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Effects of Large Wood Additions on Basal Resources, Macroinvertebrates, and Ecosystem Processes in the Narraguagus River, Maine

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EFFECTS OF LARGE WOOD ADDITIONS ON BASAL RESOURCES, MACROINVERTEBRATES, AND ECOSYSTEM PROCESSES IN THE NARRAGUAGUS RIVER, MAINE

By

Valerie Kathleen Watson

B.S. University of Maine

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(In Ecology and Environmental Sciences)

The Graduate School

The University of Maine

August 2023

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Thesis Advisor: Dr. Hamish Greig

An Abstract of the Thesis
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Ecological restoration is an increasingly common practice across ecosystems, and current practices aim to restore the biological and physical processes underlying ecosystem function, often for the sake of endangered higher-level consumers. Studies of restoration outcomes often report few or inconsistent ecological changes, and monitoring of restoration projects rarely measures ecological processes. Monitoring also usually measures outcomes at a single scale, despite the prevalence of scale-dependent phenomena across ecosystems. My thesis uses measurements of ecological processes to assess restoration response and evaluates responses across multiple scales.

I focus here on a long-term large wood addition project on the Narraguagus River of eastern Maine that aims to restore habitat for Atlantic salmon (*Salmo salar*). Like many river restoration projects, this one involves the addition of two types of large wood structures to mimic natural treefall and the physical (e.g., scour and fill) and biological (e.g., provision of habitat, retention of detrital resources) processes fallen trees support. My research asks whether a) wood addition has any generalizable or site-specific effects, b) structure type affects ecosystem response, and c) responses differ at local (site) vs regional (50-100m reach) scales in response metrics including algal biomass, leaf breakdown rate, salmon parr prey item biomass, and various taxonomic and functional metrics of macroinvertebrate community composition.

I found few generalizable ecological responses to wood additions. Site identity alone was a strong predictor of most ecological processes and macroinvertebrate community measures. Some metrics, such as leaf breakdown rate and algal biomass, showed site by treatment interactions, wherein site ID modified the response to large wood additions, but these interactions were not consistent across seasons. The two primary structure types differed in total macroinvertebrate abundance, leaf breakdown rate, and algal biomass, but again this was not consistent across seasons. It is not obvious what specific site characteristics are driving these strong site-specific responses to wood additions, though site mean macroinvertebrate taxonomic richness was predicted by site mean substrate index. However, at the regional (50-100m reach) scale, I found that the concentration of log structures is important for fine detrital and macroinvertebrate response. Total macroinvertebrate abundance was predicted by the number of structures 50m and 100m of a site.

It is common practice to consider larger-scale constraints limiting ecological potential when designing restoration projects, but my research indicates that small-scale, local conditions may be just as important, as my sites differed more from each other than did treatments. In other cases, site conditions moderated ecosystem response. Finally, it is important to consider multiple scales when monitoring restoration outcomes. In this case, the number of wood additions upstream of a sampling site (regional intensity) had a much stronger influence on ecosystem metrics than the presence of wood in the immediate site area (local). Especially in a highly connected system such as a river, restoration attempts at one location may affect the response to modifications at another site nearby, or a high concentration of projects might have an interactive, rather than additive, ecological effects.

ACKNOWLEDGEMENTS

Many thanks to the Project SHARE community, especially Steve Koenig and Chris Federico for supporting my research on their work. I hope my findings are helpful as restoration in Downeast Maine continues! I am grateful to my committee members, especially John Kocik, for their guidance and expertise on this project. Thanks to my advisor, Hamish Greig, for encouraging my endless side projects, supporting the small army of undergraduate students who occupied our lab for over a year, and tolerating my thirst for coursework not at all related to my thesis. I am incredibly grateful to the undergraduate students who assisted in the lab: Amanda, Andrew, Ash, Audrey, Braden, Gabe, Hannah, Hayden, Jessie, Josh, Kacey, Kiera, Lauren, Maria, Meg, Nick, Olivia, Parker, Ryan, Sara, Sienna, Syd, and Teemer. This thesis would not exist without their hard work.

I am especially grateful to my fantastic field assistants, bug pickers, taxonomic key wizards, and volunteer supervisors, Audrey, Ash, and Josh, and my two senior project students, Ash and Kiera. Being able to leave the lab and my volunteers in Audrey and Ash's capable hands full-time let me get all the other work of grad school done, and Ash and Kiera's excellent independent research produced additional details that give this project broader interest and applicability. Finally, thanks to mum, Neil, Brian, Dennis, Emma, Hannah(s), Kahli, Kat, Kelby, Kyle, Kirstin, Lauren(s), Lydia, Madi, Meaghan, Megan, Sam, Silas, Astro, and the crew for keeping me happy and sane.

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CHAPTER 1: MACROINVERTEBRATE RESPONSES TO IN-STREAM LARGE WOOD ADDITIONS ARE SCALE- AND SITE-DEPENDENT

ABSTRACT

Scale-dependence is common across ecosystems and ecological processes, yet scale is rarely considered in monitoring of ecological restoration. I used a multi-year river restoration project on the Narraguagus River, Maine, to test how large wood additions affect macroinvertebrate communities at local (site) and regional (50-100m reach) scales. Locally, sites tended to vary more among themselves than between treatments (restored vs not), though all restored sites did have larger and more variable macroinvertebrate communities, primarily due to changes in detritivore richness and abundance. Regional processes appear to be the primary driver of ecological change, as sites with more wood additions in the 50-100m directly upstream had more macroinvertebrates, particularly detritivores and predators, than sites with few structures directly upstream. In general, restoration in the Narraguagus does not appear to be creating the intended changes, though small changes in detritivore communities were detected. Restoration practitioners should consider changes at multiple scales and potential interactions among restoration projects when planning and monitoring restoration work.

INTRODUCTION

Across ecosystems, ecological patterns vary depending on the scale of analysis. For example, invasibility decreases with local biodiversity but increases with diversity on a regional scale (Byers and Noonburg 2003). Community assembly is associated locally with niche limitation and regionally with dispersal effects (Leibold et al. 2004; Holyoak et al. 2005). Effects of human activities can also be scale dependent; for instance urbanization can have different effects at the local and regional scales (Pautasso 2007; Pautasso and Chiarucci 2008). Scholarly discourse is often focused on negative human-ecological interactions as above, but positive relations such as restoration are increasing in frequency as social and financial support grows (BenDor et al. 2015; UN Environment Program 2020; European Comission 2022). Thus, there is increasing need to understand the scale-dependence of restoration outcomes.

It is well-accepted that scale influences restoration success in that local restoration projects are constrained by larger-scale degradation (e.g., Beechie et al. 2010). For example, re-seeding a prairie patch with native seeds may be futile if regional precipitation patterns have shifted beyond species' germination needs. Yet, restoration monitoring rarely considers the possibility of scale-dependent responses (Roni 2019; but see Lepori et al. 2005), instead tending to focus on one scale (Miller et al. 2010; Ren et al. 2016). For example, forest restoration monitoring usually focuses at the level of the forest patch (de Almeida et al. 2020; Warner et al. 2022; Suganuma and Durigan 2022), which means more local (e.g., microclimate or soil conditions) and regional (e.g., movement of migratory species) processes are overlooked. But local restoration projects are embedded in larger ecosystems (Ouellet et al. 2022), and collecting data to understand processes at multiple scales is necessary to see the full picture (Vaughn 2010; Wang et al. 2021).

In addition to interactions between local and regional-scale processes, ecological responses to restoration efforts are also likely influenced by site-specific factors (Turcotte 2022; Danhoff and Huckins 2022), where local patches respond in different or even opposite ways. These opposing patterns suggest that local scale responses may not be generalizable across sites, and large-scale studies that examine several sites at once may overlook important details. For example, a study that asks how restoration projects impact biodiversity across patches, half of which show increases in diversity and half decreases, may mistakenly conclude that the projects had no effect at all. Conversely, the same study using local, patch by patch analyses, would find strong but context dependent restoration effects.

Restoration in river ecosystems is particularly well-studied, and river systems are known to have highly scale-dependent processes due to their dendritic and directional nature (e.g., Brown et al. 2011; Tonkin and Death 2013). Scale-dependence could be driven by flow direction and strength, collection/delay of organic material on log structures, or invertebrate dispersal limitations (Parkyn and Smith 2011; Swan and Brown 2017). For example, the sediment available for work in a stream's lower reaches is limited by sediment input from reaches upstream. A restoration project downstream from a long bedrock-bottomed reach, which supplies very little sediment, has much lower potential to show any substrate response than a project downstream from a reach bordered by mobile sediment-rich glacial till. In turn, the organisms that colonize habitat patches produced during localized restoration attempts may show both direct and indirect scale dependence, as they are directed both by locally available habitat (substrate type and turnover rate) and by the pool of colonists available in reaches upstream (Townsend 1989; Leibold et al. 2004).

River restoration projects often involve removing anthropogenic structures (e.g., dams or levees), but they can also return structures to mimic those found in a healthy river. For example, addition of large wood is a common practice, intended to mimic natural logjams and associated physical and ecosystem processes. These processes, such are physical scour and deposition, detritus collection, and colonization by organisms, work on both local and regional scales, as described above. Wood addition projects often aim to improve habitat quality and/or quantity for salmonid fishes, as the wood itself acts as cover for juveniles (Beland et al. 2004), and its influence on physical processes of scour and fill create high-quality spawning and rearing habitat (MacInnis et al. 2008). However, large wood additions have ecosystem-wide importance, for example altering habitat and basal resources for macroinvertebrates (Al-Zankana et al. 2021) and reconnecting and revitalizing terrestrial floodplain vegetation communities (Gerhard and Reich 2000; Montgomery et al. 2003). Because the mechanisms through which large wood additions do their work function at multiple scales, it is reasonable to expect ecological responses to show scale-dependence as well.

Effects of wood additions on macroinvertebrate communities are well-studied but equivocal (Al-Zankana et al. 2020), and scale-dependent responses are rarely considered. Nevertheless, macroinvertebrate distribution and abundance depend upon local and regional factors, as colonists from a regional species pool are limited by local habitat availability (Townsend 1989; Winemiller et al. 2010), so scale-dependent responses to wood additions can be expected. I used common indicators of river ecological function, aquatic macroinvertebrate communities, to assess the impacts of large wood additions at local and regional scales in eastern Maine's Narraguagus river. Aquatic macroinvertebrates are common indicator taxa in stream studies, and as the primary prey item (Grader and Letcher 2006) for the juvenile salmonids that are frequent targets of restoration (e.g., Foote et al. 2020), they are a useful metric of restoration success.

Because log structures can increase habitat patchiness (and thus niche diversity) in their local area (Miller et al. 2010; de Brouwer et al. 2020) I expected that at the local scale, macroinvertebrate communities would have higher richness and abundance and be more variable in richness and abundance in test than reference sites. Because their lack of mobility concentrates their work constantly on the same location through time, I expected sites with more permanent structures (post-assisted log structures, see methods) would have more dramatic responses to wood additions than sites with more mobile (griphoist trees, see methods) structures. Individual log structures could act as sources of invertebrate colonists and basal resources (coarse and fine detritus), so at a regional scale, I predicted macroinvertebrate taxonomic richness and abundance would be higher at sites downstream of reaches with more log structures. I did not examine regional effects of PALS or GH concentration separately because their distributions were too patchy.

METHODS

Study site

The Narraguagus River is a small watershed that runs 78 km from its headwaters to its mouth in Cherryfield, Maine (**Error! Reference source not found.**). In total, the watershed covers about 600 s quare kilometers, and it is a part of the Downeast Coastal Salmon Recovery Unit designated by the National Marine Fisheries Service (National Marine Fisheries Service 2009). This region of Maine, including the Narraguagus, was used for logging and river driving of logs for over two centuries (see Chapter 3 for more details). As such, it is an important watershed for the protection and future recovery of endangered Atlantic salmon (*Salmo salar*) and has been a priority for restoration for more than a decade. So far, restoration efforts have removed all barriers to fish passage, and projects in the recent decade have aimed to restore habitat quality via in-stream wood additions.

I assessed local- and regional responses to large wood additions in the upper mainstem of the Narraguagus River in eastern Maine. Here I define “local” as the scale of a single site, approximately 10-15m long and containing one log structure, and the “regional” scale as a 50-100m long reach, containing multiple log structures and potentially multiple sites. The Narraguagus River has been the target of large wood restoration for several years, with regional differences in intensity of effort due to variation in ability to access the stream. I used intensive sampling of the macroinvertebrate community at ten site pairs (~10-15m stream segment) along a gradient of reach-scale (50-100m segment) restoration effort.

Wood additions in the Narraguagus come in two forms. “Griphoist trees” (“GH”, Figure 1-1) are trees from the riverbank that were pulled into the stream but remain connected to land by their roots. They are full trees, including branches and leaves, and because they are only attached to the bank, they are free to be moved by water flow. Post-assisted log structures (PALS, Figure 1-1) are a more heavily constructed approach, built by stacking logs and then pinning the pile down using posts driven two meters into the bed. These structures are unable to move and are much less physically complex than griphoist trees because they have no branches or leaves. Because PALS and GH structures differ in mobility, complexity, and ease of construction, I wanted to test whether they produce different local-scale restoration responses.

Figure 1-1. Examples of griphoist trees ("GH", A) and a post-assisted log structure ("PALS", B)

I selected ten log structures (five each GH and PALS) in the river's main stem, from 28 Pond downstream to the confluence with Bobcat Brook (Figure 1-2). These structures were put in place between 2017-2019, and they typically take up ¼ to $^{1}/_{3}$ of the river's wetted width (covering 15-20m longitudinally and extending 5-10m into the channel). For each of these ten sites (which covered the full longitudinal extent of a structure) I selected a paired and equivalent-sized reference site directly upstream. To avoid influence of nearby log structures, reference sites were strategically placed upstream of the test site but not immediately downstream of subsequent structures. This paired test-reference design was the basis of my local scale research questions. To assess larger-scale responses to restoration, I used GIS to count the number of human-built structures (including both PALS and griphoists) in the 50m and 100m upstream of each sampling location. I chose these bins to represent distances that commonly sampled macroinvertebrates are likely to travel in their lifetime, and avoided larger distances because number of logjams became highly bimodal in distribution. This measure includes only logjams that were present at the time of sampling, and it does not include structures that were installed but washed away before the sampling dates.

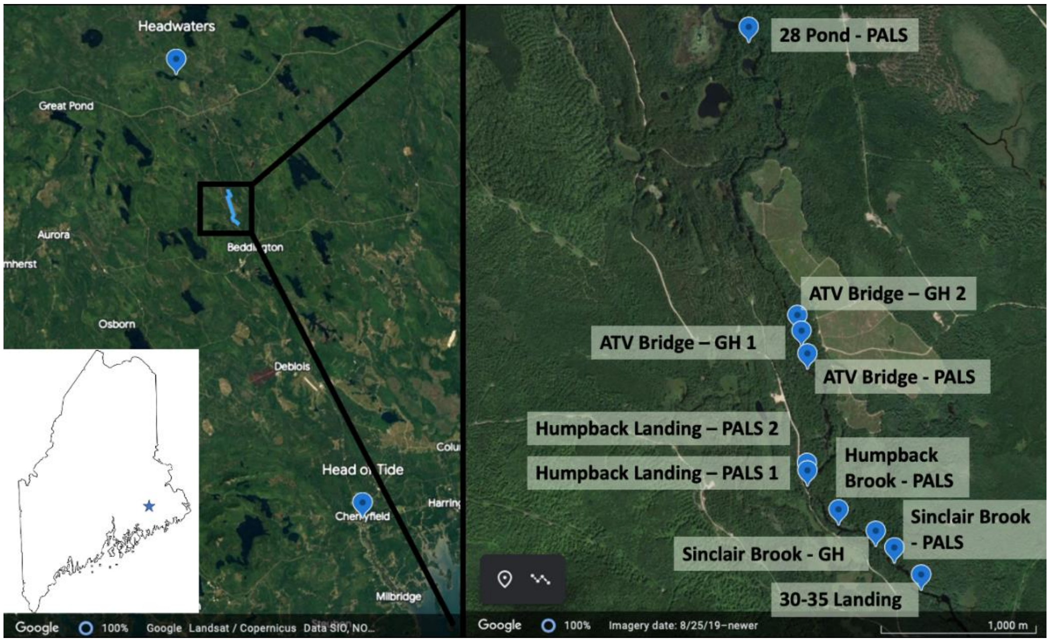

Figure 1-2. Map of study sites along the Narraguagus River, Maine

Sampling methods

Sampling design

I placed three cross-river transects at each test and reference site, one each at the upstream and downstream ends of the wood structure (defined as where the log structure first and last intersected with the water surface), and one in the middle across the approximate center of the structure (Figure 1-3). To replicate this setup at the wood-free reference site I simply used identical transect spacing to that site's test site (Figure 1-3, distances A and B). Therefore, spacing of transects was consistent within test-reference pairs but varied from site to site. Along each transect, I identified four evenly spaced sampling locations measured at 20, 40, 60, and 80% of wetted width. All sampling was completed in May-June 2021.

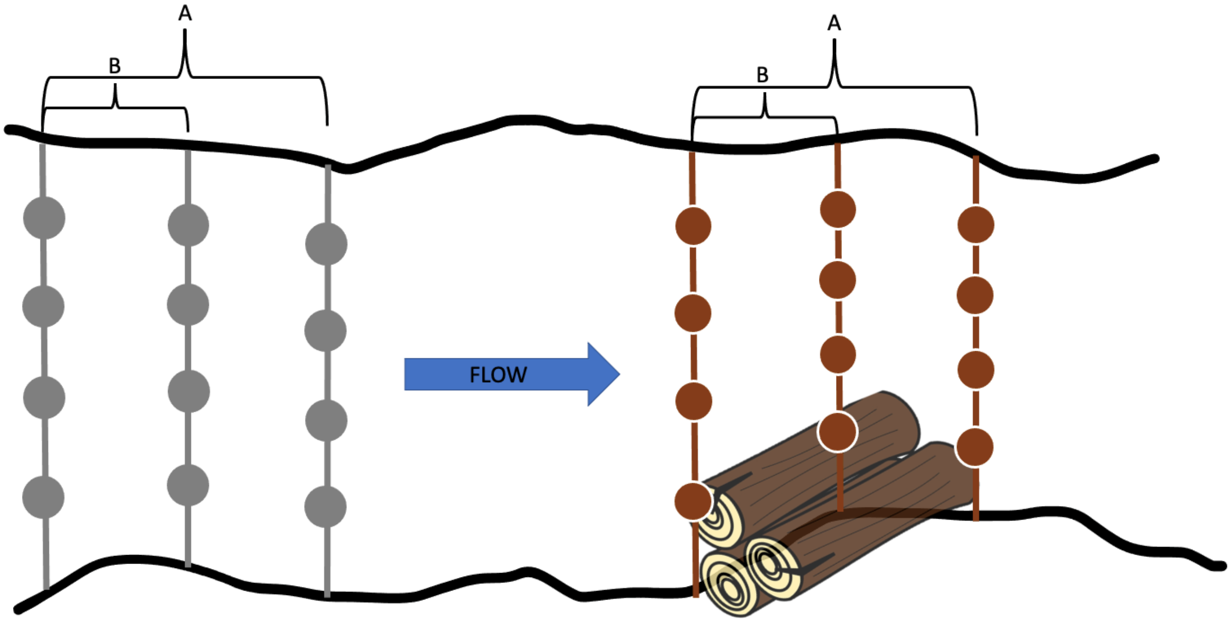

Figure 1-3. Schematic of sampling design at a single site pair.

Test site is marked in brown and the reference site in gray. Water flows from left to right. Lines represent cross-river transects and circles are sampling locations at 20, 40, 60, and 80% of river width. Note that length of test and reference sampling sites (A) as well as distance between transects (B) are equivalent within a test-reference pair but varied from pair to pair according to log structure size.

I calculated log structure area by multiplying the length of the longest axis of the structure by the length of the axis parallel to the first. I also calculated structure area proportional to site area by first multiplying length of the center transect and the distance from the downstream to the top transect to find site area, then dividing structure area by site area to find the percentage of the site area occupied by a log structure. Log structure age was defined as years from installation date to sampling date according to restoration managers' records. Reach slope values were obtained from Turcotte (2022), who used the same sites in her analyses.

Macroinvertebrate sampling

At each sampling location (4 per transect, 12 per test or reference site, 24 per site pair), I quantified macroinvertebrate community composition and structure using a Surber sampler (30 x 30cm, 243 µm mesh). Samples were immediately preserved in 70% ethanol for future lab processing. In the lab, I used a sieve to retain all sampled items greater than 500 µm. For samples with a large amount of fine material I picked 1/16 – 1/8 subsample and discarded the remainder, then corrected final invertebrate counts accordingly. Invertebrates were removed visually under a dissecting microscope, stored in 70% ethanol, and then identified to genus or the lowest level of classification possible using standard taxonomic keys (Peckarsky et al. 1990; Merritt et al. 2008; Wiggins 2014). In addition to measures of taxonomic richness and abundance, I assigned taxa to functional feeding groups (collector-filterer, collector-gatherer, predator, shredders, scrapers) according to Merritt et al. (2008) to quantify functional richness and abundance.

Physical habitat sampling

I measured additional environmental covariates including depth, velocity, substrate cover, structure area, and structure age at all sampling locations. I measured velocity at 2/3 depth from water surface, rounded to the nearest 0.1 m/s. I measured depth (nearest cm) immediately below the sampling point as indicated by a cross-river transect. To quantify substrate, I recorded percent cover of Wentworth substrate classes (sand-boulder) within the Surber sampler 30 cm by 30 cm quadrat. To convert these percent cover values into a single number that describes a substrate sample, I used an index published by Jowett et al. (1991) that considers the relative presence of each substrate class in a sample. Because this index separates fine and coarse gravel, which my sampling did not, I assumed patches of gravel were equally comprised of fine and coarse particles for my calculations. This assumption is substantiated by observations in the field.

Statistical analyses

For all analyses I quantified macroinvertebrate community composition and structure in terms of individual abundance, abundance of individual functional feeding groups (assigned using genera-specific descriptions in Merritt et al. 2008), and taxonomic and functional richness. To test for patterns in macroinvertebrate community structure at the local scale, I used paired t-tests to measure differences in mean and coefficient of variation in macroinvertebrate abundance and taxonomic and functional richness between paired test-reference sites. To look for responses at a larger scale, I took two approaches. The first was to use an ANOVA to look for patterns in macroinvertebrate community structure related to site or structure type, treatment, and their interaction. The second was to regress treatment-level means against counts of log structures in the 50 and 100m upstream of a site, using a linear regression. I also regressed macroinvertebrate community metrics against site variables including structure area, structure area relative to site area, site slope, mean site velocity, and mean site substrate index to consider site-specific drivers. All analyses were performed in R (R Core Team 2022).

RESULTS

Local responses

Restoration status

Paired t-tests comparing means between paired test and reference sites showed that there was no difference in mean macroinvertebrate taxonomic richness or abundance between treatment and reference sites at the local (site) scale ($p > 0.80$, **Error! Reference source not found.**). Paired t-tests c omparing coefficient of variation between paired test and reference sites showed a significant difference in coefficient of variation of macroinvertebrate total abundance between test and reference sites ($p < 0.01$), with test sites having more variability than reference (mean difference in CV 0.251, Figure 1-4A). In terms of functional diversity, mean shredder taxonomic richness ($p = 0.022$. mean difference = 0.33 taxa) and individual abundance ($p = 0.015$, mean difference = 4.25 individuals) was higher in restored than reference sites, as was variation in collector-gatherer individual abundance ($p = 0.018$. mean difference = 0.31, Figure 1-4B-D). All other macroinvertebrate community composition and functional group means and coefficients of variation did not show a significant difference between restored and reference sites (**Error! Reference source not found.**).

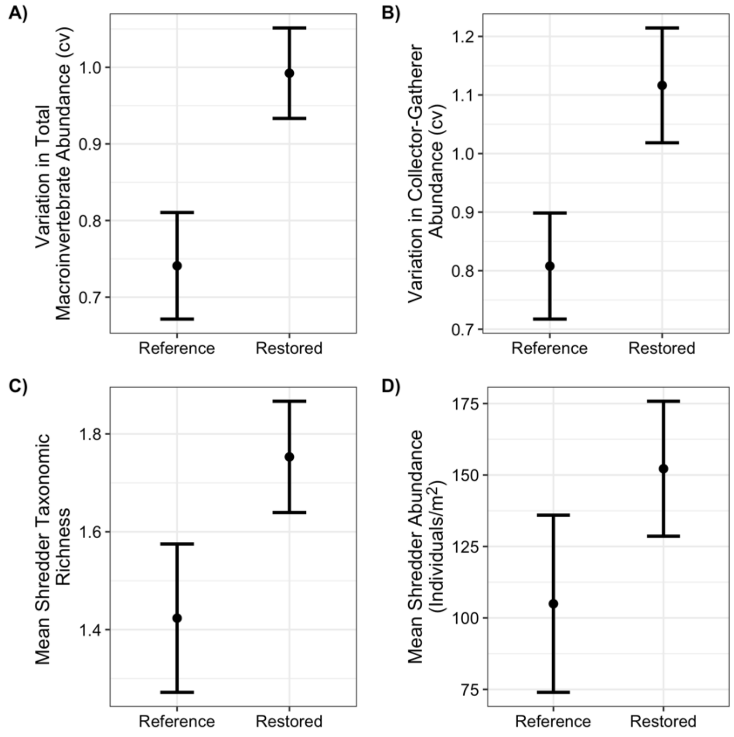

Figure 1-4. Local differences in macroinvertebrate community composition between test and reference sites.

A) *coefficient of variation (CV) in total macroinvertebrate abundance, B) CV in collector-gatherer abundance, C) mean shredder taxonomic richness, and D) mean shredder abundance across restored and reference sites of 10 sites in the Narraguagus River. All four showed significant differences between restored and reference sites across all ten sites (paired t-test, p = 0.009, 0.018, 0.022, and 0.015 respectively). Bars show mean ± 1 SE.*

Table 1-1. Summary of statistics for t-tests on all metrics of macroinvertebrate community composition. Significant p-values are italicized and bolded. "Indiv." indicates a mean count of individuals across all ten restored or reference sites

	Response Metric	P value	T statistic	Restored mean	Reference mean
Total individual abundance	Mean	0.905	-0.12	3773.3 /m^2	3715.9 /m^2
	Coefficient of variation	***0.009***	-3.29	0.99	0.74
Taxonomic richness	Mean	0.806	-0.25	28.65 taxa	28.24 taxa
	Coefficient of variation	0.892	0.14	0.34	0.346
Functional richness	Mean	0.213	-1.34	4.84 FFGs	4.73 FFGs
	Coefficient of variation	0.221	1.32	0.08	0.12
Shredder individual abundance	Mean	***0.015***	-2.98	152.20/m^2	104.96/m^2
	Coefficient of variation	0.354	0.98	0.95	1.11
Shredder taxonomic richness	Mean	***0.022***	-2.75	1.75 taxa	1.42 taxa
	Coefficient of variation	0.767	0.30	0.55	0.58
Scraper individual abundance	Mean	0.452	0.79	294.28/m^2	339.98/m^2
	Coefficient of variation	0.474	-0.75	1.08	1.00
Scraper taxonomic richness	Mean	0.196	-1.40	3.74 taxa	3.44 taxa
	Coefficient of variation	0.616	0.52	0.49	0.53
Collector-gatherer individual abundance	Mean	0.817	-0.24	2141.84/m^2	2058.33/m^2
	Coefficient of variation	***0.018***	-2.88	1.12	0.81
Collector-gatherer taxonomic richness	Mean	0.983	0.02	13.15 taxa	13.17 taxa
	Coefficient of variation	0.647	0.47	0.31	0.34
Collector-filterer individual abundance	Mean	0.939	-0.08	516.64/m^2	507.26/m^2
	Coefficient of variation	0.890	0.14	1.31	1.33
Collector-filterer taxonomic richness	Mean	0.387	-0.91	2.68 taxa	2.50 taxa
	Coefficient of variation	0.174	-1.48	0.67	0.56
Predator individual abundance	Mean	0.922	0.10	711.90/m^2	727.12/m^2
	Coefficient of variation	0.142	-1.61	0.96	0.83
Predator taxonomic richness	Mean	0.585	0.57	7.31 taxa	7.67 taxa
	Coefficient of variation	0.779	0.29	0.45	0.47

Site identity

To follow up on my t-tests, I used ANOVAs to look at the influence of site pair, treatment, and their interaction on the macroinvertebrate community at the local (site) scale. Overall, site pair alone was a stronger predictor of macroinvertebrate community composition than restoration status or their interaction (**Error! Reference source not found.**). Restoration status alone predicted shredder abundance (p = 0.028) and richness (p = 0.010), with both generally higher in restored than reference sites (Figure 1-5). Site pair also modified the effect of restoration on collector-gatherer richness (Site ID x restoration status interaction, p = 0.034) and predator abundance (p = 0.017, **Error! Reference source not found.**, Figure 1-5), with responses to restoration varying in direction and magnitude from site pair to site pair. For example, collector-gatherer richness was higher at the restored site of 28 Pond than the reference site, while the opposite was true at 30-35 Landing (**Error! Reference source not found.**B). Similarly, predator abundance was higher at the reference site of ATV Bridge – GH 1 than the corresponding restored site, but it was lower at the reference than the restored site of ATV Bridge – GH 2 (Figure 1-5C).

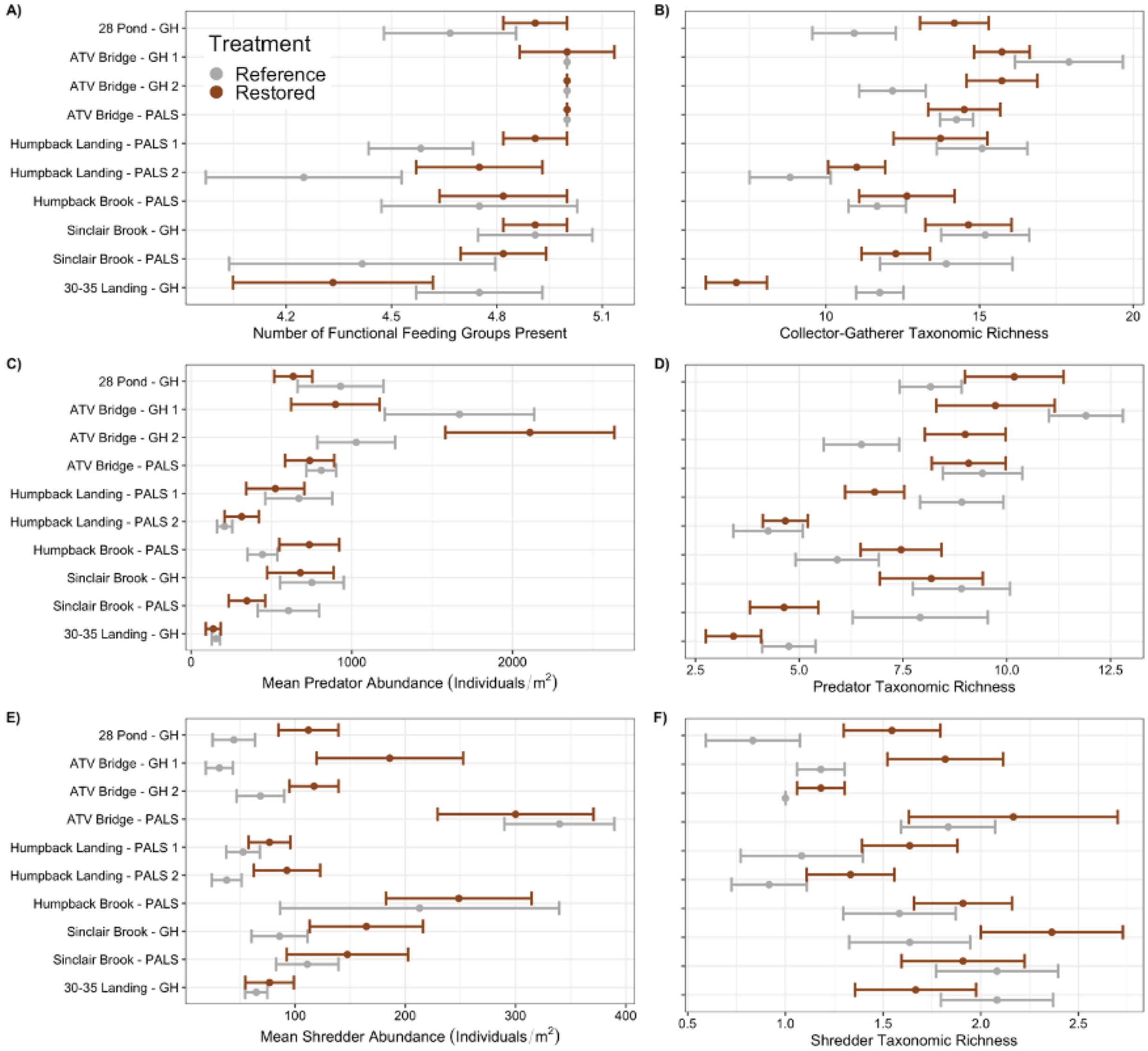

Figure 1-5. Macroinvertebrate community differences between individual test-reference site pairs.

Mean A) number of functional feeding groups present, B) collector-gatherer taxonomic richness, C) predator abundance, D) predator taxonomic richness, E) shredder abundance, and F) shredder taxonomic richness (±1 SE) in restored and reference treatments in 10 site pairs of the Narraguagus River. Restoration status alone was significant for shredder abundance (ANOVA p = 0.028) and richness (ANOVA, p = 0.010). Site pair was significant for number of FFGs present (ANOVA, p = 0.019), collector-gatherer richness (ANOVA, p = 7.55 e-08), predator abundance (ANOVA, p = 1.39 e-09), predator richness (ANOVA, p = 6.35 e-12), shredder abundance (ANOVA, p = 4.67 e-08), and shredder richness (ANOVA, p = 0.0003). Site pair x treatment interaction was significant for collector-gatherer richness (ANOVA, p = 0.034) and predator abundance (ANOVA, p = 0.017). Bars show mean ± 1 SE.

Table 1-2. Summary of statistics for ANOVAs including restoration status, site pair identity and their interaction as fixed factors. Significant p-values are bolded and italicized.

Variable	ANOVA fixed effects										
	Restoration Status				Site Pair ID				Restoration Status* Site Pair ID		
	df	F	p		df	F	p		Df	F	p
Total individual abundance	1	0.011	0.918		9	8.166	***2.26 e -10***		9	1.291	0.243
Taxonomic richness	1	0.115	0.735		9	8.137	***2.38 e -10***		9	1.638	0.106
Functional richness	1	1.928	0.166		9	2.272	***0.019***		9	1.102	0.363
Shredder individual abundance	1	4.871	***0.028***		9	6.424	***4.67 e-08***		9	0.558	0.831
Shredder taxonomic richness	1	6.774	***0.010***		9	3.672	***0.0003***		9	0.904	0.523
Collector-gatherer individual abundance	1	0.044	0.834		9	5.790	***3.42 e-07***		9	0.911	0.516
Collector-gatherer taxonomic richness	1	0.001	0.970		9	6.271	***7.55 e-08***		9	2.067	***0.034***
Collector-filterer individual abundance	1	0.00	0.991		9	10.48	***2.33 e-13***		9	0.92	0.509
Collector-filterer taxonomic richness	1	0.761	0.384		9	9.347	***6.35 e-12***		9	0.915	0.513
Predator individual abundance	1	0.025	0.876		9	7.559	***1.39 e-09***		9	2.318	***0.017***
Predator taxonomic richness	1	0.603	0.438		9	9.347	***6.35 e-12***		9	1.906	0.053
Scraper individual abundance	1	0.774	0.380		9	6.170	***1.03 e-07***		9	1.134	0.340
Scraper taxonomic richness	1	1.928	0.166		9	7.361	***2.55 e-09***		9	0.869	0.554

Site type

I also performed ANOVAs on the influence of structure type (griphoist vs PALS), treatment, and their interaction. Structure type was a stronger predictor of macroinvertebrate community composition than restoration status at the local (site) scale. Restoration status alone was only significant for shredder richness and abundance, as reported above in previous t-tests and ANOVAs. Structure type alone was significant for several factors but did not appear to modify the effect of restoration (no significant structure type x restoration status interaction, Table 1-3). For example, total macroinvertebrate abundance (**Error! Reference source not found.**A) and richness (Figure 1-6F) and abundance (Figure 1-6E) of predators were all consistently higher at griphoist than PALS sites. Only number of functional groups present showed marginal differences between restored and reference sites (p = 0.069,Table 1-3).

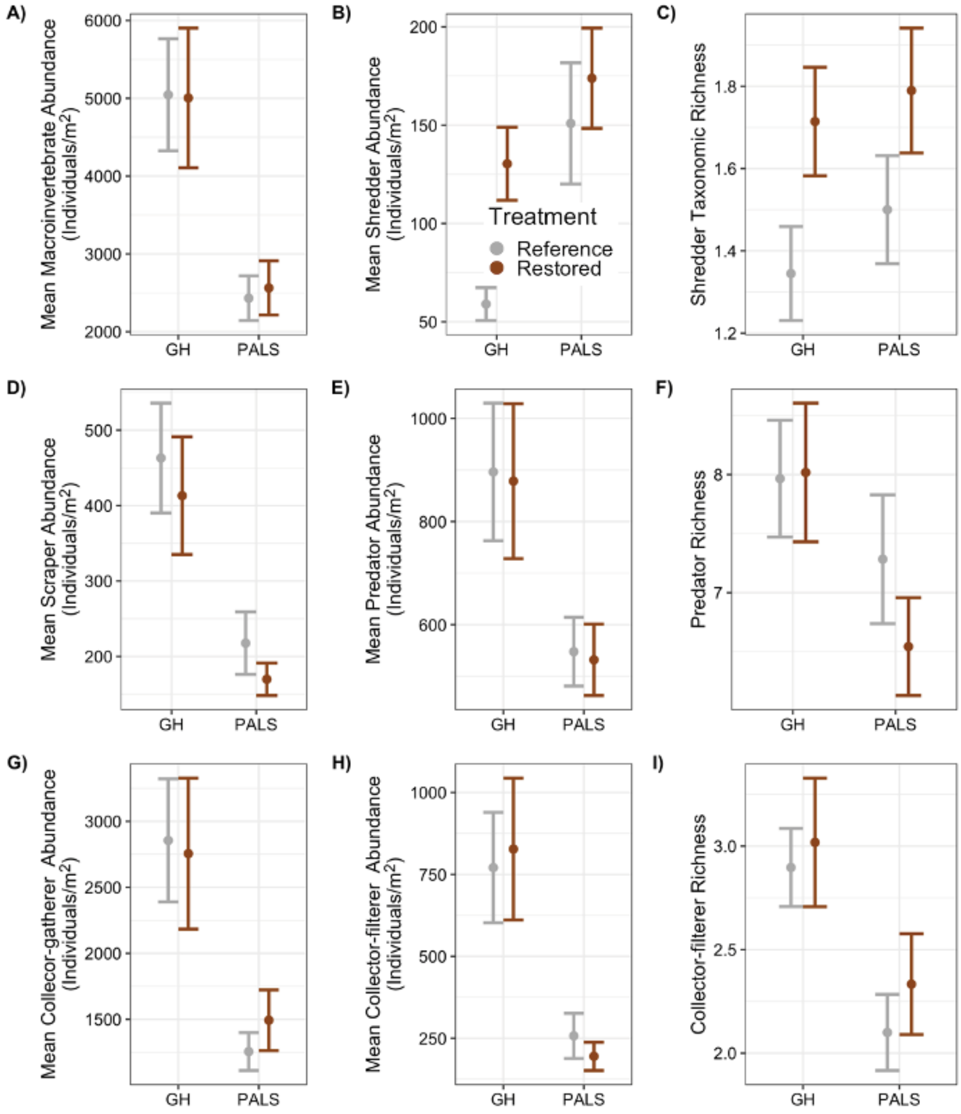

Figure 1-6. Macroinvertebrate community differences between wood structure types.

Mean A) total macroinvertebrate abundance, B) shredder abundance, C) shredder richness, D) scraper abundance, E) predator abundance, F) predator richness, G) collector-gatherer abundance, H) collector-filterer abundance, and I) collector-filterer richness in restored and reference treatments by two structure types in the Narraguagus River. Restoration status was significant for shredder abundance (ANOVA, p = 0.041) and shredder richness (ANOVA, p = 0.014). Structure type was significant for total abundance (ANOVA, p = 4.69 e-05), shredder abundance (ANOVA, p = 0.003), collector-gatherer abundance (ANOVA, p = 0.0003), collector-filterer abundance (ANOVA p = 7.06 e-05), collector-filterer richness (ANOVA, p = 0.002), predator abundance (ANOVA, p = 0.002), predator richness (ANOVA, p = 0.039), and scraper abundance (ANOVA, p = 3.45 e-05). Bars show mean ± 1 SE.

Table 1-3. Summary of statistics for ANOVAs examining the influence of restoration status, structure type (GH vs PALS), and their interaction on metrics of macroinvertebrate community composition.

Significant p-values are bolded and italicized.

Variable	ANOVA fixed effects										
	Restoration Status				Structure Type				Restoration Status* Structure Type		
	df	F	p		df	F	p		df	F	p
Total individual abundance	1	0.009	0.925		1	17.228	***4.69 e-05***		1	0.020	0.888
Taxonomic richness	1	0.089	0.766		1	2.954	0.087		1	0.000	0.998
Functional richness	1	1.856	0.174		1	1.967	0.162		1	3.341	0.069
Shredder individual abundance	1	4.219	***0.041***		1	9.064	***0.003***		1	1.139	0.287
Shredder taxonomic richness	1	6.120	***0.014***		1	0.764	0.383		1	0.091	0.764
Collector-gatherer individual abundance	1	0.039	0.843		1	13.711	***0.0003***		1	0.189	0.664
Collector-gatherer taxonomic richness	1	0.001	0.973		1	0.979	0.323		1	0.024	0.876
Collector-filterer individual abundance	1	0.000	0.992		1	16.396	***7.06 e-05***		1	0.178	0.674
Collector-filterer taxonomic richness	1	0.594	0.442		1	9.982	***0.002***		1	0.057	0.882
Predator individual abundance	1	0.019	0.889		1	9.923	***0.002***		1	0.000	0.993
Predator taxonomic richness	1	0.448	0.504		1	4.324	***0.039***		1	0.592	0.442
Scraper individual abundance	1	0.685	0.409		1	17.858	***3.45 e-05***		1	0.000	0.985
Scraper taxonomic richness	1	1.545	0.215		1	0.276	0.600		1	1.143	0.286

Site characteristics

I continued investigating local (site) scale responses to restoration by using linear models to determine what site characteristics were driving these strong site-specific differences in macroinvertebrates, using site by site effect size (t-c) as my response variable for those site characteristics that did not differ between the restored and reference sites of a site (i.e., structure area, structure area relative to site area, site slope, structure age). No effect sizes of any metrics of the macroinvertebrate community were predicted by any of the site characteristics that I measured. I also regressed reference and restoration site-level means against corresponding mean site velocity and mean site substrate index. Mean macroinvertebrate taxonomic richness across restored and reference sites decreased with increasing substrate index ($p = 0.023$, $R^2 = 0.2553$, Figure 1-7). Here a minimum possible substrate index value of 3 represents 100% sand, a maximum possible value of 8 represents 100% bedrock, and values in between represent some mix of particle sizes (Jowett et al. 1991). The range of values in my dataset therefore represent anywhere from mostly sand (3-3.5) to a cobble-boulder mix (5-5.5), and highest taxonomic richness was found in the lower end of that range.

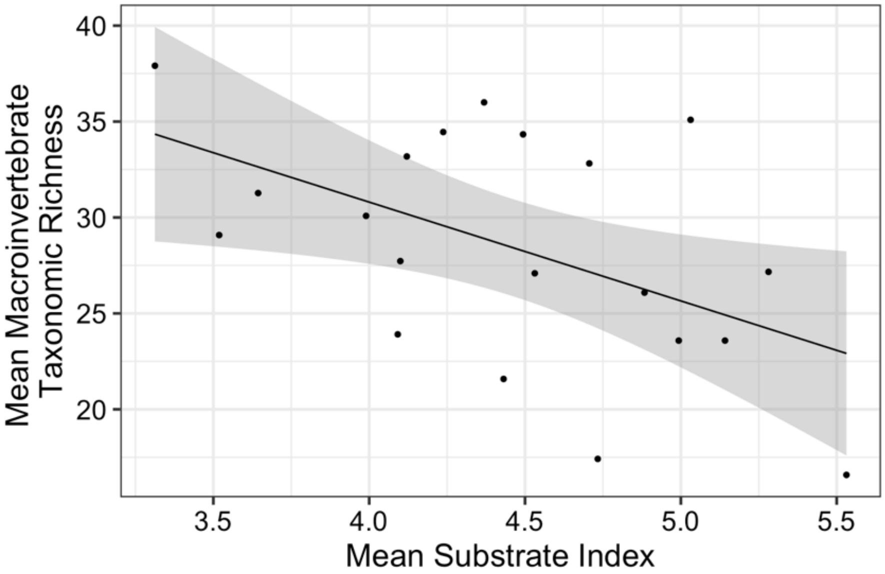

Figure 1-7. Restored or reference site mean macroinvertebrate taxonomic richness in relation to site mean substrate index. Smaller values represent dominance of smaller (sand) particles, larger values represent dominance of larger particles (cobble/boulder), and intermediate values represent some mix of particle sizes (linear model p = 0.023, R^2 = 0.255). Data represent 20 sites in the Narraguagus River, in May 2021.

Regional responses

I then broadened my analyses to a regional (50-100m reach) scale, by testing whether concentration of log structures predicted any of my variables of interest. I regressed restoration or reference site means against the count of structures in the 50 or 100 meters upstream of a site. In this analysis, the restored and reference sites at a given site were treated as two separate sites, for a total N = 20. Total macroinvertebrate abundance increased with the number of structures 50m (Multiple R^2: 0.450, p-value: 0.001) and 100m (Multiple R^2: 0.265, p-value: 0.02) of a site (Figure 1-8), but macroinvertebrate richness had no relationship with number of log structures upstream. Of metrics describing functional groups, mean collector-filterer taxonomic richness (p = 0.015, R^2 = 0.288), mean collector-gatherer abundance (p = 0.040, R^2 = 0.213), and mean predator taxonomic richness (p = 0.004,

$R^2 = 0.382$) all increased with number of structures in the 50m upstream of a sampling site, while variation in predator taxonomic richness (CV, $p = 0.045$, $R^2 = 0.205$) decreased (Figure 1-9). Mean predator taxonomic richness ($p = 0.013$, $R^2 = 0.297$) increased with the number of structures in the 100 m upstream of a sampling site (Figure 1-10), though this relationship was not as strong as that with the number of structures 50m upstream. Means and variation in all other functional groups were not related to the number of structures in the 50 or 100m upstream of a sampling site.

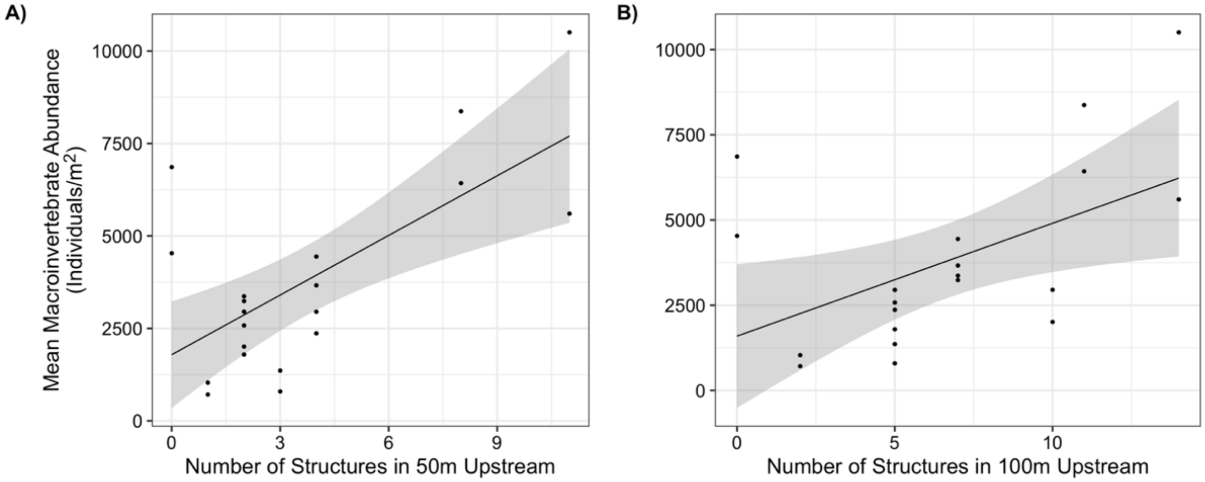

Figure 1-8. Mean macroinvertebrate abundance (individuals/m^2) in relation to restoration intensity.

Restoration intensity is here defined by the number of structures in the A) 50 m (linear model $p = 0.001$, $R^2 = 0.45$) and B) 100m upstream of a sampling site (linear model, $p = 0.020$, $R^2 = 0.265$). Data represent 20 sampling sites in the Narraguagus River, in May 2021.

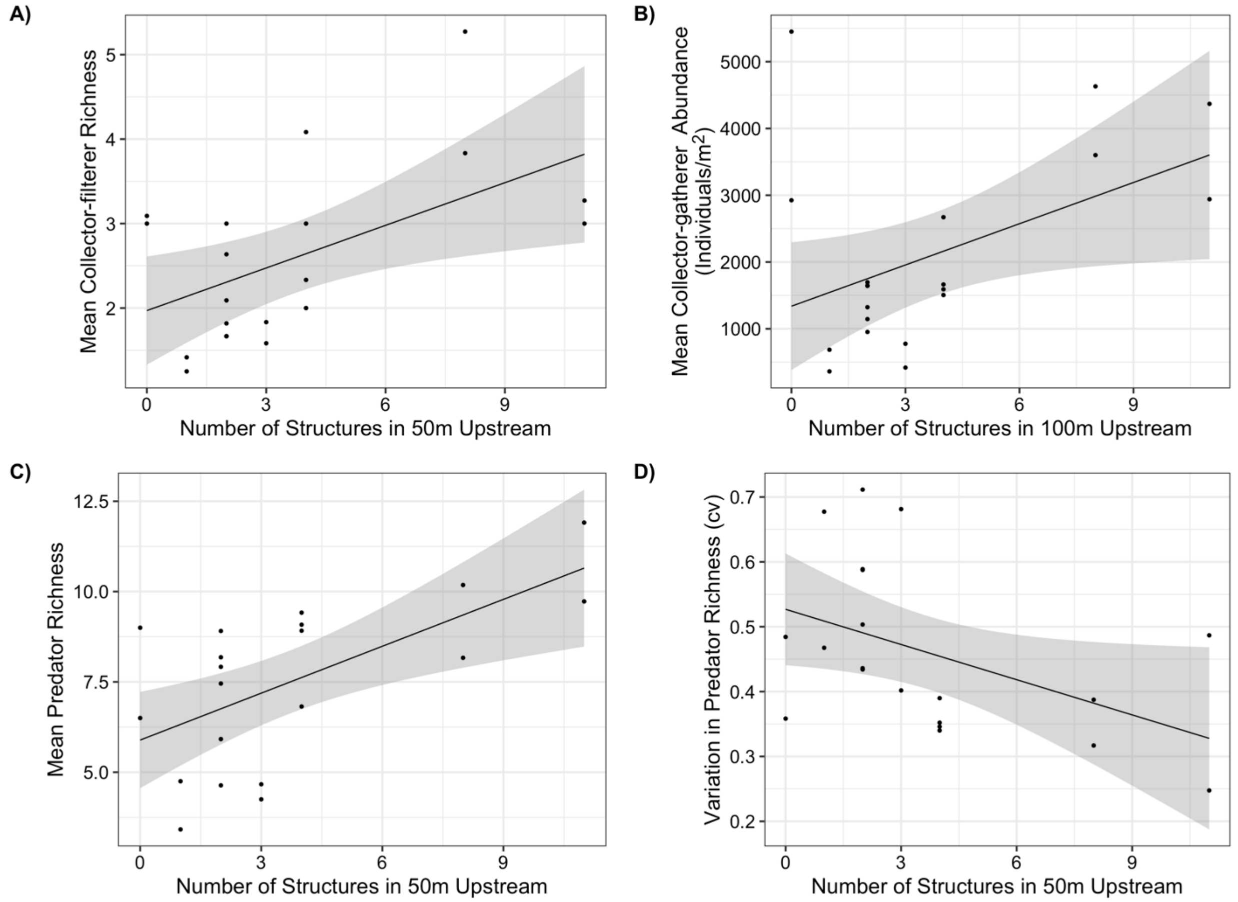

Figure 1-9. Macroinvertebrate functional community in relation to restoration intensity.

Restoration intensity is here defined by the number of structures in the 50 or 100m upstream of a site. A) Mean collector-filterer taxonomic richness against structures in 50m (linear model, $p = 0.015$, $R^2 = 0.288$), B) Mean collector-gatherer abundance against structures in 100m (individuals/m^2, linear model, $p = 0.040$, $R^2 = 0.213$), C) mean predator taxonomic richness against structures in 50m (linear model, $p = 0.004$, $R^2 = 0.382$), and D) variation in predator taxonomic richness against structures in 50m (CV, linear model, $p = 0.045$, $R^2 = 0.205$). Data represent 20 sampling sites in the Narraguagus River, in May 2021.

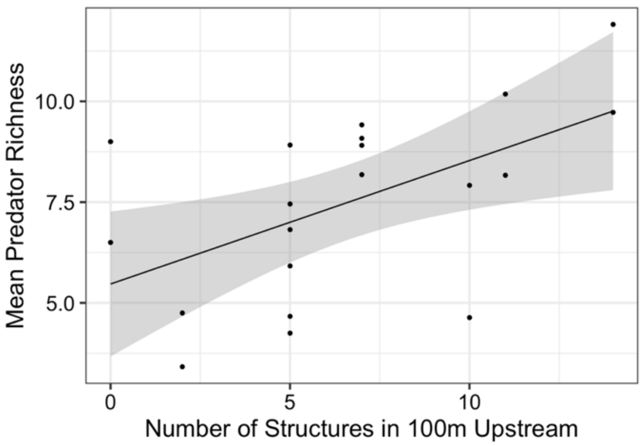

Figure 1-10. Mean predator taxonomic richness in relation to the number of structures in the 100 m upstream of a sampling site. Data represent 20 sampling sites in the Narraguagus River, in May 2021. Linear model, p = 0.013, R^2 = 0.297.

DISCUSSION

Contrary to my hypotheses, I found few generalizable differences in aquatic macroinvertebrate communities between paired restored and reference sites. Out of more than 25 macroinvertebrate community metrics, only shredder richness and abundance, variation in macroinvertebrate abundance, and variation in collector-gatherer abundance showed consistent local (site) scale responses, all higher in restored than reference sites. Nevertheless, these few detectable patterns were consistent with my expectations and the common view that wood additions increase habitat heterogeneity, which in turn increases variability and/or abundance in macroinvertebrate communities. Across most community metrics, site pair or structure type alone was the dominant predictor at the local scale, though some functional groups (collector-gatherers, shredders, and predators) also responded to restoration or the interaction between restoration and site. These results are consistent with the many published studies that have found equivocal responses of macroinvertebrate communities to wood additions and gives some insight into a potential reason: that sites are responding differently from one another, erasing any generalizable effect when sites are considered replicates in restoration assessment.

In addition, I found that several measures of the macroinvertebrate community demonstrated regional responses to wood additions, as macroinvertebrate total abundance, collector-filterer richness, predator mean and variation in richness, and collector-gatherer abundance all were predicted by the number of structures in the 50- and/or 100-m reach upstream of the sampling location. These measures all increased with restoration intensity, except for variation in predator richness, which decreased. This is a promising line of evidence that large-scale restoration effects may become primary ecological drivers over any responses at the local scale. Together, these two explanations may begin to explain why sites respond differently to restoration, and they demonstrate the importance of considering the cumulative effects of local-scale restoration projects on the regional-scale ecosystem.

It is clear from my analyses that site-level constraints are important in determining restoration success. Nearly all metrics of the macroinvertebrate community differed more between sites than between treatments; for example, macroinvertebrate richness was best predicted by substrate rather than presence of wood additions, which is consistent with research showing that substrate is an important driver of macroinvertebrate distribution (Bourassa and Morin 1995; Buss et al. 2004). The importance of such site-level constraints should not be surprising: restoration literature has long held that managers should consider site constraints that may limit project success, but these constraints are generally only considered at larger scales like a whole forest or watershed (e.g., Beechie et al. 2010). My findings indicate that small-scale site constraints also need to be considered, as local differences between sites can result in no or even opposing responses to restoration efforts.

Like many previous studies (e.g., Al-Zankana et al. 2020), I found few generalizable local (within restored-reference pair) responses to wood additions in the macroinvertebrate communities I measured. This may be due to the small physical scale of restoration structures and the relatively short time they have been in the river. Wood structures alter riverine habitat by directing flows that create patterns of scour and fill (Montgomery et al. 2003). These patches may be frequently disturbed by flow, with most or all organisms removed, or they may be protected by the wood and disturbed only in very high flows. Together, this creates a mosaic of patches that differ in their disturbance history and successional state, each collecting different amounts of detritus and suitable to different algal and macroinvertebrate taxa (Pringle et al. 1988). Macroinvertebrate community richness, evenness, and composition are known to respond to disturbance frequency (Death 1996; Haghkerdar et al. 2019), so if wood is acting as expected macroinvertebrate communities should respond by increasing in variation, which they did overall (Figure 1-4). It is notable that the functional groups that did respond consistently to restoration were the shredders and collector-gatherers, invertebrates that eat coarse and fine organic matter, which suggests that wood additions may be changing dynamics of organic matter retention.

Even so, consistent responses to restoration across sites were limited to only two functional groups and apparently to changes in food resources, indicating that wood additions are not changing the physical habitat at the scale of the local site. This is consistent with visual assessment in the field, as most of the substrate within both restored and reference sites did not appear to be recently disturbed. This is also consistent with geomorphic findings of a parallel project using the same sites (Turcotte 2022), which found limited and often opposite physical responses to wood additions. Small (<1m) scour pools and bars were only noticeable directly adjacent to wood, if at all, suggesting that flows may have been insufficient thus far to create much change, or structures are too small to interact with flows. Most of the time the structures under study were in the river were drought years (NDMC et al. 2023), and these structures may not have had the opportunity to interact with sufficient flows to direct processes of sediment mobilization and resulting recolonization.

This is somewhat expected, as this system prior to colonization likely contained logjams composed of large, old-growth trees which no longer exist. In comparison to historic wood loading, the structures in this study (<0.5m diameter) are not “large” at all and are unlikely to create geomorphic change. Without periodic high flows, the structures are limited in their ability to mobilize sediment, and so unable to create this mosaic of disturbance history. This may be exacerbated by the logging history of the river, as substrate is highly embedded (personal observation) in many reaches and difficult to move. It is notable that restoration responses seem to be propagating up levels of ecological organization, and it is possible the macroinvertebrates simply have not yet felt the effects. According to ANOVAs (Appendix 2), restoration had the strongest and most generalizable influence on physical habitat variables such as velocity, depth, and substrate. At the level of basal resources (algae and detritus), generalizable effects weakened and began to be replaced by site-specific responses, with each site responding differently to wood structures. At the level of the macroinvertebrates, all restoration effects have disappeared, replaced by site as the sole predictor of macroinvertebrate communities. There is some possibility that with more time and stronger flows, the response to restoration may continue moving up the ecosystem to higher trophic levels. However, this seems unlikely, as I observed macroinvertebrates responding to regional-scale changes, so any local response to wood additions should also be detectable.

In fact, there is good evidence that macroinvertebrate communities typically respond very quickly to disturbance (Haghkerdar et al. 2019; Greig et al. 2022). This requires larger scale processes, such as the presence of regional pools of colonists (Pringle et al. 1988; Townsend 1989), to occur. My research supports the idea that macroinvertebrates are instead responding to regional-scale dynamics. Total macroinvertebrate abundance, collector-gatherer abundance, collector-filterer richness, and predator richness all increased with the number of structures in the 50 and/or 100m upstream of a sampling location, suggesting these functional groups may drive the pattern in overall macroinvertebrate abundance. Conversely, variation in predator richness declined with increasing number of structures upstream, implying that the regional species pool provided by a series of log structures may increase similarity among communities downstream. These regional patterns may be driven by alterations to food availability by structures in series, as the two collector groups rely mostly upon fine detritus for food, and availability of fine particulate organic matter (FPOM, 0.5 – 1.0 mm) also increased with the number of structures in the 50m upstream of a sample (Appendix 2).

Local and regional patterns in detritivore richness and abundance suggest that log structures in series increase organic matter retention capacity, a phenomenon that has been documented in other large wood restoration projects, especially for coarse leaf material (Nilsson et al. 2015) and in streams with low discharge (Koljonen et al. 2012) similar to the Narraguagus. Organic material retention can be related to biofilm colonization (Shogren et al. 2020), flow patterns (Brookshire and Dwire 2003), substrate complexity (Webster et al. 1987), or collection by the wood itself (Brookshire and Dwire 2003), all of which can be altered by wood structures. The retention and slow release of fine detritus in turn supports communities of shredder, collector-gatherer, and collector-filterer invertebrates that rely on it for a food source. This idea is further supported by overall higher predator richness and abundance, collector-gatherer richness, and collector-filterer richness and abundance at griphoist than PALS sites (Figure 1-6). Griphoist structures are larger and more physically complex that PALS because they still retain their branches and leaves, making them better able to collect detritus (personal observation). Structures may also act as sources of colonists to the larger metacommunity, sheltering invertebrates during particularly high or low flows who then are able to colonize downstream depauperated reaches when normal water levels return (Thompson and Townsend 2006; Brown et al. 2011). In this way, pools of invertebrates and detritus held by log structures at the regional (50-100m reach) scale could moderate patch dynamics at the local (site) scale.

In this system, regional (reach) scale processes seem to dominate the limited local scale effects of wood additions. While I did observe several small-scale (≤ 2m) scour pools directly adjacent to log structures during sampling, these features are insignificant compared to the scale of change wood additions were intended to create. These small patches may function as novel or recently disturbed habitat, so my findings do not discount the possibility of very fine patch-scale macroinvertebrate responses to restoration. Future analyses should consider a deeper examination of macroinvertebrate community composition to reveal which, if any, taxa are responding to restoration and inform managers of implications for higher-level consumers, such as salmonid fishes, that primarily prey upon a subset of these taxa.

To summarize findings across scales, it appears that log structures create limited physical complexity at the very fine scale, as my field assistants and I, as well as project managers (Chris Federico, pers. comm.) have observed scour pools of 1-2 meters directly around the base of log structures at a subset of wood addition sites. Scaling up to an individual site, or the full width of a section of river containing a log structure, site characteristics such as substrate are dominant, and any effects of restoration are not detectable. Zooming out to a 50-100m reach, the concentration of structures in that reach becomes important to the communities downstream, as structures in series seem to retain and slowly release both detrital resources and colonists to the sites below. Overall, wood additions in the Narraguagus are creating little ecological change and falling far short of project goals to increase substrate mobility across the watershed.

To my knowledge, this is the first study that has examined effects of restoration intensity, or cumulative effects of projects individual at a regional (river reach) scale, so the extent to which my findings can be extrapolated to other projects, biogeographic areas, and ecosystems is unclear. Therefore, more work is needed to establish the frequency of multiscale responses to restoration.

Restoration monitoring should consider processes directing ecosystem response at multiple scales, as appropriate to restoration goals to better understand what factors most directly drive restoration response in their systems. This information can help practitioners better prioritize projects when facing limited financial or human capacity.

CHAPTER 2: ECOSYSTEM PROCESSES RESPOND DIFFERENTLY TO RESTORATION ACROSS SITES

ABSTRACT

Process-based restoration is an increasingly common approach to ecological rehabilitation, yet practitioners rarely monitor ecosystem processes when assessing project success. Large wood additions are a common form of process-based restoration in rivers, as they are intended to alter physical and biological processes through their interactions with river flows. My study assesses how direct and indirect measures of three ecosystem processes (leaf breakdown, algal biomass as a proxy for production, and macroinvertebrate food items of salmon parr as a proxy for biomass) respond to large wood restoration in the Narraguagus River, Maine. I find that in general, variation in ecological metrics is determined mostly by site identity rather than restoration status, across all three processes. Site-specific differences in restoration response may help to explain the frequency of equivocal outcomes of restoration in the literature, as responses can only be detected when sites are analyzed individually. Restoration in the Narraguagus us not creating the intended effects, possibly because structures are too small and flows too low for wood additions to be effective. Alternatively, site-specific constraints may be limiting restoration response, causing the large among-site differences in restoration effect. Restoration managers should consider constraints at the site level when designing and implementing projects, and consider alternative restoration approaches that could be more effective in specific site contexts.

INTRODUCTION

Ecological restoration is a globally growing field of practice (UN Environment Program 2020; European Comission 2022), research (Palmer et al. 2014; Wortley et al. 2013), and funding interest, garnering billions of dollars yearly in state and federal funding in the US alone (BenDor et al. 2015). Yet restoration outcomes are equivocal, with projects showing few or no detectable results as compared to reference systems or natural regeneration alone in systems including grasslands, forests, and rivers (e.g., Crouzeilles et al. 2017; Seabloom et al. 2003; Tong et al. 2017). Moreover, outcomes are often taxa- or context-specific (Crouzeilles et al. 2016; Lortie et al. 2022; Meli et al. 2014), suggesting that traditional restoration approaches are not effective at rehabilitating ecosystems as a whole.

As a result, many practitioners are focusing restoration efforts on repairing the ecological processes that underlie species or ecosystems of interest, known alternately as process-based (rivers, Beechie et al. 2010) and augmentative (terrestrial, Sheley et al. 2009) restoration frameworks. By improving ecosystem function overall, these methods aim to bring in the ecosystem as a partner in its own restoration, supporting natural systems that can reinforce and sustain themselves. Thus, the benefits of restoring ecosystem function extend beyond the target species, providing greater ecological benefits than structural restoration (Ford 2021) and offering managers a stronger or broader rationale to support their projects (Beechie et al. 2010). Unfortunately, restoration projects rarely use ecological processes as response metrics (Al-Zankana et al. 2020; Kollmann et al. 2016; Ruiz-Jaen and Mitchell Aide 2005)—an essential part of a process-based approach—or examine the ecosystem comprehensively enough to detect such changes (Meli et al. 2014).

Trophic processes, such as primary production, consumption, and the capture of cross-ecosystem subsidies are fundamental to all ecosystems, and are thus make an ideal functional metric to assess restoration (Loch et al. 2020). They give an indication of energy flow within and beyond the project area (Kupilas et al. 2016), connecting biodiversity with ecosystem function (Kollmann et al. 2016; Thompson et al. 2012), and underlie the stability of ecosystems as a whole (Rooney and McCann 2012). Trophic processes also underlie responses of the higher-level consumers that are frequently the nominal targets of restoration (e.g., salmonid fishes, bald eagles, wolves). Because of their fundamental nature in an ecosystem and the existence of established methodology for their measurement, trophic processes are promising tools for estimating the success of process-based restoration (Fraser et al. 2015).

Here I focus on using trophic processes as a measure of process-based restoration outcomes in an in-stream river restoration project in the Narraguagus River of eastern Maine, USA. Rivers worldwide have a long history of degradation due to centuries of use for transporting people, materials, and timber (Young et al. 1994; Erskine and Webb 2003; Reuss 2004; Wohl 2014). Process-based restoration, particularly in the form of wood additions that mimic natural logjams, is a common and well-established tool in river ecosystems (Roni et al. 2015). Process-based approaches often generate more success than traditional restoration techniques (Al-Zankana et al. 2020) and large wood additions are particularly popular for salmonid habitat restoration (Foote et al. 2020). There are two styles of wood additions in this river, which are similar to those applied elsewhere. “Griphoist trees” (“GH”, Chapter 1 figure XX) are riparian trees that have been pulled over into the channel, still connected to the bank by roots but the full tree is able to move as it is pushed by the current. They closely resemble natural treefall, as they retain their branches and leaves. The second structure type is post-assisted log structures (PALS, Chapter 1) that are constructed stacks of logs that are held in place by posts driven two meters into the bed, making them completely unable to move without being washed out entirely. PALS are made of trimmed logs and lack the physical complexity of a naturally fallen tree.

Despite the popularity of wood additions as a restoration tool, their efficacy remains equivocal, with outcomes for physical habitat (de Brouwer et al. 2020; Dolph et al. 2015; Gerhard and Reich 2000), macroinvertebrate taxonomic richness or diversity (Dolph et al. 2015; Entrekin et al. 2009; Gerhard and Reich 2000; Testa et al. 2011; Thompson et al. 2018), and retention of organic matter (Lepori et al. 2006; Wallace et al. 1995) varying across sites and studies. While wood additions are a form of process-based restoration, rarely do researchers monitor indicators of processes linked to ecosystem function such as functional diversity, biomass, or leaf breakdown.

This is an important oversight, as process-focused metrics have been argued as more likely to show a response than general measures of habitat and community (Al-Zankana et al. 2020; Kupilas et al. 2016). Processes such as algal and invertebrate production or leaf breakdown reflect a combination of geomorphic and biotic responses to river restoration. For example, changes in flow resulting from large wood installation can create dynamic patches of scour and fill with different substrate sizes and turnover frequencies (Gerhard and Reich 2000; Montgomery et al. 2003). Ecological theory suggests that the heterogeneous habitat created by large wood structures should beget diverse communities at all levels of the ecosystem, because diverse habitat patches provide niches for a wide range of algal and invertebrate taxa (Winemiller et al. 2010). Similarly, leaf breakdown is influenced by the structure of macroinvertebrate detritivore assemblages, as well as the availability of riparian litter and physical abrasion due to substrate mobilization. Therefore, leaf breakdown represents the output of intertwined physical and biotic processes, making it an excellent metric of general ecosystem function (Young et al. 2008) and one likely to respond to wood addition activities.

Biomass and production are especially important metrics in streams in regions subject to warming water temperatures, as changes in food availability limit or enhance the ability of fish to compensate for rising metabolic costs; this is especially important for coldwater salmonids at their southern range edges where river water temperatures are changing dramatically. In parts of eastern Maine, for example, June water temperatures are rising 2°C per decade, and winter of 2022-2023 was the river’s first recorded ice-free winter at long-term monitoring stations (Craig 2023). Moreover, much research on large wood restoration has focused on the Pacific Northwest (Roni et al. 2002, 2015; Roper et al. 2010; Bennett et al. 2016) or agricultural regions of the Midwest and UK (Dolph et al. 2015; Thompson et al. 2018) while little research has addressed large wood additions in the context of northeastern USA streams and their unique geological and natural history.

This study examines the responses of ecosystem processes to an in-stream wood addition project in the Narraguagus River, Maine. The project was initially designed to improve habitat for Atlantic salmon (*Salmo salar*) but has evolved to consider numerous of Maine's 13 diadromous fish species, making a broad, ecosystem process approach to monitoring especially appropriate. I measured how in-stream large wood restoration affected three ecosystem processes: leaf breakdown, algal production, and production of Atlantic salmon parr prey items, using standing biomass of algae and macroinvertebrates as well-established proxies for production (Morin et al. 1999; Cusson and Bourget 2005). In this project there are two types of wood structures, more mobile griphoist trees (GH) consisting of a riparian tree pulled into the stream and more constructed post-assisted log structures (PALS) made of a stack of limbed logs held in place by posts driven two meters into the bed (Figure 2-1).

Figure 2-1. Examples of griphoist trees ("GH", A) and post-assisted log structures ("PALS", B) from the Narraguagus River

Because large wood is likely to increase heterogeneity, complexity, and suitability of physical habitat for algae and invertebrates, I expected that leaf breakdown rate and algal biomass would be both higher overall and more variable in restored than reference reaches. With a wider variety of food options, I also expected that biomass of macroinvertebrates which make up juvenile salmonid diets will be higher in test sites than in reference sites. Because of physical differences in mobility and complexity between PALS and GH structures, I wanted to test whether they produce different results in the river.

Because of their immobility, focusing their interactions continuously on the same patch over time, I expected PALS structures would have stronger influences on ecosystem processes then griphoist structures.

METHODS

Study site

The Narraguagus River of eastern Maine contains critical habitat for endangered Atlantic salmon (*Salmo* salar) as part of the Downeast Coastal Salmon Habitat Recovery Unit (U.S. Fish and Wildlife Service and National Marine Fisheries Service 2018). It is a small watershed of mixed and evergreen forest, encompassing about 600 square kilometers between its source in Eagle Lake, T34MD, Maine, to its mouth in Cherryfield, Maine (Arter 2003). Rivers in this region were used for driving timber for more than two hundred years, from settlement in the 1700s through about 1970 (See Chapter 3 for more details). The Narraguagus is typically 20-30m wide in its main stem, with a bed comprised predominantly of small boulders and large cobbles, with some areas of sand and gravel often holding rooted vegetation (mostly bayonet rush, *Juncus militaris*). It has naturally tannic waters, circumneutral pH (range 6.3 – 7.4), attains the highest (class AA) Maine DEP water quality classification (Whiting et al. 2008), and water temperatures were typically 15° – 20° C during May sampling. As a salmon-bearing river with reasonably high water quality, the Narraguagus has been the focus of over a decade of restoration work. Currently, there are zero remaining barriers to fish passage, and restoration activities since the 2010s has targeted habitat complexity via additions of large wood.

I chose five griphoist and five PALS sites along the approximately 6.5km of the upper mainstem of the Narraguagus River, from 28 Pond downstream to Bobcat Brook (Figure 2-2). At each structure I subsequently selected a wood-free site of equivalent longitudinal extent just upstream as a reference site. I strategically placed reference sites to be upstream of the test site (range: 1 – 60m) but not directly downstream of the subsequent logjam (distance to next logjam upstream range 2 – 2500m). The spacing among logjams varied across reaches, so I also measured the distance from the upstream boundary of the reference site to the nearest upstream logjam.

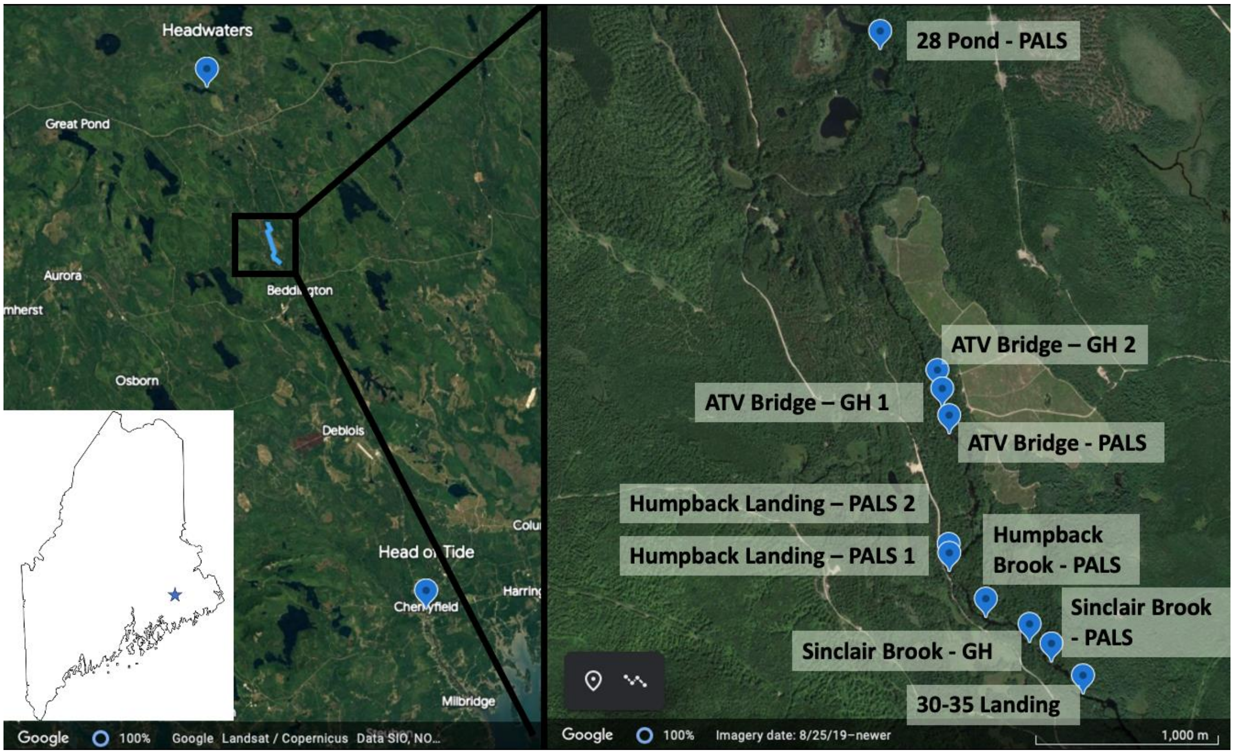

Figure 2-2. A map of the study sites along the Narraguagus River, Maine.

Sampling methods

Sampling design

I placed three cross-river transects equally spaced across each test site, with one transect at where the upstream-most point the structure intersected with the water surface, one at the downstream-most point it intersected with the water surface, and one in the middle. I also established three transects at the reference site, with identical spacing to their paired test site (Figure 2-3, distances A and B). This ensured spacing of transects was consistent within sites but varied among test-reference pairs. Along each transect I took four samples, equally spaced at 20, 40, 60, and 80% of the measured wetted width. I completed all sampling in May-June 2021. Leaf breakdown samples were taken at a subset of 4 locations per test or reference site (one sample per up- and downstream transect and two from the middle, example in Figure 2-3), and they were collected in both June and August 2021 to account for phenological differences in velocity, decomposer activity and availability of alternative food sources (e.g., algae). Leaf sample locations were consistent within test-reference pairs but among pairs.

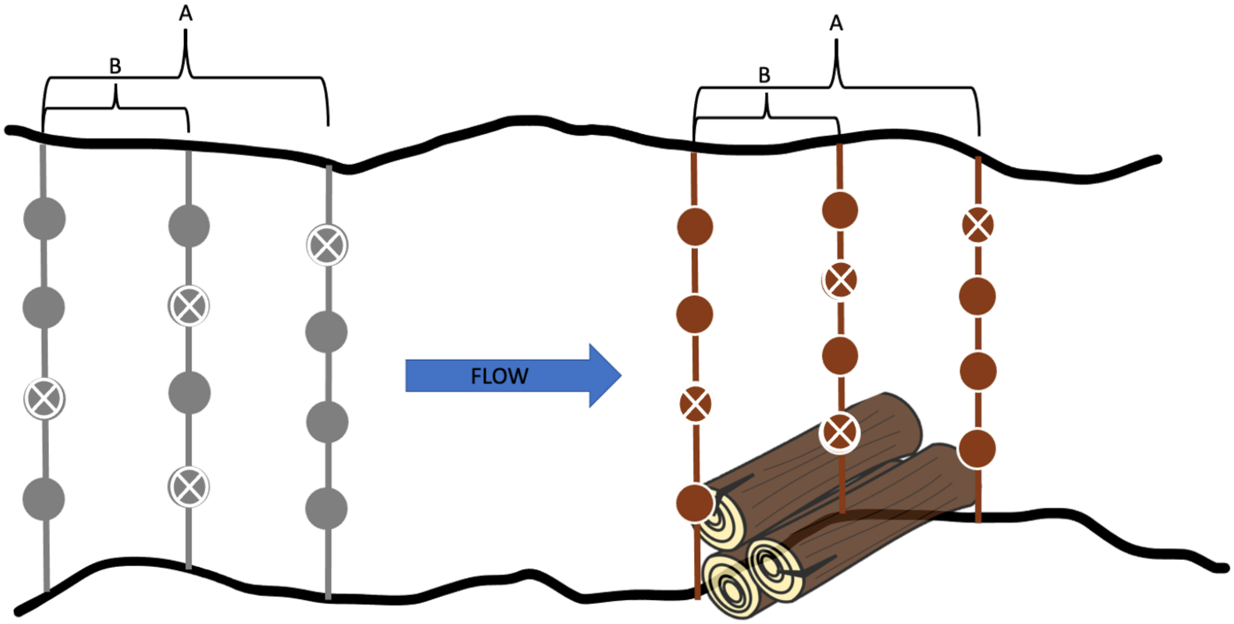

Figure 2-3. Schematic of sampling design at example test-reference site pair.

Test site is marked in brown and the reference site in gray. Water flows from left to right. Lines represent cross-river transects and circles are sampling locations at 20, 40, 60, and 80% of river width. Circles marked with an "X" are example leaf breakdown sampling locations, though exact configuration varies among site pairs. Note that length of test and reference sampling sites (A) as well as distance between transects (B) are equivalent within a test-reference pair but varied from pair to pair according to log structure size

I calculated site area by measuring the length of the center transect and the distance from the downstream to the top transect and multiplying those two values. I measured logjam size by measuring the length of the longest axis of the wood structure and the axis parallel to the first. I then calculated absolute area by multiplying those dimensions, and relative area by dividing logjam area by site area. Logjam age represents years from installation date to sampling date based on project managers' records.

I measured three ecosystem processes: leaf breakdown rate, algal biomass (as a measure of basal resource availability), and biomass of invertebrate prey items of salmon parr. Leaf breakdown rate provides a measurement of consumption of detrital resources, and algal standing biomass gives an indication of algal production, both important metrics of basal resource use and availability. I focused on availability of macroinvertebrate prey items for salmon parr specifically because rapid parr growth can reduce an individual's vulnerability to predation (Stanfield and Jones 2003) and parr size and condition (Rowe et al. 1991; Jonsson et al. 1998) are directly linked to smolt production (i.e., population output from a given river). Here algal and invertebrate standing biomass are surrogates for the actual process of production, which was not measured.

Leaf breakdown sampling

I constructed leaf packs by placing ~10 grams (range = 9.5-10.5) of air-dried red maple (*Acer rubrum*) leaves into nylon mesh bags with 8mm openings, large enough to permit entry by aquatic macroinvertebrates. Leaf packs were deployed at a subset of four randomly selected sampling locations (one each from the end transects and two on the middle) to measure leaf breakdown. I used rebar to secure leaf packs to the stream bed. Leaf bags were deployed twice, with the first round of leaf bags remaining in place for 30 days from mid-June to mid-July and for the same duration from early August to early September, to account for phenological changes in decomposer activity level and life stage, stream flow, and availability of algal food sources (Siebenmann 1995). An additional ten bags in each sampling period were transported and from the field site to account for mass lost through transit and handling.

Upon collection, I immediately placed the leaf pack in a cooler on ice for transport, then transferred to a freezer for storage. In the lab, I rinsed the contents of each leaf pack through a 1.0 mm sieve and discarded all material less than 1.0 mm. I removed all invertebrates, stored them in 70% ethanol, and identified them to genus (or the lowest level of classification possible) using standard taxonomic keys (Peckarsky et al. 1990; Merritt et al. 2008; Wiggins 2014). Leaf material was placed in a 60°C oven to dry for at least 48 hours, then ashed at 550°C oven for two hours to calculate ash-free dry mass (Suberkropp and Chauvet 1995; Hauer and Lamberti 2007; Nuven et al. 2022). Because all leaf packs were deployed for the same number of days, I measured leaf breakdown rate as amount of mass (dry and ash-free) lost over the experimental period. I corrected for mass lost in transport using 10 leaf pack replicates that were brought to the site, installed, then immediately removed and processed.

Algal biomass sampling

At every sampling location I collected a piece of gravel or small cobble (approx. 2-10 cm along longest axis) from the streambed, and immediately placed it in a Whirl-Pak in a dark cooler of ice. Upon returning to the lab, samples were transferred to a black plastic bag in a freezer for storage. I used chlorophyll concentration per unit area of stone as a proxy for algal biomass. In the lab, I added 50 ml of 90% ethanol buffered with magnesium carbonate, enough to completely submerge the stones. I then re-sealed the bags and placed them in a 78° C hot water bath for five minutes to improve cell lysing by boiling the ethanol. Samples were refrigerated overnight (12-18 hours) before measuring absorbance at 664, 665, and 750 nm on a spectrophotometer (Thermo Helios Aquamate). To standardize for rock size, I measured rock surface area using the particle layer method described by Bergey & Getty (2006) and calculated chlorophyll-a concentration per square centimeter of substrate following equations in Hauer and Lamberti (2007).

Salmon parr prey biomass sampling

I used a Surber sampler (30 x 30cm, 243 µm mesh) to collect a quantitative sample of the macroinvertebrate community at each sampling location. Samples were immediately preserved in 70% ethanol. I used 1.0 mm and 500 µm sieves to separate samples into a coarse and fine section and removed all invertebrates using a dissecting microscope. I subsampled $^{1}/_{16}$ to ½ of the fine material when samples had too much fine material to process in a two-hour session. Invertebrates were stored in 70% ethanol and identified to genus or the lowest level of classification possible using standard taxonomic keys (Peckarsky et al. 1990; Merritt et al. 2008; Wiggins 2014).

To quantify biomass of available salmon food items (Appendix 1), I separated all invertebrates described in the literature as primary food sources for salmon parr (Grader and Letcher 2006; Ojala 2008). This included Simuliidae and Chironomidae (Diptera); Baetidae, Ephemerellidae, and Heptageniidae (Ephemeroptera); and Glossosomatidae, Helicopsychidae, Hydropsychidae, and Rhyacophilidae (Trichoptera). I assigned each individual to a body size bin (<1.0mm, 1.0 – 5.0 mm, 5.0 – 10.0 mm, 10.0 – 15.0 mm, 15.0 – 20.0 mm) and applied published length-mass regressions (Benke et al. 1999) to the mean value of each bin to estimate total invertebrate biomass. For these calculations, all Ephemeroptera were assigned to the order-level equation and Diptera and Trichoptera to family-level equations because of differences in body shape across families.

Physical habitat sampling

At all sampling locations I collected additional physical habitat data including depth, velocity, and substrate cover. Depth was recorded to the nearest centimeter at the bed location directly below the sampling location mark on a cross-river transect tape. Velocity was taken at $^{2}/_{3}$ depth from water's surface and recorded to the nearest 0.01m/s using a Marsh-McBirney FlowMate velocity meter. Substrate cover data was initially recorded as percent cover of Wentworth substrate classes (sand-boulder), then transformed into a single-value substrate index that accounts for relative cover of each substrate class following Jowett et. al. (1991). This calculation considers fine and coarse gravel separately, which my data did not, so I assumed gravel areas were equally split between fine and coarse gravel and made calculations accordingly. This assumption is supported by visual assessment in the field.

Statistical analyses

I used paired t-tests to assess whether means and variation (measured as coefficient of variation) of ecosystem processes (including leaf breakdown rate, algal biomass, and salmon prey biomass) differed between paired test and reference sites. Variables were untransformed prior to the calculation of means and CV, and no transformations were necessary for paired t-tests. To test for site-specific patterns, I used ANOVAs comparing ecological metrics to factors of site identity, restoration treatment (restored or reference), and the interaction of the two using each unique sample as a replicate. I then used linear models to evaluate the relationship between site characteristics such as logjam size and age with the effect size in ecosystem processes at each site, to test potential drivers of site-specific differences. All analyses were performed in Program R (R Core Team 2022) on untransformed data.

RESULTS

I found no significant differences ($p \geq 0.11$, $t < 1.80$, Table 2-1) in means or coefficients of variation between test and reference for any metrics of ecosystem processes (paired t-tests, paired by site). I followed up with ANOVAs testing whether site, treatment, or their interaction predicted metrics of ecosystem processes. In general, site was a much stronger predictor than treatment or their interaction (Table 2-2). Site also significantly altered the effect of treatment on algal biomass in May (treatment x site interaction, $p < 0.05$) and leaf breakdown rate in July ($p < 0.01$), demonstrated by the fact that restored-reference differences were not consistent in direction or magnitude from site to site

(Figure 2-4, Figure 2-5). For example, mean algal biomass was much higher in the restored than the reference site at 28 Pond in May, but reference algal biomass was higher than restored at 30-35 Landing in May (Figure 2-4A). Similarly, leaf breakdown rate in July at 28 Pond was higher at the restored than the reference site, while the opposite was true at Humpback Landing – PALS 1 (Figure 2-5B). Parr food biomass was only significantly related to site (Figure 2-6).

Table 2-1. Summary of statistics for all paired t-tests comparing restored to upstream reference sites. Values are rounded to nearest 0.01.

Variable	**Response Metric**	**p value**	**T statistic**	**Restored mean**	**Reference mean**
Leaf breakdown rate (May)	Mean	0.26	1.20	0.13 g/day	0.14 g/day
	Coefficient of variation	0.47	-0.75	0.08	0.07
Leaf breakdown rate (July)	Mean	0.26	1.20	0.15 g/day	0.14 g/day
	Coefficient of variation	0.11	-1.80	0.11	0.08
Algal biomass (May)	Mean	0.64	0.49	0.98 μg/cm^2	1.06 μg/cm^2
	Coefficient of variation	0.75	0.33	0.68	0.72
Algal biomass (July)	Mean	0.78	0.29	1.12 μg/cm^2	1.64 μg/cm^2
	Coefficient of variation	0.26	1.20	0.73	0.92
Parr food biomass (May)	Mean	0.53	-0.78	233.31 mg/m^2	219.24 mg/m^2
	Coefficient of variation	0.36	-0.96	0.87	0.79

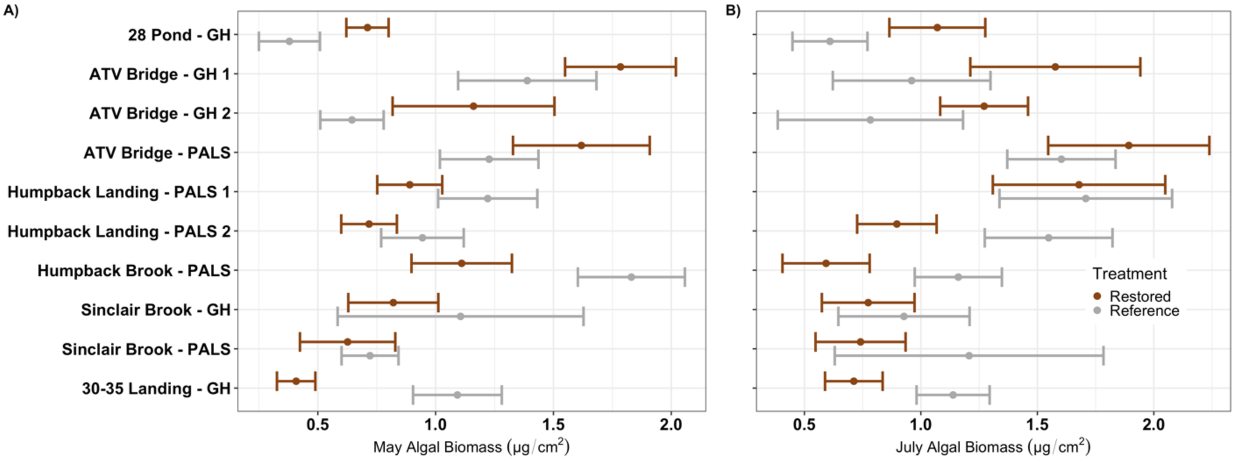

Figure 2-4. Mean algal biomass in A) May and B) July of 2021 10 test and reference site pairs of the Narraguagus River. Site (ANOVA $p < 0.001$) and the site x treatment interaction (ANOVA, $p < 0.05$) was significant in May, and only site was significant in July (ANOVA, $p < 0.01$). Bars show mean ± 1 SE.

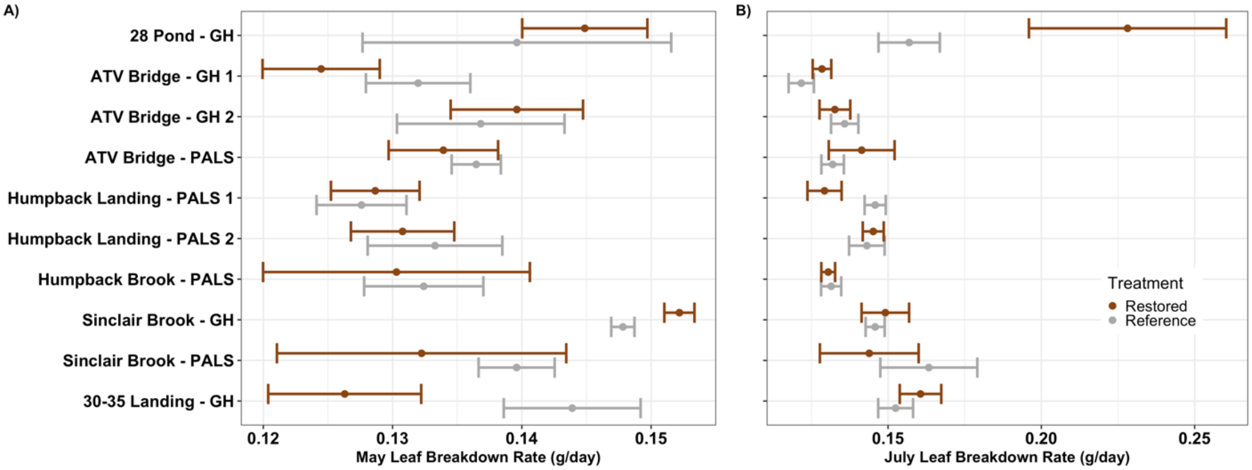

Figure 2-5. Mean leaf breakdown rate in A) May and B) July of 2021 in 10 test and reference site pairs in the Narraguagus River. Site was significant in May (ANOVA, $p < 0.05$) and both site (ANOVA $p < 0.001$) and the site x treatment interaction (ANOVA, $p < 0.01$) were significant in July. Bars show mean ± 1 SE.

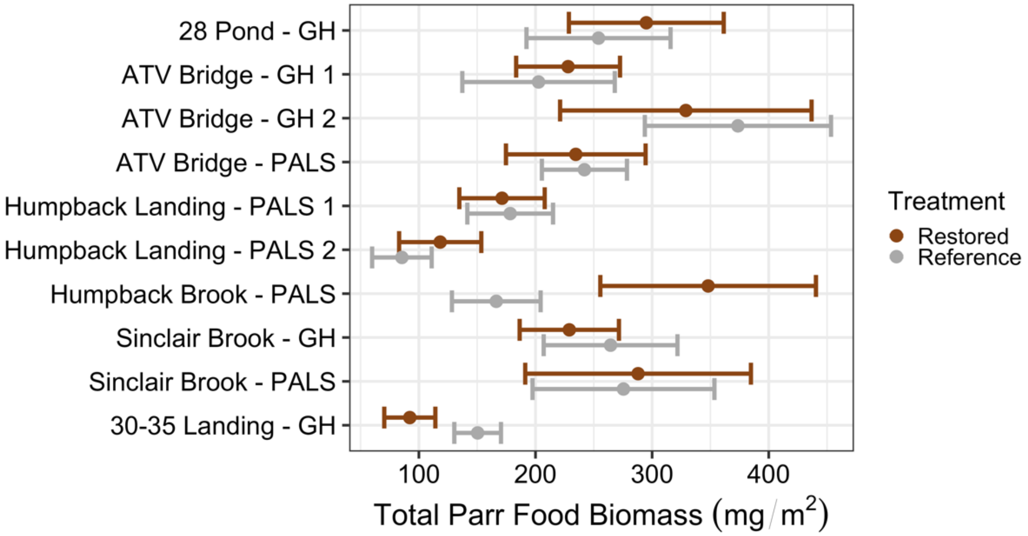

Figure 2-6. Mean parr food biomass (mg per m2 ±1 SE) in May 2021 in in 10 test-reference site pairs in the Narraguagus River. Site was significant (ANOVA, p = 0.001). Bars show mean ± 1 SE.

Table 2-2. Summary of statistics for ANOVAs including restoration status, site identity and their interaction as fixed factors. Significant p-values are bolded and italicized.

Variable	Fixed effects										
	Restoration Status				Site ID				Restoration Status*Site ID		
	DF	F	p		DF	F	p		DF	F	
Leaf breakdown rate (May)	1	1.07	0.305		9	2.57	***0.015***		9	0.69	0.718
Leaf breakdown rate (July)	1	1.77	0.189		9	6.99	***7.95 e -07***		9	2.96	***0.006***
Algal biomass (May)	1	0.38	0.537		9	5.48	***9.52 e -07***		9	2.22	***0.022***
Algal biomass (July)	1	0.10	0.754		9	2.88	***0.003***		9	1.43	0.178
Parr food biomass (May)	1	0.22	0.641		9	3.23	***0.001***		9	0.63	0.771

I performed a second set of ANOVAs testing whether structure type (griphoist vs PALS), treatment, and their interaction predicted ecosystem process metrics (Table 2-3). In these analyses, algal biomass had a significant relationship ($p < 0.05$) with structure type in July, with higher biomass in reference than test sites treated with PALS, but the opposite pattern in GH sites (Figure 2-7B). Algal biomass had no relationship with either predictor in May. Leaf breakdown rate was related to structure type in May ($p < 0.05$) and marginally related to both structure type and its interaction with site ($p < 0.1$ for both) in July. In May, leaf breakdown was higher at GH than PALS sites, while in July restored sites in GH sites had the highest breakdown rates (Figure 2-7C-D). Biomass of invertebrate foods of salmon parr in May was not related to any of my predictors (ANOVA, $p>0.23$, Figure 2-8).

Table 2-3. Summary of statistics for ANOVAs examining the influence of restoration status, structure type (GH vs PALS), and their interaction on ecosystem processes.

Significant p-values are bolded and italicized.

Metric	Fixed effects										
	Restoration Status				Structure Type				Structure Type* Restoration Status		
	DF	F	p		DF	F	p		DF	F	p
Leaf breakdown rate (May)	1	0.97	0.328		1	4.99	***0.029***		1	0.45	0.505
Leaf breakdown rate (July)	1	0.97	0.328		1	2.94	0.091		1	3.27	0.075
Algal biomass (May)	1	0.31	0.577		1	1.77	0.184		1	1.32	0.252
Algal biomass (July)	1	0.09	0.760		1	6.35	***0.012***		1	3.61	0.059
Parr food biomass (May)	1	0.20	0.652		1	1.44	0.232		1	0.97	0.326

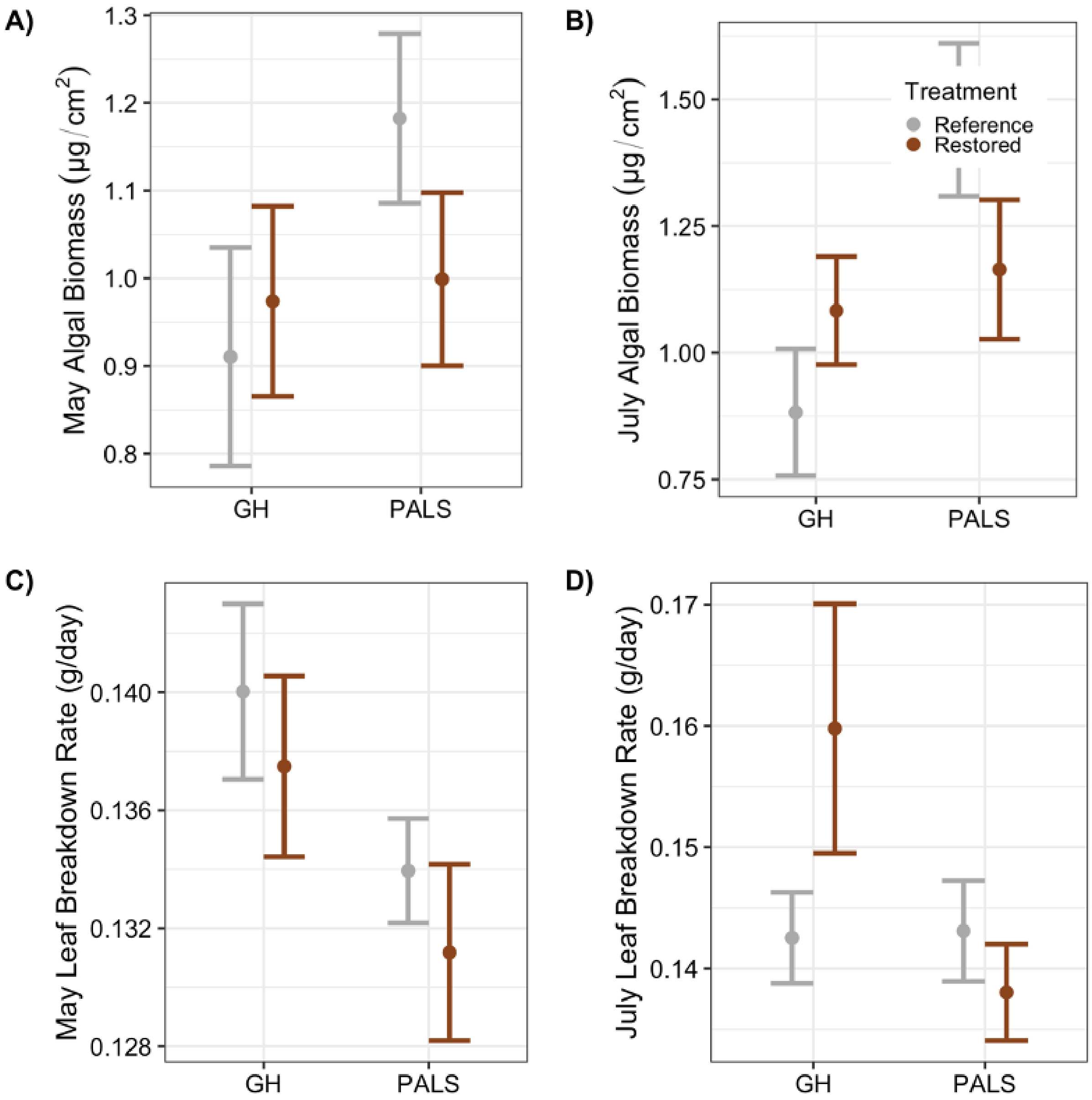

Figure 2-7. Differences in algal biomass and leaf breakdown rates between griphoist and PALS sites, in the Narraguagus River, May and July 2021.

Mean algal biomass in A) May and B) July of 2021, with mean leaf breakdown rate in C) May and D) July of 2021 in restored and reference treatments by two restoration structure types in the Narraguagus River. Structure type was significant for May leaf breakdown rate and July algal biomass (ANOVA $p < 0.05$). Structure type x treatment interaction was marginally significant for leaf breakdown rate in July (ANOVA $p = 0.075$) and for algal biomass in July (ANOVA $p = 0.059$). Bars show mean ± 1 SE.

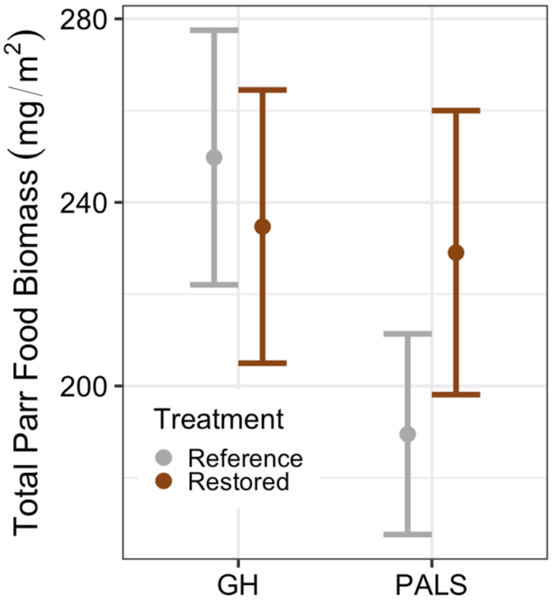

Figure 2-8. Differences salmon parr prey biomass between griphoist and PALS sites in the Narraguagus River, May 2021.

Structure type, treatment, and their interaction were all not significant (ANOVA $p > 0.23$). Bars show mean ± 1 SE.

Because so many variables had site-specific responses, I used linear models to test whether any specific site characteristics predicted ecosystem process response, by regressing effect size (site-specific difference in means between treatments) against site characteristics describing logjam dimensions, age, and concentration. Site-specific characteristics, including log structure length, width, area, area proportional to the stream, age, reach slope, and proximity to upstream structures poorly predicted responses to restoration, in terms of both means and variation (linear model $F<3.18$, $p>0.11$). I also looked for patterns at larger regional scales by regressing site means and coefficients of variation against the count of structures in the 50 and 100 meters upstream of a site. I found no patterns ($p> 0.25$, $F<1.37$).

DISCUSSION

I found no significant differences in mean or coefficient of variation in leaf breakdown rate, algal biomass, or macroinvertebrate biomass between restored and reference sites, contrary to my hypotheses. While restoration had no generalizable effects, there were some differences between restored and reference sites at individual sites for all three ecosystem processes I measured, but these differences were not consistent from site to site. This is consistent with numerous studies that found equivocal or site-specific responses of basal resources, macroinvertebrate communities, and stream bottom substrate to in-stream restoration projects (Palmer et al. 2010; Al-Zankana et al. 2020). However, my findings contradict the suggestion made by some authors (e.g., Al-Zankana et al. 2020) that ecosystem processes may show stronger and more consistent responses than community, population or habitat metrics (e.g., macroinvertebrate abundance, physical habitat characteristics) more commonly measured. Thus, even ecosystem processes may not respond strongly or consistently to restoration actions, and instead, baseline characteristics describing the local site where structures are placed may be more important in constraining restoration success.

It is interesting that wood additions produced different or even opposite results from one site to the next, as this suggests log structures are interacting differently with water and substrate at different locations. If working as expected, wood structures change the direction and intensity of flow by diverting water aside or forcing it into a smaller channel. Especially during high flows, that water is then more able to do its work of scour and fill, creating and disturbing substate patches by mobilizing sediment and depositing it in new locations (Montgomery et al. 2003). These patches of different disturbance history and substrate composition are colonized by different assemblages of algal and macroinvertebrate taxa with their own inherent levels of productivity (Palmer et al. 2000), so a restored site should be highly heterogeneous. Similarly, these patches would experience different velocities, physical abrasion, invertebrate activity, and natural leaf accumulation (de Brouwer et al. 2020), leading to heterogeneity in breakdown rate of added leaf packs (Young et al. 2008). Each of these variables (e.g., detritus accumulation, velocity, and invertebrate community) may respond differently to wood additions, obscuring the overall signal of restoration at a sampling location.

It follows that larger structures in sites with sediment that is not deeply embedded might be more effective, because they affect a larger proportion of flow and sediment is more able to be mobilized. It is possible that log structures simply did not have enough time or were too small to make significant ecosystem changes by the time of my study. Compared to historic wood inputs prior to colonization, which were likely comprised of old-growth trees wood additions in this project were very small (<0.5m diameter), so it is perhaps not surprising that they had limited impact in this system. Log structures in the Narraguagus have been in place for four years or less, several of which were drought years, giving them very little time and high flows to work with in creating physical and ecological changes. They also had difficult material to work with, as much of the streambed is highly embedded and immobile due to historic log drives. Visual assessment supports the existence of scattered localized responses in the form of small (<1m) scour pools, but no broader influence on the site was detectable. While my previous chapter demonstrated the presence of reach-level effects, the number of structures in the 50-100 m above a site was not a significant predictor of any of these ecosystem processes. This contrasts with responses observed for macroinvertebrate metrics, particularly detritivores, which had increasing richness and abundance with increasing number of structures directly upstream (Chapter 1). This is contrary to expectation because processes are interactions among ecological components including macroinvertebrates, embedded in that larger regional context. Regional effects of restoration may differ for metrics at different levels of ecological complexity.

It is possible that generalized responses to restoration activities simply take longer than the period of this project to emerge. Looking lower in the ecosystem, metrics of physical habitat including velocity, depth, and substrate had no generalizable responses to restoration, though such abiotic metrics did show stronger responses when accounting for site-by-site differences (see Chapter 1). Algal biomass and detritus availability, in turn, showed moderate site-by-site responses, while macroinvertebrate communities showed the weakest responses. This may support the hypothesis that logjam age is important, as restoration effects seem to be propagating up the food web, and that process takes time. This sort of lag in restoration effect is likely common across systems (e.g., Wortley et al. 2013; Griffith and McManus 2020; Gilby et al. 2021), as responses propagate through the ecosystem, and managers should consider this phenomenon when planning project monitoring.

My results also indicate some phenological differences in the strength of site by treatment interactions, where sites responses differed between July and May. The Narraguagus is a wide, shallow, and dark-watered river, so the primary ecological differences between spring and summer are in water depth, velocity, and temperature. May flows are high and dominated by snowmelt, so they are cooler, while by July water levels have dropped and the channel has warmed with summer heat (Craig 2023). Under warmer and dryer conditions differences between sites are increased, as shallower sites warm in the sun and acquire dry patches, while deeper sites remain watered and retain possible cooling groundwater influence. Under these conditions, differences in algal and invertebrate communities will also increase, and sites may move toward or away from particular organisms' thermal tolerances, altering both their communities and their ecological interactions (e.g., leaf breakdown). In addition, the specific organisms present change through the season, as late-instar macroinvertebrates remain in the river in May, while by July these individuals have emerged and been replaced by small, recently hatched individuals. These different instars likely have different habitat, dietary, and metabolic requirements (Holomuzki and Short 1990; Lancaster and Robertson 1995), resulting in a changing distribution through the season. Similar phenological patterns exist across systems and organism life-histories, so seasonal differences in the outcome (or metrics of success) of restoration is likely a common phenomenon across ecosystems.

It is important to acknowledge that biomass is an imperfect proxy for production because it only measures a single point in time and does not account for turnover. Standing biomass measurements of algae and invertebrates cannot differentiate between a standing stock that is composed of the same individuals through time and one with rapid and continuous turnover of individuals due to consumption or immigration and emigration (Biggs 1996). Restored sites may have more frequent bed movement and scour than sites without logs (Montgomery et al. 2003), resulting in fluctuations in biomass as algae and invertebrate populations are removed, substrate is recolonized, and individuals regrow. Early in the recolonization process, production is high and biomass low as small-bodied, fast-growing diatoms dominate. Later on, larger, slower-growing filamentous diatoms and green algae take over, creating a higher-biomass, lower-production community (Biggs 1996). Similar patterns exist in macroinvertebrate communities, where variation in factors such as feeding guild, life cycle traits, and taxonomic diversity determine production in a patch (Cusson and Bourget 2005; Clare et al. 2022). A biomass measurement captures only a single snapshot of that cycle and obscures the volume of production actually contributing to the food web via consumption. Nevertheless, primary and secondary standing stock biomass is often correlated to production and likely reflects coarse differences in production between sites (Morin et al. 1999; Cusson and Bourget 2005).

Regardless of these imperfect metrics of ecosystem production, my study indicates that site-specific responses are possible for multiple metrics of ecosystem response, which could explain the largely equivocal responses to restoration found across the literature (e.g., Nilsson et al. 2015; Theodoropoulos et al. 2020). Differing or opposite site-specific responses would obscure overall patterns, which means the common assessment strategy of looking for responses across multiple replicate sites overlooks the details of restoration response, potentially making an incorrect conclusion that restoration has done nothing. This is exactly what happened in my study: when all sites were analyzed together, restoration seemed to have no effect. It was not until sites were analyzed individuals that responses could be detected.

This predominance of site-specific responses and lack of any generalizable effect on ecological means and variation indicates that restoration may not create the widespread environmental heterogeneity intended by practitioners. It is well-accepted that restoration projects are constrained by large-scale environmental limitations (e.g., ongoing human impact to a watershed or climate change pushing a region beyond species' tolerances, Beechie et al. 2010; Theodoropoulos et al. 2020), but my study suggests this perspective needs to be applied to finer-scale site selection as well. For restoration practitioners to maximize ecological return on restoration investment requires a deeper understanding of the ultimate drivers of restoration response. Ecological responses are also generated by a combination of direct and indirect effects mediated by other responses (e.g., grazing pressure by herbivores can be directly altered by predator presence or indirectly by substrate size which determines refuge availability Albariño et al. 2022). Analyses such as structural equation models could be useful tools for disentangling the direct and indirect drivers of site-level response.

In some cases, stream degradation may be so severe, occurring at the full valley scale and separating the river from its floodplain, that it constrains the potential for restoration to work. It is notable that despite some site-specific responses, most metrics at most of my study sites had no response to restoration, which indicates a larger failure of wood additions of this size to generate large-scale ecological change. In this case, a process-based approach was not sufficient to overcome site- or larger-scale constraints. Emerging restoration approaches such as the stage-0 stream evolution model (Cluer and Thorne 2014) could account for the lack of response: in this model the Narraguagus would likely be in the earlier stages, possibly the stage 3s “zombie river,” too incised in its bed and disconnected from its floodplain to recover without significant physical modification. Substrate embeddedness is particularly important in this scenario, as loss of mobile sediment constrains the ability of large wood to do any work on the bed even during high flows (Montgomery et al. 2003). Stage-0 restoration takes a valley-scale approach, focusing on raising the bed level to reconnect the river to its floodplain and raise the water table back to pre-incision levels (Cluer and Thorne 2014). The Narraguagus will soon be evaluated for its potential for highly intensive stage-0 work, but it is unique as one of the first east coast sites to undergo such an evaluation. It is worth considering in restoration projects whether traditional approaches to restoration are sufficient to overcome the ecological inertia evident in “zombie rivers” and their equivalents across ecosystems. If not, a larger scale and more intensive approach may be needed.

For restoration managers planning new projects or monitoring old ones, this study brings up some important considerations. Most obviously, it is important to consider factors that might limit restoration efficacy at the site level along with larger scale constraints. Doing so will aid in maximizing ecological return on restoration investment. Second, it is important to measure multiple metrics of ecosystem response, as each of my metrics alone tell a different story at the site level. But even processes, previously proposed to be the most sensitive metrics of restoration success, may not show any pattern. It is useful to collect pre-restoration data (not done in this project) to increase confidence in any pattern (or lack thereof) revealed by future monitoring. In the case that no responses are found, it is worth considering other restoration frameworks, such as stage-0 in the case of streams, to determine which is most appropriate for the site and its context.

CHAPTER 3: IMPLICATIONS FOR RESTORATION PROFESSIONALS

ABSTRACT

Rivers in the northeastern United States and many other forested regions of North America have a long history of log drives by European settler states, in some cases lasting over 200 years. This history sets the context for river restoration practitioners today, and it influences how restoration monitoring studies such as this one should be interpreted. This project has potential implications for how restoration should be conducted moving forward, including in the planning, implementation, and monitoring stages. In addition, the overall lack of predictable outcomes of restoration described in the previous two chapters suggests practitioners should keep other approaches and frameworks in mind.

A BRIEF HISTORY OF LOG DRIVES IN EASTERN MAINE AND BEYOND

To set some context for large wood as a restoration tool, I want to provide some history on the historic and widespread degradation of rivers by the practice of log driving in Maine and elsewhere. As European colonists settled new areas, one of their first tasks was often to begin harvesting timber (Whitney 1994). Rivers were used to transport this timber, as well as people and materials, so settlers used draft animals and dynamite to remove physical obstacles (e.g., large rocks or bedrock outcrops, logjams) and straighten channels (Young et al. 1994; Reuss 2004). Rivers were also cleared to protect infrastructure from flooding and erosion (Erskine and Webb 2003). This clearing of natural complexity resulted in extreme physical and ecological simplification and channelization of rivers around the world (Wohl 2014).

This story is also true in Maine, including the smaller rivers of eastern Maine, where timber harvesting began soon after European settlement. For example, the January 30, 1883 Machias Union newspaper documented active harvesting operations in the entire Machias River watershed (1883), and it is reasonable to assume that similarly comprehensive logging occurred in nearby watersheds in the same era. Veteran log driver Richard Gaddis described the extent of modifications as follows: “They’d done a lot of work on it (the river). In other words, they’d gone up in the summer, and they’d blow rocks out of it, and they cut the sweepers… And they built some crib work where they wanted to turn the water in a place” (Gaddis and Ives 1986). The Machias River was heavily modified using dynamite, bank armoring, and logjam removal, which Gaddis interprets as typical tools for the trade.

Driver Frank Dowling, who began working on the Machias as a teenager in 1908, reflected on stories from his old-timer colleagues: “When this river was first used, it must have been… bothered by hundreds of trees, which had been uprooted by water and toppled into it, to beat here and there until the brush, the trunk, with its roots, were all that was left… in places there would be a hundred feet or more wide strip of this trash to impede the drive, bothering the passage of logs” (Dowling and Ives 1986). What Dowling imagines is what the river looked like before log drives, and what rivers should look like today. It would be a significant challenge, though, to find a modern river that is so full of physical complexity, and this is why restoration remains a large important project for rivers in Maine and beyond.

IMPLICATIONS OF THIS PROJECT FOR MANAGEMENT DECISIONS

The goal of this project was to assess common community- and process-based responses to river restoration in the Narraguagus River across multiple spatial scales. I found few generalizable responses to restoration across sites. Instead, sites are highly unique in their ecological communities, both before and after restoration. In some cases, site characteristics or structure type modify restoration response, with some sites showing increases and others decreases relative to unrestored areas in various measures of ecological function and macroinvertebrate community composition. In others there is no obvious signal of restoration at all. Finally, the concentration of restoration structures in a reach seems to matter more than restoration status of a given site for more mobile parts of the ecosystem, including macroinvertebrates and fine detritus (an important food resource of many insects). These patterns lead me to some general considerations for restoration managers, some applicable across systems and others to streams only:

Consider conditions limiting or enhancing restoration response at multiple scales.

It is common to consider large (e.g., watershed) scale conditions that might limit a site's potential to be restored. For example, it is impossible to restore high-quality salmonid spawning and rearing habitat in a segment of river that has a dam or levee, at least until that structure is removed. My results indicate that similar limits exist at the site level. It is unclear what exactly limited the responses of particular sites in my study, but factors such as substrate type and embeddedness, velocity, and existence of remnant log drive structures all should be considered when choosing a project site. On the other hand, having many structures in one area seems to have a stronger ecological effect than the same number of structures widely dispersed, as the intensity of restoration in a reach seems to become a primary driver over local scale responses. To maximize return on investment, it may be productive to creating many less sturdy (i.e., griphoist) structures rather than a few well-anchored (i.e., PALS) structures.

Consider monitoring restoration at multiple scales.

Despite the intensive sampling, my study failed to detect very small-scale (< 1m) responses such as small scour pools directly adjacent to log structures that could be observed visually. While small, these structures may also be disproportionately important to salmonid fishes as they provide excellent spawning and rearing habitat. Monitoring should be structured to measure responses at this very local scale as well, especially if managers are interested in salmonid fishes. In addition, the Narraguagus has been the target of restoration for many years, and as a result there are reaches that contain a nearly constant sequence of log structures, alternating from one bank to the other. Especially in this situation, when restoration effort is intense, it is possible for the intensity of restoration in a reach to become a primary driver over any responses at an individual site. Instead, restoration could be defined on a spectrum of intensity rather thana binary of restored vs non-restored.

Try to collect baseline data *prior* to implementing restoration projects.

Like the previous point, it is difficult to detect restoration responses when most of the river has been altered – there are simply no sites that can be confidently described as "unrestored." The ideal way to solve this problem is to collect data prior to restoration. This way you can be sure that you have a solid understanding of non-restored conditions, and you'll be more likely to detect results (and be confident in them). Alternatively, measuring an unrestored control stream at the same two times (before and after restoration of the restored stream) can provide baseline data to improve confidence in conclusions.

Try to continue monitoring for several years post-restoration.

Restoration can take some time to have any effect, especially if it happens in low-flow years that give the newly built structures very little water to work with. It is ideal to monitor intermittently for several years post-restoration to understand how the projects work over time.

Structure type seems to matter.

This is intuitive, but structures that are physically complex seem to be better at collecting detritus, thus forming habitat and food supply for macroinvertebrates and possibly enriching algal growth with added nutrients. If this is an important project goal, griphoist trees may be ideal for a project. On the other hand (we did not test this), PALS may be better for influencing velocity and bed scour because of their physical sturdiness and anchoring to one place.

Consider alternative restoration frameworks.

So far, my discussion of restoration effects (or lack thereof) has taken the optimistic view that restoration is doing important work, it's just difficult to detect. However, it is also important to consider that there is a very real lack of response, and this method of wood additions is not working well in this system. In this case, we need to consider other models. Two examples are Stage-0 and Resist-Accept-Direct (RAD, Thompson et al. 2021). Stage-0 restoration is an emerging method specifically for low-gradient stream segments that takes a full-valley approach to reconnect the river to its floodplain (Cluer and Thorne 2014). It is a dramatic and intensive approach, but there is growing evidence it is highly and rapidly effective in low-gradient settings, and managers of low-gradient streams should keep aware of developments in that area. Importantly, there are tools available to assess a given stream for its suitability to a Stage-0 approach (Powers et al. 2018) to test for suitability without the expenditure of test projects.

RAD is more a philosophy of prioritization than a methodology, and it works nicely with my earlier considerations. RAD accepts the fact that some sites are simply not possible to restore, especially in the context of global changes such as rising water temperatures that managers cannot address on their own (Thompson et al. 2021). This is especially useful in the situation that restoration managers eternally find themselves in: limited funding and people power, and a lifetime's worth of potential projects. In this framework, managers choose to resist, accept, or direct ecosystem change at a site based on their ultimate goals and site constraints. For example, managers working on salmon streams at the southern extent of their range (i.e., Maine) might choose to prioritize reconnecting cooling groundwater springs in areas that have high-quality spawning habitat or existing stable salmon populations (resist), abandon the southern-most sites (accept), and try to incorporate genes from heat-tolerant southern populations in northern rivers (direct).

CONCLUSION

It is important for restoration practitioners to consider the changes they expect or want to see produced by their projects as well as the limitations that might prevent a desired response from the site to the ecosystem scale. In addition, monitoring should be designed to maximize confidence in results, i.e., having a true pre-restoration or unrestored reference site along with data collected at several time intervals post-restoration in both the reference and restored sites. Realizing this list of recommendations could require an unrealistic level of labor and financial investment, having a true control should be a top priority, as it dramatically increases confidence in interpretation of results. Project design, implementation, and monitoring should all be done with the understanding that restoration projects near one another can have cumulative effects beyond the impacts of an individual project, and so data such as project proximity, size, and age is important and relatively simple to track if done from the project's start. Thinking through these considerations from the very inception of a project is essential, as building them into project design makes execution simpler and more cost-effective than trying to reformat things later on. Finally, managers should keep abreast of developments in other restoration approaches such as Resist-Accept-Direct and Stage-0, the former being applicable to all systems and the latter to stream valleys only.

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APPENDIX 1: RESPONSES OF DETRITUS AND PHYSICAL HABITAT TO RESTORATION

Table 3-1. Summary of statistics for t-tests on all metrics of physical environment and detrital resources. Significant p-values are italicized and bolded.

Variable	Response Metric	P value	T statistic	Restored mean	Reference mean
May velocity	Mean	0.051	-2.25	0.266 m/s	0.204 m/s
	Coefficient of variation	0.768	-0.30	0.639	0.614
July velocity	Mean	0.231	-1.28	0.220 m/s	0.184 m/s
	Coefficient of variation	0.855	-0.19	0.653	0.639
May depth	Mean	0.311	-1.07	39.37 cm	44.73 cm
	Coefficient of variation	0.746	-0.33	0.347	0.331
July depth	Mean	0.135	1.64	38.04 cm	45.96 cm
	Coefficient of variation	0.589	0.56	0.303	0.328
May percent cover aquatic vegetation	Mean	0.346	1.00	24.21%	32.71%
	Coefficient of variation	0.444	-0.80	1.793	1.489
July percent cover aquatic vegetation	Mean	0.483	0.73	26.92%	32.83%
	Coefficient of variation	0.531	-0.65	1.58	1.39
May substrate index	Mean	0.894	-0.14	4.47	4.45
	Coefficient of variation	0.585	0.57	0.163	0.178
July substrate index	Mean	0.614	-0.52	4.55	4.45
	Coefficient of variation	0.405	0.87	0.149	0.168
May ash-free dry mass fine particle organic matter	Mean	0.565	-0.60	0.29 g	0.27 g
	Coefficient of variation	0.943	0.07	1.126	1.134
May ash-free dry mass coarse particle organic matter	Mean	0.542	-0.63	3.27 g	2.88 g
	Coefficient of variation	0.716	-0.38	1.161	1.552

Table 3-2. Summary of statistics for ANOVAs including restoration status, site identity and their interaction as fixed factors, for measures of the physical environment and detrital resources

Significant p-values are bolded and italicized.

Variable	ANOVA fixed effects								
	Restoration Status			Site ID			Restoration Status* Site ID		
	df	F	p	df	F	p	df	F	p
May velocity	1	10.17	***0.002***	9	7.44	***1.76 e-09***	9	2.00	***0.040***
July velocity	1	4.24	***0.041***	9	4.14	***6 e-05***	9	2.57	***0.008***
May depth	1	8.20	***0.005***	9	25.26	***<2 e-16***	9	7.13	***4.74 e-09***
July depth	1	20.55	***9.54 e-06***	9	24.55	***<2 e-16***	9	7.62	***1.01 e-09***
May percent cover aquatic vegetation	1	4.04	***0.046***	9	8.70	***3.72 e-11***	9	4.08	***7.35 e-05***
July percent cover aquatic vegetation	1	1.86	0.174	9	8.33	***1.15 e-10***	9	3.48	***0.0005***
May substrate index	1	0.06	0.808	9	12.11	***1.79 e-15***	9	2.09	***0.032***
July substrate index	1	1.00	0.318	9	16.37	***<2 e-16***	9	3.67	***0.0003***
May ash-free dry mass fine particle organic matter	1	0.16	0.686	9	3.97	***0.0001***	9	0.35	0.957
May ash-free dry mass coarse particle organic matter	1	0.32	0.632	99	1.44	0.174	9	0.62	0.784

Table 3-3. Summary of statistics for ANOVAs including restoration status, structure type (GH vs PALS) and their interaction as fixed factors, for measures of the physical environment and detrital resources.

Significant p-values are bolded and italicized.

Variable	ANOVA fixed effects										
	Restoration Status				Structure Type				Restoration Status* Structure Type		
	df	F	p		df	F	p		df	F	p
May velocity	1	8.20	***0.005***		1	7.34	***0.007***		1	2.63	0.106
July velocity	1	3.60	0.059		1	0.26	0.614		1	1.76	0.186
May depth	1	3.95	***0.047***		1	5.01	***0.026***		1	7.34	***0.007***
July depth	1	9.79	***0.002***		1	0.36	0.549		1	3.40	***0.012***
May percent cover aquatic vegetation	1	2.98	0.086		1	2.86	0.092		1	7.98	***0.005***
July percent cover aquatic vegetation	1	1.39	0.239		1	3.05	0.082		1	5.66	***0.018***
May substrate index	1	0.04	0.840		1	4.76	***0.030***		1	0.21	0.650
July substrate index	1	0.60	0.439		1	4.59	***0.033***		1	0.06	0.805
May ash-free dry mass fine particle organic matter	1	0.15	0.696		1	7.25	***0.008***		1	0.18	0.677
May ash-free dry mass coarse particle organic matter	1	0.23	0.633		1	0.55	0.459		1	0.45	0.505

Table 3-4. Summary of statistics for linear models including number of structures in either 50m or 100m upstream from sampling site, for measures of the physical environment and detrital resources.

Significant p-values are bolded and italicized. All linear models had 1 (for structures upstream) and 18 (for sample variables) degrees of freedom.

Variable	Linear model fixed effects						
	Structures in 50m upstream				Structures in 100m upstream		
	F	Multiple R^2	p		F	Multiple R^2	p
May velocity	2.63	0.127	0.122		1.18	0.061	0.292
July velocity	1.50	0.077	0.236		0.46	0.025	0.507
May depth	0.03	0.002	0.871		0.01	0.0004	0.936
July depth	0.14	0.008	0.713		0.19	0.011	0.665
May percent cover aquatic vegetation	2.81	0.135	0.111		0.28	0.015	0.602
July percent cover aquatic vegetation	2.20	0.109	0.155		0.10	0.006	0.754
May substrate index	2.96	0.141	0.103		0.43	0.024	0.519
July substrate index	1.51	0.077	0.236		0.02	0.0008	0.904
May fine particle organic matter ash-free dry mass	4.48	0.199	***0.049***		5.30	0.228	***0.033***
May coarse particle organic matter ash-free dry mass	2.11	0.105	0.164		2.35	0.116	0.143

APPENDIX 2: TABLE OF MACROINVERTEBRATES DESIGNATED AS FOOD FOR ATLANTIC SALMON PARR, WITH SOURCES

Table 3-5. Macroinvertebrates included in analyses of salmon parr food availability (biomass), along with source literature showing they are important diet items.

Order	Family	Source
Ephemeroptera	Baetidae	Grader and Letcher 2006; Ojala 2008
	Heptageniidae	Grader and Letcher 2006; Ojala 2008
	Ephemerellidae	Grader and Letcher 2006; Ojala 2008
Trichoptera	Glossosomatidae	Ojala 2008
	Helicopsychidae	Ojala 2008
	Hydropsychidae	Ojala 2008
	Limnephilidae	Grader and Letcher 2006
	Rhyacophilidae	Grader and Letcher 2006
Diptera	Chironomidae	Grader and Letcher 2006; Ojala 2008
	Simuliidae	Grader and Letcher 2006; Ojala 2008

BIOGRAPHY OF THE AUTHOR

Val was born in Randolph, Massachusetts, but she made an early escape to the woods of the Blue Hills and pretended she was from there instead. There, she quickly went feral and made friends with seven foxes, an unsuspecting skunk, two aloof frogs who knew more than they let on, and a hemlock with a penchant for snarky limericks. After escaping the incomprehensibly ordered confines of Catholic middle school, Val reverted to her natural form at Norfolk Country Agricultural High School, where she fixed tractors and climbed trees for grades, much to her glee and her former captors' disdain. She then roamed north to the University of Maine, where she earned her Baccalaureate in Ecology and Environmental Sciences in 2018 by taking too many classes, tolerating the bothersome nonsense of a cackling ornithologist, and tapdancing her way through her thesis. During a particularly challenging independent study, she made a full suit of armor made of nothing but sarcasm.

Throughout and after her university years, Val wandered her way through intermittent employment and in-between adventures in 34 states, with a sum total of 2.5 hours with dry feet. Between trips to civil war dinosauria, she spent summers digging through avalanche debris in Colorado for plants older than she was and using leaves for clothes. During the school year Val worked hard to corrupt the minds of schoolchildren around the nation, dragging them through woods, marsh, and beach to put mud on their faces and befriend giant spiders. After poor global hygiene shut down the world, Val reluctantly accepted a graduate position because she had nothing better to do. She has steadfastly refused to be properly scholarly, instead talking to random unsuspecting strangers about science and taking way too many classes for the fun of it. Somehow, she managed to still win some fancy awards and finish grad school gainfully employed. Val is known for her enthusiasm for good science communication and disdain for formal nonsense. She is a candidate for the Master of Science in Ecology and Environmental Sciences from The University of Maine in August 2023.