**Stream invertebrate and fish feeding response to increases in light availability in the forested headwaters of the Cascades**

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**Introduction**

Streams and their biota are inherently linked to riparian vegetation in forested systems: when we alter streamside vegetation we are altering streams. In the Pacific Northwest (PNW) region of North America, riparian forests have undergone a drastic shift in the past half century, with decades of heavy harvesting resulting in a landscape dominated by dense second-growth vegetation. For streams that run thought these forests, dense vegetation decreases light availability and subsequent light limitation reduces benthic primary production. In many systems, higher trophic levels can be disproportionately supported by algae, and a shift in this basal resource can have substantial effects on stream biota. Earlier research has shown that relieving light limitation by clear-cutting riparian forests can result in an increase in stream primary and secondary productivity (Bilby and Bisson, 1992), but clear cutting along streams is no longer a common practice in the Pacific Northwest. Even in managed landscapes riparian buffers are left. Unmanaged forests and these riparian forest buffers are in the early stages of stand regeneration with dense homogenous canopy cover and low stream light. As forest succession continues, natural disturbances and tree mortality will increase canopy heterogeneity through the introduction of gaps. While studies on forest clearing demonstrate a clear response in benthic primary producers, invertebrates, and fish when a whole reach is relieved of light limitation (Wootton, 2012), the effects of localized light patches – that reflect a more realistic picture of future stream conditions in forested landscapes – have not been evaluated. To understand how aquatic food webs respond to an increase in light associated with canopy gaps, I investigate the response of macroinvertebrates and fish feeding to canopy-opening manipulations.

Stream food webs are influenced by light in multiple ways. Light can enhance algal growth, acting as a bottom-up driver of secondary production, but it can also increase foraging efficiency of fish (Wilzbach et. al, 1986), imposing a top-down pressure on macroinvertebrates. Understanding the predator-prey dynamic between invertebrates and fish when a small gap is cut requires fish diet data. However, diet contents can be hard to identify and, in this study, were only identified down to the family level. In order to ensure that family level identification was still representative of community shifts in benthic taxa, I will compare benthic analyses performed at both the family level and the lowest taxonomic resolution of the data to ensure that family level analysis results in similar conclusions as those drawn from lower levels of identification.

**Methods**

*Study location*

The study consists of five reach pairs on five separate streams in the western Cascade Mountains of Oregon. Each reach pair consisted of one treatment reach and one control reach. Two of the reach pairs (W-100, W-113) are located on private Weyerhaeuser Co. land, and three (LOON, CHUCK, MCTE) are located on U.S. Forest Service land, one of which (MCTE) is situated in the HJ Andrews Experimental Forest. Stream reaches were 90 meters in length and treatment gaps were 30 to 40 meters in diameter and situated approximately in the middle of treatment reaches. Reach pairs were spaced at least 30 meters apart to limit any effects of the upstream reach on downstream conditions.

All of the streams are wadeable, fish-bearing streams with bankfull widths of 1-8 meters. Fish-bearing streams were purposefully selected to provide management-relevant results for key species such as salmonids. The streams run through 40-60-year-old forests that had previously been harvested without leaving a riparian buffer. These forests have a homogenous canopy structure with heavy understory shading, as defined by their early seral stage. Small streams were chosen for ease of sampling and to maximize the effect of a canopy opening manipulation since small streams can be completely shaded by overhead vegetation.

Sampling lasted two years with pre-treatment data gathered during summer 2017 and post-treatment data gathered during summer 2018. Canopy gaps were cut in the treatment reach during the winter of 2017-18 to permit adequate time for response to the canopy manipulation. The reach-pair design with pre and post treatment years is intended to account for inherent environmental variation among streams and between years.

*Data Collection*

Three benthic invertebrate samples were taken at each stream reach at meters 15, 45, and 75, or the closest area with non-boulder substrate. Samples were collected once per year over the course of one week using a Surber sampler with a .09 m2 sampling area. Substrate was disturbed to a depth of approximately 4 inches for one minute. The sample was then preserved in 95% ethanol for identification and enumeration in the lab. Fish diets were collected during three-pass depletion of fish standing stock and were only taken from a subset of fish greater than 100 mm in length. Fish were gastro-lavaged, and stomach contents were collected in filter paper and preserved in 95% ethanol for lab processing. In order to measure the response of primary producers to the canopy gap, three tiles were set out every ten meters for two weeks for each stream and Chlorophyll values were measured using a Bentho Torch™.

*Data Analysis*

In the lab, the three benthic samples per reach were combined and subsampled by randomly sampling whole squares from a Caton tray until the cutoff of 300 individuals or greater was reached. Benthic invertebrates were then identified down to genus or the lowest taxonomic unit (LTU) for cryptic taxa. Counts from subsamples were then converted to densities using the formula where *s* is the fraction subsampled. Singleton taxa (taxa occurring in only one SU) were removed from the original matrix and density values were square-root transformed to reduce the effect of abundant taxa (Chironomidae, *Baetis*, *Micrasema*) on community relationships. The resulting matrix of benthic invertebrates at the LTU level of identification (20 reaches by 64 taxa) was then used for analysis.

All diets were processed (9 to 13 fish diets per reach) with aquatic invertebrates identified down to the family level and terrestrial invertebrates identified to order. Because the number of fish dieted in each reach varied, the average of all fish diets was used. The resulting matrix was then filtered for aquatic species and appended to a matrix of 2018 benthic invertebrate families (10 reaches by 38 families), producing a matrix of 20 sample units (SU’s) by 40 families consisting of both fish diets and benthic samples. Singleton taxa were then removed to create a matrix of combined diet and benthic families of 20 SU’s by 36 families. At this point, the combined matrix was relativized by row maxima to compensate for the difference between benthic sampling—measured in density per m2—and fish diets.

Statistical analyses were performed in PC-ORD (Version 7; McCune and Mefford 2011). Blocked multi-response permutation procedure (MRBP) was used to assess differences between treatment and control reaches in the pre and post treatment years. MRBP was followed up with blocked indicator species analysis (ISA) to determine underlying taxa driving any grouping detected by MRBP. This two-step procedure was performed twice for the benthic community, once with family level community data and once at the LTU level in order to compare any differences in results. The combined benthic and diet matrix was subsequently tested for any differences between treatment and control reaches using the same MRBP and ISA methods.

To test for any pre-treatment reach differences in 2017, MRBP was run on 2017 data only with Treatment as the two *a priori* groups and blocked by Stream. The 2018 post-treatment data was then assessed using the same MRBP grouping and blocking. MRBP is a nonparametric method used to test for differences betweengroups. This method accommodates paired or blocked study designs by accounting for variation related to study design variables that have little bearing on the question being addressed. In this case, MRBP accounts for any between-stream variation. MRBP outputs a p-value for the observed within-group distance (smaller distances constituting stronger grouping) by shuffling SU’s between groups to generate a distribution of possible within-group distances (McCune and Grace, 2002).

The follow-up ISA calculates an indicator value (IV) for each species. The IV is a composite of a taxon’s fidelity and exclusivity to a group. If a taxon is consistently abundant in one group and never present in any other, then it would receive a high IV. Conversely, a taxon rarely abundant in SU’s of one group and present in other groups would receive a low IV (McCune and Grace, 2002). A Monte Carlo test of 1,000 permutations of the taxa matrix was used to generate a p-value for each taxon’s IV.

The taxon resolution was lowered from the LTU level to family level for benthic samples in order to create a matrix of both fish and benthic samples. In order to judge the impact of reducing taxon resolution on interpreting benthic community relationships, two ordinations of benthic invertebrates were performed, one in LTU space and one in family space using nonmetric multidimensional scaling (NMS) in order to determine whether different conclusions would be drawn from lower levels of identification (Kruskal, 1964). Sorensen distance was used for both ordinations to reduce the impact of outliers. Ties were not penalized, although there were no ties in either matrix, and the ordination was rotated to maximize the environmental variable BenthoTotal along axis 1. A random start was used ../Thesis/PC-ORD/nms%20benthic%20LTU.emfand the real data were run 250 times to ensure an absolute stress minima was reached. A Monte Carlo test with 100 permutations was used to generate a p-value for the probability of the final ordination have a lower than expected p-value by chance.

To further test for differences between the level of identification used, a mantel test was applied to the original family and LTU benthic distance matrices. The distance matrices were calculated using Sorensen distances and a Monte Carlo test of 1000 permutations was used to generate a p-value.

Fig. 1a

Ordination in LTU space with an environmental joint plot overlaid. Pre-treatment reaches (2017) are coded as triangles, post treatment (2018) as circles, treatment reaches (Y) are filled shapes, and non-treatment reaches (N) are empty.

**Results**

*Benthic Community Differences*

|  |  |  |
| --- | --- | --- |
| Identification and Year | A Statistic | p-value |
| Family 2017 | 0.033 | 0.161 |
| Family 2018 | -0.243 | 0.833 |
| LTU 2017 | 0.041 | 0.071 |
| LTU 2018 | -0.022 | 0.838 |

../Thesis/PC-ORD/nms%20benthic%20family.emfThere was little difference between benthic LTU-level communities in the treatment versus reference reaches in the 2017 pre-treatment year (MRBP: A = 0.041, p = 0.071), or the post-treatment year (A = -0.022, p = 0.838). When the family-level benthic community data was used, the results were similar (Table 1). The results from the NMS ordinations support the results of the MRBP, showing similar results for both LTU space and family space (Fig. 1a and Fig. 1b). The NMS ordination of benthic invertebrates in LTU space converged on a 2D solution with a final stress of 12.031, whereas in family space a 3D solution was more desirable. To make comparisons easier, a 2D solution was forced for the ordination in family space. The forced 2D solution in family space had a similar stress value (stress = 11.412) to the 2D ordination in LTU space, and they captured similar amounts of variance in original taxa space (genera level = 89.3% of variance, family level = 91.3% of variance). In addition, the family ordination and the LTU ordination had similar relationships with the environmental variables BenthoTotal (total chlorophyll values from the Bentho TorchTM) and YearTreatQ (a binary variable coded with 1’s for 2018 treated reaches and 0’s for all other reaches) with positive r values with axis 1 of 0.272 and 0.298 for YearTreatQ, and 0.304 and 0.41 for BenthoTotal respectively. The mantel test showed a similar level of relatedness between the original family and LTU distance matrices (r = 0.986, p = 0.001).

Table 1.

Results of MRBP analysis for both levels of identification in the pre and post treatment years

Fig. 1b

Ordination in LTU space with an environmental joint plot overlaid. See Fig. 1a for symbol meanings.

*Trout Diet Analysis*

There was little difference between SU’s for the combined diet and benthic sample units as supported by the MRBP (A = 0.011, p = 0.161). The NMS converged on a 3D solution with a final stress of 10.015. The three axes captured 90.3% of the variation in the final matrix and found some relationship between families in terms of community composition (A = 0.171, p = 0.02), and there was some separation between the treatment diet sample units and the rest of the SU’s. However, there was a fair amount of overlap between groups (Fig 2a, 2b), reflecting the very weak grouping from the MRBP analysis. It appears that the invertebrate community that comprises fish diets is separate from the benthic community in the NMS, suggesting selective feeding behavior. The NMS results are diminished by MRBP results using stream and treatment as the blocking variable and benthic sample or fish diet as the grouping variable, which shows very weak grouping (A = 0.051, p = 0.023).

*Conclusions*

../../../../../../Desktop/Thesis/PC-ORD/diet%20axi../../../../../../Desktop/Thesis/PC-ORD/diet%20axi There seemed to be very little difference between conclusions drawn from the family level or the LTU level of identification. Both the original distance matrices and the 2D ordinations were highly related, and while the ordinations are not identical, the relationships with environmental variables and the general arrangement of points are similar. To better understand why there was such similarity between the two matrices, the differences

Fig. 2b

Axis 1 and 3 of the 3D ordination of the combined benthic and diet SU’s. Benthic samples are coded as triangles and fish diets are coded as circles. Filled shapes represent treatment reaches (Y), empty shapes are control reaches (N).

Fig. 2a

Axis 1 and 2 of the 3D ordination of the combined benthic and diet SU’s. Benthic samples are coded as triangles and fish diets are coded as circles. Filled shapes represent treatment reaches (Y), empty shapes are control reaches (N).

in taxon richness between the two matrices were analyzed. The LTU matrix had 168.42% more taxa than the family level matrix, but of the 38 families, only 13 consisted of more than one genera (Fig. 3). The similarity between the LTU and family matrices may be due to the large amount of families consisting of only one sub-taxa. However, including the lower level of taxonomic identification resulted in stronger relationships with both environmental variables in the NMS ordination, suggesting that the family level of identification for aquatic invertebrates does not capture all of the community variation. But for systems with low taxonomic richness within families, the amount of information lost by reducing the taxonomic resolution is small.

Biologically, the treatment seemed to have little effect on both the benthic community and the community within fish diets. Total chlorophyll was the strongest environmental correlate with axis 1 in the ordination, but the relationship was due to an increase in chlorophyll in both the control and treatment reaches in the post-treatment year. At the highest trophic level within these stream systems, trout diets showed little to no response to the treatment, but they seem to occupy a different region of family space when compared to the benthic community. The lack of response in both the benthic invertebrate community and trout diets to small gaps suggests that stream food webs will remain relatively stable as forests mature and canopy cover becomes more heterogeneous­­­.

Fig. 3.

Number of lower taxa within each family. Note the large number of families consisting of only one lower taxonomic unit.

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