. To reduce this source of error across all sample sites, we increased the total sample area by using a customized Surber sampler with a larger sampling area (0.25 m^2) than the standard (0.096 m^2) (Bellmore et al., 2013). In addition, to better capture diversity in the macroinvertebrate assemblage, sampling in the restored reach was stratified into three distinct reach-scale aquatic habitat patches, distinguishable by overall differences in dominant substrates, surface morphology, and stream flow, factors that strongly influence the macroinvertebrate assemblage. We called these habitat patches "Main Channel", "Side Channel", and "Wetted Forest" (Figure 2). The Main Channel habitat (which generally overlaps with the pre-restoration main channel) features interbraided channels with gravel and small to medium cobbles, islands, pools, slow-water areas with sand and

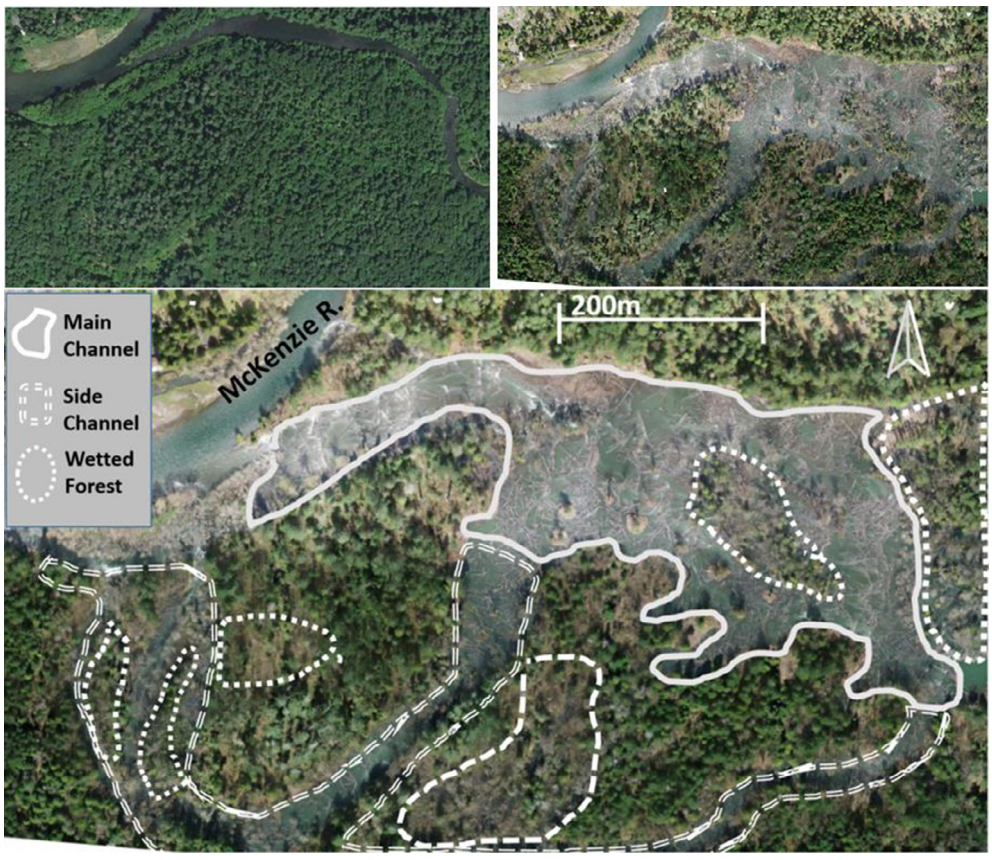

FIGURE 2 Stratified habitat patches where macroinvertebrate samples were taken in the restored reach of the South Fork McKenzie River, OR. Top left image, before restoration. Top right image, after restoration. [Color figure can be viewed at wileyonlinelibrary.com]

unconsolidated sediments, and a high density of large wood. The Wetted Forest habitat consists of perpetually 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 floodplain channels that maintained perrenial connection with the main stem following restoration, these channels contained an abundance of large wood and a substrate dominated by mud, aquatic macrophytes, and small gravels. We did not stratify the sampling in the reference reaches by habitat patch because the reference reaches were simpler, single-channel systems.

Each season, five total benthic macroinvertebrate biomass samples were collected from each habitat patch/reach of the restored area and from each reference reach, for a total of 20 samples ($n = 20$) from each reach every season: summer 2019, fall 2019, winter 2020, spring 2020. Each benthic sample consisted of several subsamples, collected in proportion to the occurrence of the dominant hydraulic habitat types within each patch. For example, in the Main Channel of the restored reach, each benthic sample consisted of five sub-samples collected with the large (0.25 m^2) Surber sampler: two from riffles, two from runs, and one from less common stagnant water habitat, for a total area of 1.25 m^2 per sample. Each sample in Reference reaches A and B also consisted of five sub-samples collected with the large Surber sampler: two from riffles, three from runs and for a total area of 1.25 m^2 per sample. Fewer sub-samples were taken in the Side Channel and Wetted Forest patches of the restored reach because they were smaller in area. In the Side Channel, each sample consisted of only four sub-samples collected with the large (0.25 m^2) Surber sampler: three from non-vegetated substrate and one from vegetated substrate, for a total area of 1 m^2 per sample. Each sample in the Wetted Forest also consisted of four subsamples, randomly placed with no stratification, and collected with a standard Surber sampler (0.096 m^2) to minimize the amount of organic detritus in the samples for better preservation and processing, for a total area of 0.36 m^2 sampled. Finally, three submerged wood surface samples were also collected each season in the Main and Side Channels of the restored reach. Each wood surface sample consisted of four kick-net sub-samples, for a total area of 0.6 m^2 per sample.

In order to estimate annual secondary production, annual growth rate estimates for individual taxa are needed. High temporal resolution data on the size-frequency and abundance of each taxa are frequently required to estimate annual growth rates, especially for high turnover taxa. Samples to estimate annual growth rates for common taxa were collected from Reference reach A, with each sample consisting of three sub-samples taken from riffles, for a total area of 0.75 m^2 per sample, elutriated with a $\sim$ 250-micron sieve, and preserved in jars with 95% ethanol. Due to a combination of unpredictable flows from Cougar Dam and dangerous conditions during the winter and spring of 2020, only six total samples were collected for growth rates (July, Aug., Sep., Nov., Dec. 2019, and Feb. 2020), resulting in a lack of temporal resolution needed for estimates of the faster growing taxa (e.g., chironomidae, baetidae). For those taxa, we used published growth rates from peer-reviewed literature (Bellmore et al., 2013; Benke, 1984; Cross et al., 2013; Guan, 2000; Hamill et al., 1979; Huryn, 1990; Huryn & Wallace, 1987; Lugthart et al., 1990; O'Doherty, 1985; Ramírez & Pringle, 1998).

Preserved macroinvertebrates were picked from each sample in the lab, removing the largest (>10 mm) individuals first and subsampling with Caton tray or gridded sieve until 500 total individuals were picked (Vinson & Hawkins, 1996). All macroinvertebrates were identified to family, genus, or species/group level according to the Pacific Northwest Aquatic Monitoring Partnership standard taxonomic level 2 (Wisseman et al., 2015), measured to the nearest 0.5 mm 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 (Benke et al., 1999; Ganihar, 1997; Gowing & Recher, 1984; Hawkins et al., 1997; Hódar, 1996; Lang, 1997; Rogers et al., 1977; Sabo et al., 2002; Sage, 1982; Sample et al., 1993; Schoener, 1980; Wrubleski & Rosenberg, 1990) for each taxon and standardized to 1 m^2 sample area.

2.4 | Macroinvertebrate data analysis

Total annual mean biomass estimates and 95% confidence intervals for community assemblages were calculated for each reach/patch by bootstrap resampling the biomass estimates from the seasonal sample sets with a custom script written in R using the tidyr package 1.3.0 (Wickham, 2020). Biomass values were randomly selected, with replacement, from each set of seasonal estimates for each taxa, and the total annual mean was calculated. The process was repeated for 10,000 iterations to generate a bootstrap distribution of means for each macroinvertebrate assemblage in each habitat patch in the restored reach, and each reference reach. The percentile method was used to obtain the upper and lower bounds of the 95% confidence interval from the bootstrap distributions.

Taxon-specific annual growth rates were calculated using the size-frequency method, where differences between the abundances of size classes through time are used to account for the total biomass produced by an average cohort over that time (for details on this approach, see Benke & Huryn, 2017). 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. Taxa-specific production estimates were then divided by the total annual biomass (B) of each taxa to obtain taxon-specific P:B estimates:

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

Annual secondary production for each taxa in the restored patches and reference reaches was then calculated by multiplying bootstrap annual biomass estimates by the taxon-specific growth rate (P/B), using a combination of P/B values calculated from the monthly data and those from the published literature:

$$\text{Bootstrap annual B} \times \text{annual growth rate} \frac{\text{P}}{\text{B}} = \text{annual P}$$

Annual production totals for each reach were then obtained by summing the taxon-specific production estimates. Confidence intervals for production were obtained by scaling the upper and lower bounds of the bootstrap biomass 95% CIs by the total reach P/B ratios. Finally, the annual production estimates and 95% CIs 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 1 km of valley length by dividing the total estimate by valley length and then multiplying by 1000. To evaluate differences in prey production between sites, we visually compared 95% confidence intervals (Bellmore et al., 2013; Cross et al., 2013). Means with nonoverlapping confidence intervals were interpreted as significantly different.

To examine compositional differences between patches and reaches, we conducted a 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 zeros and large spread of values in the dataset. The standardized mean biomass estimates were then plotted via NMDS ordination, and groups (treatment and season) were analyzed for statistically significant differences via Analysis of Similarity (ANOSIM) using the Vegan (version 2.6–4; Oksanen et al., 2020) and Ecodist (version 2.0.9; 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).

3 | RESULTS

3.1 | Seasonal macroinvertebrate biomass

Seasonal per-area macroinvertebrate biomass estimates (g DM/m^2) were generally higher in unrestored reference reaches, especially in reference reach A (the site closest to the restoration site and farthest from the dam outflow), which had 3× higher macroinvertebrate biomass than patches in the restored site in fall 2020 (Figure 3). Most sites exhibited the highest macroinvertebrate biomass in the summer or autumn, and we found no evidence for consistent differences in the seasonal biomass patterns between the reference reaches and the three 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 (Figure 3).

3.2 | Total annual macroinvertebrate biomass and secondary production

Average annual biomass and production of aquatic macroinvertebrates were 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

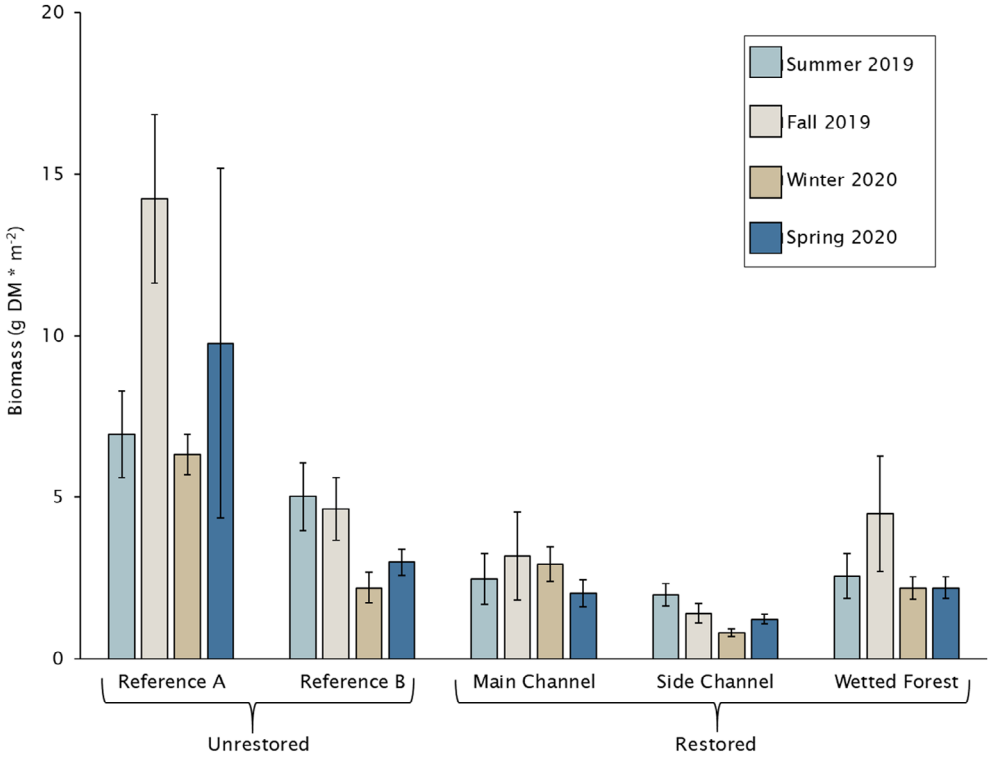

FIGURE 3 Seasonal average benthic macroinvertebrate biomass per-area (mean ± SE) in the unrestored (Reference A and B) reaches and Stage 0 restored habitat patches in the restored reach of the South Fork McKenzie River. $n = 5$, except as indicated by asterisk ($n = 2$). [Color figure can be viewed at wileyonlinelibrary.com]

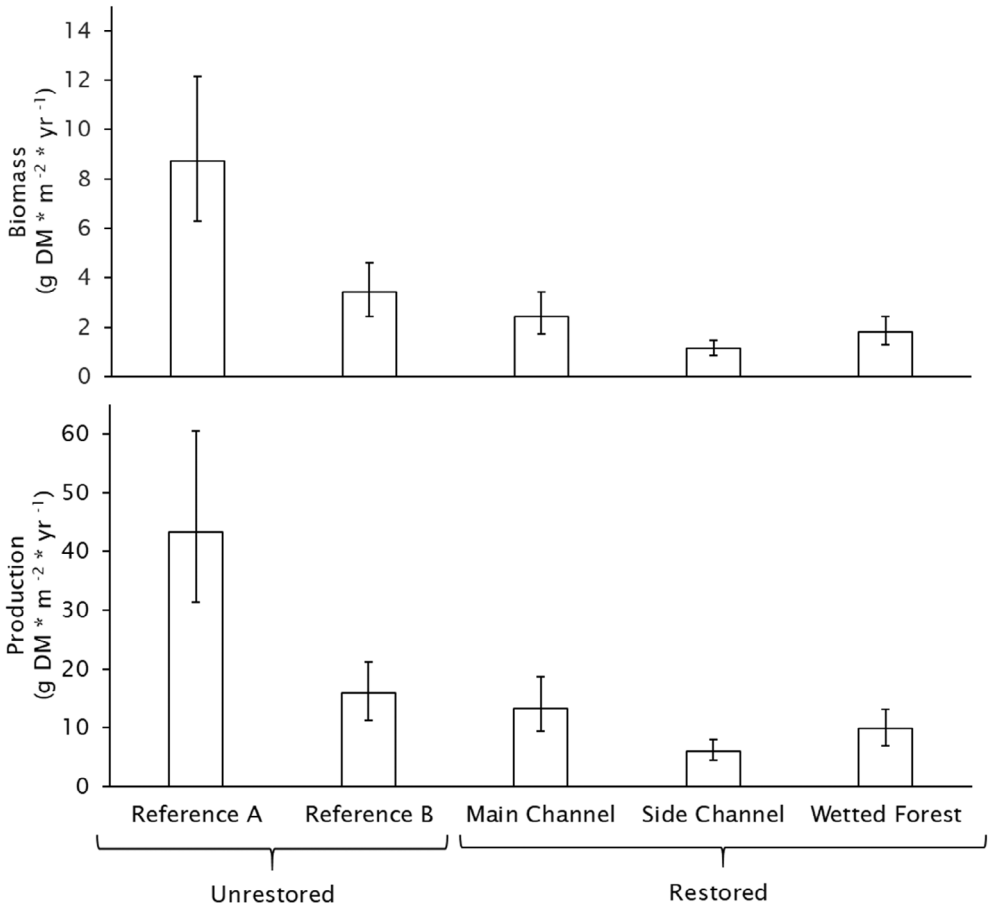

FIGURE 4 Bootstrap estimates of mean total annual macroinvertebrate biomass and secondary production (mean ± 95% confidence interval [CI]) on the benthos in the unrestored reaches and the habitat patches in the Stage 0 restored reach of the South Fork McKenzie River, Oregon.

production (8.7 and 43.3 g DM/m^2/year), which was significantly higher than habitat patches in the restored reach (non-overlapping 95% CIs) and ~3× greater than the highest estimate from the restored reach, the Main Channel patch (2.4 and 13.3 g DM/m^2/yr), and this pattern was similar to that observed in the macroinvertebrate abundance estimates (Appendix A; Figure A1).

However, there was about 4.5× greater aquatic habitat area in the restored reach than in the unrestored reaches. When per meter square estimates of biomass and production were scaled by the amount of aquatic habitat area available, the restored reach had at least 2× as much macroinvertebrate biomass (24.2 kg DM/yr in Reference A and 8.6 kg DM/yr in Reference B vs. 50.3 kg DM/yr in the restored reach) and production (120.4 kg DM/yr in Reference A and 40.0 kg DM/yr in Reference B vs. 274.4 kg DM/yr in the restored reach) per 100 m of valley length than the reference reaches (Figure 5). As a result, the restored site had significantly greater total food biomass and annual production (non-overlapping 95% CIs) relative to both reference sites. 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 in the restored reach supported 218 mg/m^2 of biomass and 1.3 g/m^2/yr of production in the Main Channel, and 317 mg of biomass and 1.9 g/m^2/yr of production in the Side Channel.

3.3 | Assemblage composition

The macroinvertebrate assemblages accounting for the majority of production in the reference reaches were different from those in the aquatic habitat patches sampled in the restored reach. 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 slower watered Side Channel and Wetted Forest aquatic habitat patches in the restored reach was dominated by Baetidae and Chironomidae, accounting for ~50% of total production, while Hydropsychidae, Baetidae, and Ephemerellidae made up ~60% of the total production in the swifter-watered reference reaches.

Annual production in the Main Channel habitat patch was distributed more evenly across a larger assemblage of taxa (Figure 6) 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 Heptageniidae contributed about equally (11%–17%) to the production totals. Limnephilidae, 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.

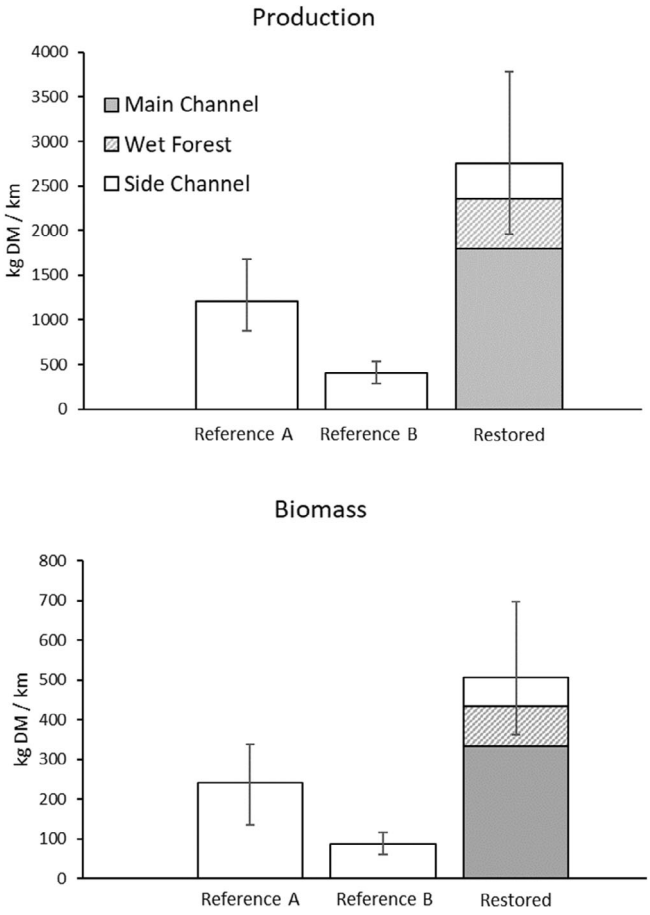

FIGURE 5 Total kilograms of biomass and production per kilometer of valley length for the unrestored reference reaches and habitat patches of the restored reach of the South Fork McKenzie River, Oregon.

The macroinvertebrate taxa contributing to annual production on submerged wood surfaces were a similar assemblage to the taxa contributing the majority of the benthic production 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.

These differences in aquatic macroinvertebrate assemblages were reflected in our NMDS analysis, which showed distinct differences in macroinvertebrate composition of reference reaches versus aquatic habitat patches in the restored reach (Figure 8, ANOSIM $R = 0.4235$, $p < 0.05$). Restored patches were separated from reference reaches along both axes 1 and 2, with the differences largely driven by a greater prevalence of different Chironomidae spp. and Heptageniidae in the restored patches. The NMDS also showed substantial, but consistent, seasonal shifts in macroinvertebrate composition across all sites. Summer biomass was positively associated with Ephemerellidae and Chironomidae (*Cladotanytarsis*), whereas winter biomass was positively associated with Heptageniidae, Hydropsychidae, and other Chironomidae taxa (*Cricotopus*, *Tanytarsis*).

4 | DISCUSSION

We examined short-term (1–2 year) aquatic macroinvertebrate production responses to Stage 0 floodplain restoration in the South Fork McKenzie River (SFMR), Oregon. We expected the Stage 0 restored reach to support higher densities of secondary macroinvertebrate production relative to the unrestored reference sites, yet this expectation was only partially confirmed. Per-meter-squared estimates of production were actually higher in the upstream unrestored reference reaches than in any of the habitat patches in the restored reach. However, aggrading and widening the channel resulted in 4.5× greater wetted area available to support macroinvertebrate production. As a result, when production was scaled to the total wetted habitat area available, the restored reach supported 2× greater production per unit of valley length than in reference reach A and 7× higher than reference reach B. This finding illustrates one way that floodplain restoration actions, like Stage 0 restoration, may increase aquatic macroinvertebrate productivity: by simply increasing habitat quantity that can be rapidly colonized (within 1 year) by aquatic macroinvertebrates. However, our findings also suggest that restoration may result in short-term declines in macroinvertebrate production per unit area of stream bed, creating tradeoffs between habitat quantity and quality that could have important implications for insectivorous fishes. Greater habitat area could support larger fish populations, but individual fishes may require larger foraging territories or more time searching for prey to meet their energetic requirements if per area resource abundance is lower (Chapman, 1966; Rossi et al., 2021), which could result in lower fish densities (fish per unit area) until per area macroinvertebrate production recovered.

Although we did not directly measure colonization in this study, our finding suggest that macroinvertebrates can quickly recolonize new habitats following the disturbance associated with restoration implementation, which for the SFMR included dewatering the channel and using heavy equipment to fill the channel with rocks and logs (see Powers et al., 2019). It may not be surprising that macroinvertebrate production can rapidly recover following this disturbance. Many aquatic insect larvae are known to behaviorally drift downstream, which can provide a ready supply of colonizers following disturbances (Mackay, 1992). Many taxa that were early colonizers, such as Baetidae mayflies and Chironomidae midges (Mackay, 1992)—both of which accounted for a greater proportion of total production in the restored reach—are considered to be "*r*-selected" and can exhibit high rates of turnover (Huryn & Wallace, 2000). Larger bodied and slower growing "*k*-selected" taxa (e.g., Hydropsychidae and Epehemerillidae) may take longer to colonize and establish post-disturbance, and these taxa accounted for a larger proportion of the production observed in the unrestored reference reaches than in the restored reach (Figure 6). These findings are consistent with other studies on post-restoration aquatic community responses to valley-wide floodplain stream restoration. On the River Lippe, Germany, researchers found that the species that were "opportunistic", short-lived, fast-growing, and produced multiple generations a year responded rapidly in post-disturbance colonization and benefited the most from restoration

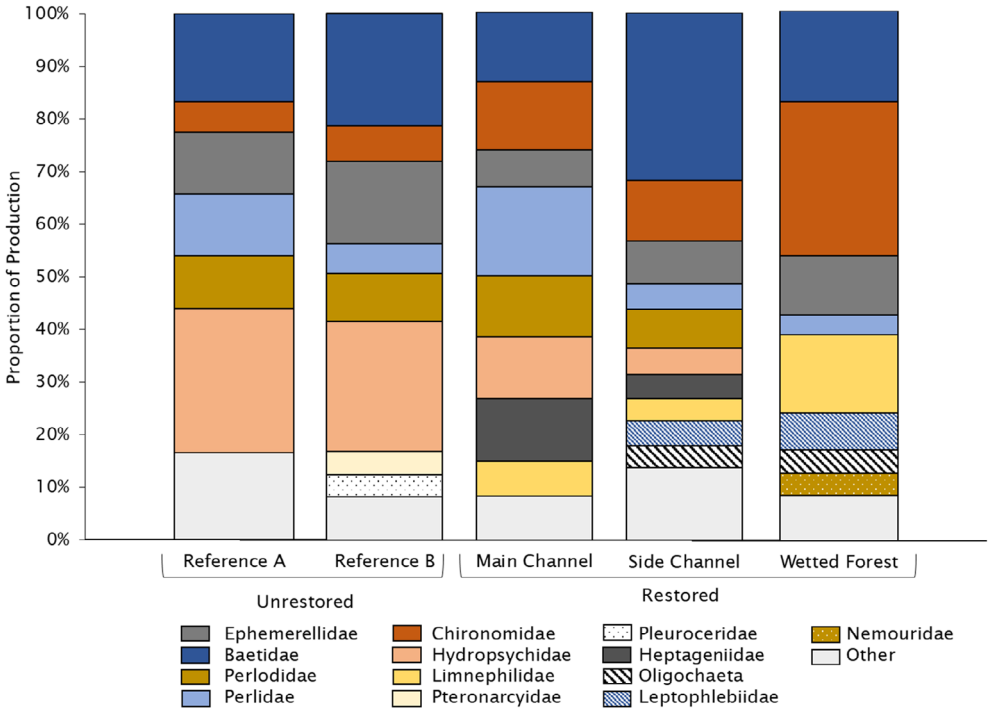

FIGURE 6 Proportions, by dominant taxa, of the total mean annual benthic macroinvertebrate production for each unrestored reach and each habitat patch in the Stage 0 restored reach of the South Fork McKenzie River, Oregon. [Color figure can be viewed at wileyonlinelibrary.com]

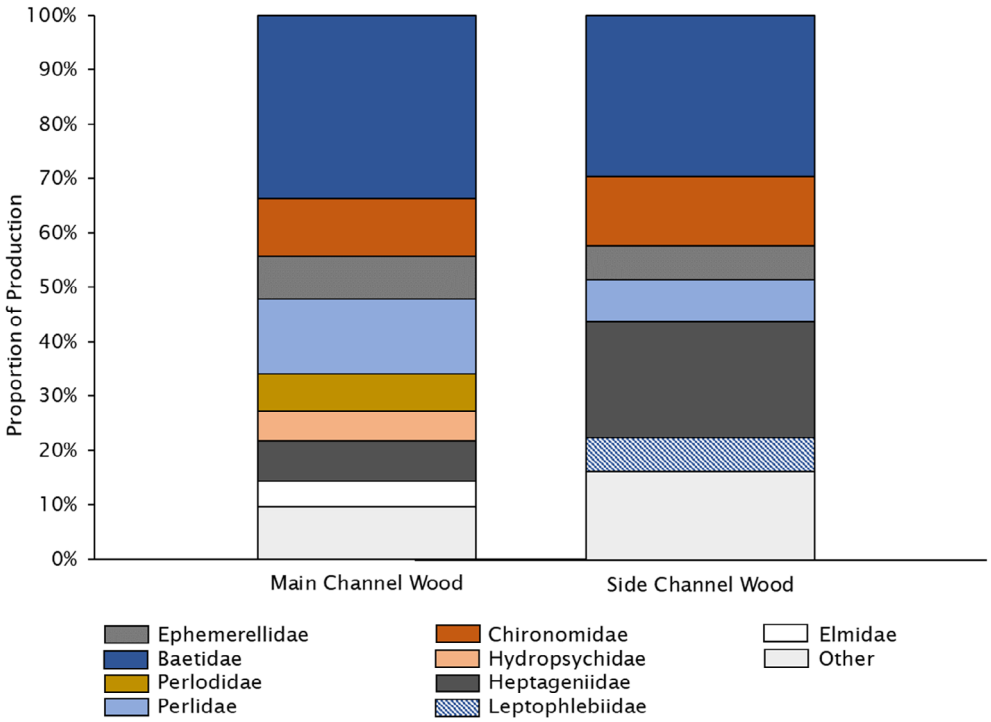

FIGURE 7 Proportion of total annual wood surface macroinvertebrate production by family in the Main and Side Channel habitat patches in the Stage 0 restored reach of the South Fork McKenzie River, OR. [Color figure can be viewed at wileyonlinelibrary.com]

actions (Höckendorff et al., 2017). Additionally, on the Rhone River, France, just 1 year after restoration to restore floodplain connectivity, macroinvertebrate communities had reestablished and were skewed toward "pioneering" taxa with short generation times and multiple generations a year (Paillex et al., 2009). Similar findings have been observed in dam removal studies, where macroinvertebrate communities can quickly re-establish in downstream and former reservoir habitats following the removal of the dam (Bellmore et al., 2019; Mahan et al., 2021).

Despite encouraging evidence about biological recovery time, the assumption that intact Stage 0 river-floodplain systems are more biologically productive than single-thread river segments requires further evaluation (Castro & Thorne, 2019; Cluer & Thorne, 2014). Few studies have actually compared primary or secondary production in intact floodplains relative to other river channel types, and those that have found that confined single-thread river segments supported similar total primary and secondary production (per unit of valley length) relative to paired floodplain segments (Bellmore & Baxter, 2014).

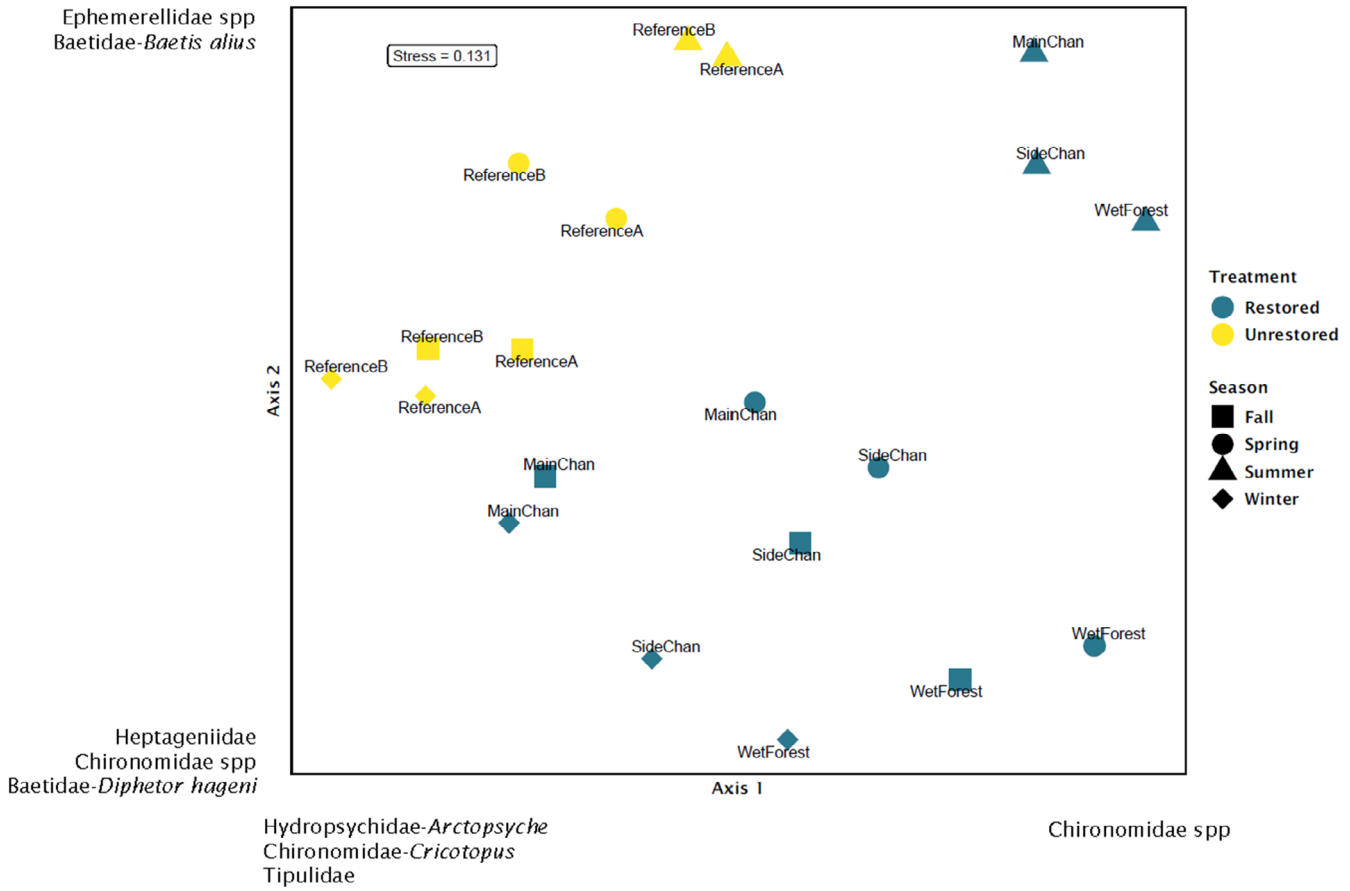

FIGURE 8 Nonmetric Multidimensional Scaling (NMDS) ordination plot of average seasonal benthic macroinvertebrate biomass, for each taxon, in each sample reach (stress = 0.131). Taxon names next to each axis account for the majority of variation along that axis. [Color figure can be viewed at wileyonlinelibrary.com]

Estimates of macroinvertebrate production in unrestored single-thread reaches of the SFMR were quite high, up to three times higher than other estimates for Pacific Northwest streams (Bellmore et al., 2013; Bellmore et al., 2015; Robinson & Minshall, 1998) and equivalent to estimates from productive rivers in the southeastern United States (Smock et al., 1985). Indeed, the SFMR is known as a productive trout fishing stream, with populations likely supported by these high rates of macroinvertebrate production.

River regulation may be one explanation for the high macroinvertebrate production estimates in our unrestored reference reaches. Our study was conducted downstream of a high-head dam. The operation of Cougar Dam has attenuated peak flows, simplified the channel, and reduced the proportion of small gravels in favor of large, immobile cobbles (Ligon et al., 1995); it is possible that these changes may have counterintuitively increased biological production in the SFMR. The absence of scouring flows combined with the stability of the stream bed and potential presence of reservoir plankton available to filter-feeding insects (Murphy et al., 2021) may have contributed to the high rates of production observed in our reference reaches. Indeed, some of the highest estimates of aquatic invertebrate production have come from similar contexts, such as lake outlets (Huryn & Wallace, 2000; Wotton, 1988), where high-turnover filter-feeding taxa are common. Given the proximity of reference reaches to the restored reach, it is likely that the restored reach had similarly high macroinvertebrate production prior to project implementation. If true, it would indicate that Stage 0 restoration may strongly depress macroinvertebrate production (per unit area), at least for the first few years following restoration. It is also likely that continued dam operation in the SRMR, which strongly alters the natural flow and sediment regimes (Poff et al., 1997; Wohl et al., 2015), will influence trajectories of geomorphic and ecological recovery in the Stage 0 restored reach. With Cougar Dam in place, the SFMR will continue to be sediment starved and less likely to experience high scouring flows that create and maintain floodplain habitat mosaics (Stanford et al., 2005).

A second expectation of our study was that habitat heterogeneity created via stage restoration would support a diversity of distinct aquatic macroinvertebrate communities (i.e., higher beta diversity), and our observations from this study support this expectation. Unlike the single-thread reference reaches with relatively homogeneous habitat, the restored reach contained a diversity of distinct aquatic habitats: main channel habitat with deep pools and submerged wood, flooded forests with standing water and organic-rich soils, and perennial side channels with substantial submerged aquatic vegetation (primarily sedges and grasses). These aquatic habitat patches were found

to have statistically distinct macroinvertebrate communities, suggesting that habitat heterogeneity in Stage 0 restored valley bottoms provides a template for a diversity of distinct biological communities to exist in different aquatic habitats (e.g., Benke, 1984; Scholl et al., 2023). In turn, this portfolio of macroinvertebrate assemblages could support a spatial mosaic of patch-scale aquatic food webs (Bellmore et al., 2013), which provide a broader range of foraging opportunities for mobile fishes that can move between floodplain patches in search of favorable foraging and growth conditions (Abrahms et al., 2021; Armstrong et al., 2013, 2016; McMeans et al., 2019). When considered in aggregate, this portfolio may result in a more complex and spatially structured meta-community (and meta-food-web), which has been shown to promote ecological stability (Bellmore et al., 2015; Stouffer & Bascompte, 2011), increasing the likelihood that interacting species persist despite fluctuations in environmental conditions such as floods (McCann, 2000). Our findings provide further support that complex floodplain mosaics support diverse ecological structures and functions (Hauer et al., 2016; Stanford et al., 2005).

Another unique aspect of our study was the potential importance of wood surfaces in supporting secondary production. Although estimates of the amount of wetted large wood surface area do not yet exist in the restored reach, studies from lowland streams in the southeastern U.S. found that snag/wood surface area ranged from about 6% of the available benthic area in the Satilla River, Georgia, to 50% of total benthic surface area in the Ogeechee River, Georgia (Benke, 1984; Benke & Wallace, 2015). If we conservatively assume the amount of submerged wood surface is equivalent to 20% of the area of benthic substrate, this would contribute an additional 8.8 kg/km of biomass and 53.4 kg/km of production to the annual totals in the restored reach, equal to about 2% of the benthic production total. These values are lower than observed in sand-bed rivers in the southeastern United States where almost all observed macroinvertebrate production occurs on stable wood surfaces (Benke, 1984). Nevertheless, it illustrates that wood surfaces can contribute to total secondary production even in more stable gravel-bed rivers. However, the potential contribution of wood surfaces to secondary production is likely to vary significantly depending on the suitability of benthic habitats and how much wood is added during restoration. In a context where the stream bed is less stable (sand or pebble bed rivers) and wood loading is high, wood surfaces could support a substantial fraction of total production (Benke, 1984; Benke & Wallace, 2015). Furthermore, large wood can contribute to multiple facets of aquatic biodiversity, including hosting unique communities of insects (Wondzell & Bisson, 2003).

5 | CONCLUSION

Our study suggests that Stage 0 restoration has multiple effects on aquatic productivity in the short term. The disturbance from project implementation may reduce aquatic macroinvertebrate production on a per-unit-area basis, but this reduction may be offset by channel aggradation and widening, which can provide substantially more wetted area for production. As Stage 0 restoration becomes more common, especially in the western United States (Flitcroft et al., 2022), studies are needed to examine longer term trajectories in geomorphology (Hinshaw et al., 2022) and associated biological productivity and food web dynamics to better understand the duration of initial disturbance responses, and whether or not restoration has positive impacts on macroinvertebrate and fish production in the long term. Furthermore, there are other—more passive—approaches to valley-scale floodplain restoration where disturbance responses to project implementation may be relatively minimal (Pollock et al., 2014; Wohl et al., 2021), which also need to be quantitatively evaluated.

Our study clearly showed that restoration increased biological diversity by creating a heterogeneous template for different aquatic macroinvertebrate assemblages, and potentially unique food webs. This increase in aquatic habitat and community diversity could be especially relevant to the production of mobile aquatic consumers like fish and also important for terrestrial consumers such as insectivorous birds (dippers, swallows, etc.), bats, and piscivorous birds (kingfishers, osprey, etc.), that can move across the floodplain, selecting from a diversity of local aquatic communities and food webs that intact floodplain mosaics may support (Bellmore et al., 2013, 2015; O'Mara et al., 2021). This biological portfolio may also help stabilize the dynamics of the aquatic ecosystem (Schindler et al., 2015) and aid in maintaining biological production and diversity as extreme events (e.g., floods, fires, and droughts) become more frequent and severe in a changing world.

ACKNOWLEDGMENTS

The authors express sincere appreciation for the financial and material support of the Oregon Watershed Enhancement Board, McKenzie Watershed Council, US Forest Service (USFS) Pacific North West (PNW) Research Station, and McKenzie River Ranger Station. Special thanks to Kate Meyer, Matt Helstab, Carla Rothenbeucher, Mickey Means-Brous, and Logan Bodiford from the McKenzie River Ranger Station; Bruce Hansen and Kelly Christiansen from the USFS PNW Research Station, Corvallis; Jared Weybright and Chase Antonovich from the McKenzie Watershed Council; Jonathan Burnett from PNW Olympia Forestry Sciences Laboratory; and Matthew Barker from Oregon State University Aerial Information Systems Laboratory.

CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest relevant to this research article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Jeremy C. Jennings https://orcid.org/0000-0002-0585-9741

REFERENCES

Abell, R., Thieme, M. L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S. C., Bussing, W., &

Stiassny, M. L. (2008). Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. *Bioscience*, *58*(5), 403–414.

Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2021). Emerging perspectives on resource tracking and animal movement ecology. *Trends in Ecology & Evolution*, *36*(4), 308–320.

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.

Arscott, D. B., Tockner, K., & Ward, J. V. (2005). Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *Journal of the North American Benthological Society*, *24*(4), 934–954.

Beechie, T., Beamer, E., & Wasserman, L. (1994). Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. *North American Journal of Fisheries Management*, *14*(4), 797–811.

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. (2014). Effects of geomorphic process domains on river ecosystems: A comparison of floodplain and confined valley segments. *River Research and Applications*, *30*(5), 617–630.

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.

Bellmore, J. R., Pess, G. R., Duda, J. J., O'Connor, J. E., East, A. E., Foley, M. M., Wilcox, A. C., Major, J. J., Shafroth, P. B., Morley, S. A., & Magirl, C. S. (2019). Conceptualizing ecological responses to dam removal: If you remove it, what's to come? *Bioscience*, *69*(1), 26–39.

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* (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.

Benke, A. C., & Wallace, J. B. (2015). High secondary production in a coastal plain river is dominated by snag invertebrates and fuelled mainly by amorphous detritus. *Freshwater Biology*, *60*(2), 236–255.

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

Chapman, D. W. (1966). Food and space as regulators of salmonid populations in streams. *The American Naturalist*, *100*(913), 345–357.

Cluer, B., & Thorne, C. (2014). A stream evolution model integrating habitat and ecosystem benefits. *River Research and Applications*, *30*(2), 135–154.

Corline, N. J., Peek, R. A., Montgomery, J., Katz, J. V., & Jeffres, C. A. (2021). Understanding community assembly rules in managed floodplain food webs. *Ecosphere*, *12*(2), e03330.

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

Davies, P. M., Jr., Bunn, S. E., Jr., & Hamilton, S. K., Jr. (2008). Primary production in tropical streams and rivers. In *Tropical stream ecology* (pp. 23–42). Academic Press.

Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., & Peres-Neto, P. R. (2014). Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: The case of floodplain-fish communities. *Ecography*, *37*(5), 464–475.

Flitcroft, R. L., Brignon, W. R., Staab, B., Bellmore, J. R., Burnett, J., Burns, P., Cluer, B., Giannico, G., Helstab, J. M., Jennings, J., & Mayes, C. (2022). Rehabilitating valley floors to a stage 0 condition: A synthesis of opening outcomes. *Frontiers in Environmental Science*, *10*(892268), 1–27.

Foster, A. D., Claeson, S. M., Bisson, P. A., & Heimburg, J. (2020). Aquatic and riparian ecosystem recovery from debris flows in two western Washington streams, USA. *Ecology and Evolution*, *10*(6), 2749–2777.

Funk, A., Schiemer, F., & Reckendorfer, W. (2013). Metacommunity structure of aquatic gastropods in a river floodplain: The role of niche breadth and drift propensity. *Freshwater Biology*, *58*(12), 2505–2516.

Ganihar, S. R. (1997). Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences*, *22*(2), 219–224.

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.

Gowing, G., & Recher, H. F. (1984). Length-weight relationships for invertebrates from forests in South-Eastern New South Wales. *Australian Journal of Ecology*, *9*(1), 5–8.

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.

Hauer, F. R., Locke, H., Dreitz, V. J., Hebblewhite, M., Lowe, W. H., Muhlfeld, C. C., Nelson, C. R., Proctor, M. F., & Rood, S. B. (2016). Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. *Science Advances*, *2*(6), e1600026.

Hauer, F. R., & Resh, V. H. (2017). Macroinvertebrates. In *Methods in stream ecology* (Vol. 1, pp. 297–319). Academic Press.

Hawkins, J. W., Lankester, M., Lautenschlager, R. A., & Bell, F. (1997). Length–biomass and energy relationships of terrestrial gastropods in northern forest ecosystems. *Canadian Journal of Zoology*, *75*(3), 501–505.

Hinshaw, S., Wohl, E., Burnett, J. D., & Wondzell, S. (2022). Development of a geomorphic monitoring strategy for stage 0 restoration in the south fork McKenzie River, Oregon, USA. *Earth Surface Processes and Landforms*, *47*, 1937–1951.

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.

Hódar, J. A. (1996). The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica (Montrouge)*, *17*(5), 421–433.

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.

Jeffres, C. A., Holmes, E. J., Sommer, T. R., & Katz, J. V. (2020). Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. *PLoS One*, *15*(9), e0216019.

Katz, J. V., Jeffres, C., Conrad, J. L., Sommer, T. R., Martinez, J., Brumbaugh, S., Corline, N., & Moyle, P. B. (2017). Floodplain farm

fields provide novel rearing habitat for Chinook salmon. *PLoS One*, *12*(6), e0177409.
Keddy, P. A., Fraser, L. H., Solomeshch, A. I., Junk, W. J., Campbell, D. R., Arroyo, M. T., & Alho, C. J. (2009). Wet and wonderful: The world's largest wetlands are conservation priorities. *Bioscience*, *59*(1), 39–51.
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.
Lamberti, G. A., & Hauer, F. R. (Eds.). (2017). *Methods in stream ecology*. Academic Press.
Lang, A. (1997). Mass-length relationships of epigeal arthropod predators in arable land (Aranae, Chilopoda, coleoptera). *Pedobiologia*, *41*, 327–333.
Layman, C. A., & Rypel, A. L. (2020). Secondary production is an underutilized metric to assess restoration initiatives. *Food Webs*, *25*, e00174.
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.
Mackay, R. J. (1992). Colonization by lotic macroinvertebrates: A review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(3), 617–628.
Mahan, D. C., Betts, J. T., Nord, E., van Dyke, F., & Outcalt, J. M. (2021). Response of benthic macroinvertebrates to dam removal in the restoration of the Boardman River, Michigan, USA. *PLoS One*, *16*(5), e0245030.
McCann, K. S. (2000). The diversity–stability debate. *Nature*, *405*(6783), 228–233.
McMeans, B. C., Kadoya, T., Pool, T. K., Holtgrieve, G. W., Lek, S., Kong, H., Winemiller, K., Elliott, V., Rooney, N., Laffaille, P., & McCann, K. S. (2019). Consumer trophic positions respond variably to seasonally fluctuating environments. *Ecology*, *100*(2), e02570.
Meyer, K., Hammons, B., Hogervorst, J., Powers, P., Weybright, J., Bair, B., Robertson, G., & Mazullo, C. (2018). *Lower South Fork McKenzie River Floodplain Enhancement Project 80% design report*. McKenzie Watershed Council. https://www.mckenziewc.org/?page_id=884
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.
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., Stevens, M. H., & Wagner, H. (2020). Vegan: Community ecology package. R Package Version 2.5–7. https://CRAN.R-project.org/package=vegan
O'Mara, K., Venarsky, M., Stewart-Koster, B., McGregor, G. B., Schulz, C., Kainz, M., Marshall, J., & Bunn, S. E. (2021). Connectivity of fish communities in a tropical floodplain river system and predicted impacts of potential new dams. *Science of the Total Environment*, *788*, 147785.
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), 250–258.
Palmer, M., & Ruhi, A. (2019). Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration. *Science*, *365*(6459), eaaw2087.
Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, *47*(11), 769–784.
Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. *Bioscience*, *64*(4), 279–290.
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.
R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. URL https://www.R-project.org/
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.
Richardson, W. B., Bartsch, L. A., Bartsch, M. R., Kiesling, R., & Lafrancois, B. M. (2019). Nitrogen cycling in large temperate floodplain rivers of contrasting nutrient regimes and management. *River Research and Applications*, *35*(5), 529–539.
Robinson, C. T., & Minshall, G. W. (1998). Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. *Archiv für Hydrobiologie*, *142*, 257–281.
Rogers, L. E., Buschbom, R. L., & Watson, C. R. (1977). Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, *70*(1), 51–53.
Rossi, G. J., Power, M. E., Pneh, S., Neuswanger, J. R., & Caldwell, T. J. (2021). Foraging modes and movements of Oncorhynchus mykiss as flow and invertebrate drift recede in a California stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(8), 1045–1056.
RStudio Team. (2019). *RStudio: Integrated development for R*. RStudio, Inc., URL. http://www.rstudio.com/
Rypel, A. L., Pounds, K. M., & Findlay, R. H. (2012). Spatial and temporal trade-offs by bluegills in floodplain river ecosystems. *Ecosystems*, *15*(4), 555–563.
Sabo, J. L., Bastow, J. L., & Power, M. E. (2002). Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, *21*(2), 336–343.
Sage, R. D. (1982). Wet and dry-weight estimates of insects and spiders based on length. *American Midland Naturalist*, *108*, 407–411.
Sample, B. E., Cooper, R. J., Greer, R. D., & Whitmore, R. C. (1993). Estimation of insect biomass by length and width. *American Midland Naturalist*, *129*, 234–240.
Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257–263.
Schoener, T. W. (1980). Length-weight regressions in tropical and temperate forest-understory insects. *Annals of the Entomological Society of America*, *73*(1), 106–109.
Scholl, E. A., Cross, W. F., & Guy, C. S. (2023). Geomorphology shapes relationships between animal communities and ecosystem function in large rivers. *Oikos*, *2023*(2), e09431.
Smock, L. A., Gilinsky, E., & Stoneburner, D. L. (1985). Macroinvertebrate production in a southeastern United States Blackwater stream. *Ecology*, *66*(5), 1491–1503.
Sparks, R. E. (1995). Need for ecosystem management of large rivers and their floodplains. *Bioscience*, *45*(3), 168–182.
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.
Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, *108*(9), 3648–3652.
Tank, J. L., Rosi-Marshall, E. J., Griffiths, N. A., Entrekin, S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*, *29*(1), 118–146.
Thorp, J. H., Delong, M. D., Greenwood, K. S., & Casper, A. F. (1998). Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia*, *117*, 551–563.
Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. *Environmental Conservation*, *29*(3), 308–330.

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/

Vinson, M. R., & Hawkins, C. P. (1996). Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. *Journal of the North American Benthological Society*, *15*(3), 392–399.

Walther, D. A., & Whiles, M. R. (2011). Secondary production in a southern Illinois headwater stream: Relationships between organic matter standing stocks and macroinvertebrate productivity. *Journal of the North American Benthological Society*, *30*(2), 357–373.

Wickham, H. (2020). Tidyr: Tidy messy data. R Package Version 1.1.2. https://CRAN.R-project.org/package=tidyr

Wisseman, R., Sullivan, S., Pfeiffer, J., Salter, S., & Puls, A. (2015). Northwest standard taxonomic effort taxa lists 2015-11-03. Manuscript in Preparation. Retrieved from https://www.pnamp.org/project/northwest-standard-taxonomic-effort

Wohl, E., Bledsoe, B. P., Jacobson, R. B., Poff, N. L., Rathburn, S. L., Walters, D. M., & Wilcox, A. C. (2015). The natural sediment regime in rivers: Broadening the foundation for ecosystem management. *Bioscience*, *65*(4), 358–371.

Wohl, E., Castro, J., Cluer, B., Merritts, D., Powers, P., Staab, B., & Thorne, C. (2021). Rediscovering, reevaluating, and restoring lost river-wetland corridors. *Frontiers in Earth Science*, *9*, 653623.

Wondzell, S. M., & Bisson, P. A. (2003). Influence of wood on aquatic biodiversity. *The Ecology and Management of Wood in World Rivers*, *37*, 249–263.

Wotton, R. S. (1988). Very high secondary production at a lake outlet. *Freshwater Biology*, *20*(3), 341–346.

Wrubleski, D. A., & Rosenberg, D. M. (1990). The Chironomidae (Diptera) of bone pile pond, Delta marsh, Manitoba, Canada. *Wetlands*, *10*(2), 243–275.

How to cite this article: Jennings, J. C., Bellmore, J. R., Armstrong, J. B., & Wisseman, R. W. (2023). Effects of process-based floodplain restoration on aquatic macroinvertebrate production and community structure. *River Research and Applications*, *39*(9), 1709–1723. https://doi.org/10.1002/rra.4174

APPENDIX A: MEAN ABUNDANCE OF MACROINVERTEBRATES PER UNIT AREA OF BENTHOS

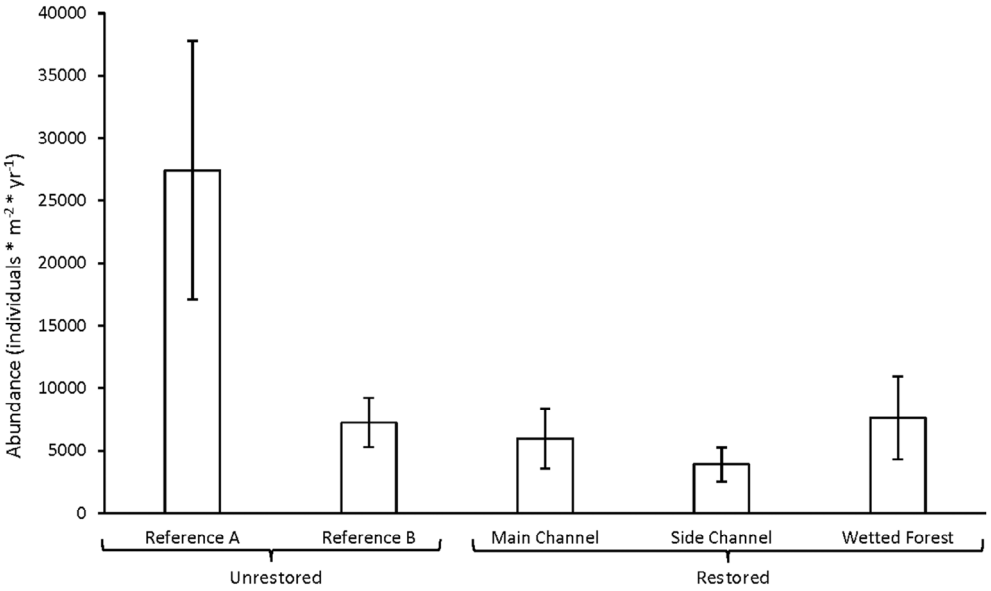

FIGURE A1 Mean abundance of macroinvertebrates (mean +/−SE) per square meter of the benthos across all study sites on the South Fork McKenzie River, Oregon.