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LongitudinalPatterns in Riverine Ecology within and among Seven Pacific Northwest Rivers:Implications for River Research, Monitoring & Management

Running Title: Longitudinal Patterns in River Ecological Indicators

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Abstract: Rivers vary because of their different geographic settings and their differing levels of anthropogenic disturbances. Relative to wadeable streams, boatable or raftable riversare much less studied because they require more expensive gear and are more dangerous to sample. Because of the importance of Pacific Northwest rivers for water supply, recreation, and endangered fish species, we selected seven rivers of interest to state, tribal, or federal agencies. Our objectives were to determine the degree to which fish and macroinvertebrate assemblages varied with water chemistry, habitat structure, and distance along each river, as well as the degree to which each river differed from the others. We sampled the rivers by inflatable rafts and assessed spatial patterns in fish and macroinvertebrate assemblages as well as water quality and physical habitat structure at 20 sites spread out longitudinally along each river.By analyzing site-to-site similarity matrices for fish, macroinvertebrates, chemistry, habitat, and river distance, we found that water quality-river distance relationships were relatively strong, but habitat structure-distance relationships were usually weak or absent.Also, site-to-site similarity in water quality was unrelated to site-to-site similarity in habitat structure.

Among-river variability was much greater than within-river variability for both fish and macroinvertebrate assemblages. We observed very different patterns among the seven rivers regarding the importance of distance, water quality, and physical habitat similarities relative to fish and macroinvertebrate assemblage similarities. The best set of environmental variables for distinguishing bioticassemblage similarities varied widely among rivers, and among the two assemblage types. We conclude that the riverscape concept is valuable for river monitoring, research, and management, as well as the value of rigorously sampling both water quality and physical habitat as well as both fish and macroinvertebrate assemblages.

KEYWORDS: fish, macroinvertebrates, water quality, physical habitat structure.

1. Introduction

Rivers vary naturally because of differences in the climate, lithology, physiography, surficial geology, and soils of the lands through which they flow (Whittier et al., 1988; Pinto et al., 2009; Omernik& Griffith, 2014) and because of their discharges (McGarvey & Hughes, 2008; McGarvey & Ward, 2008; McGarvey & Terra, 2016). In addition, rivers arechanged by point and diffuse pollution, channel and riparian modifications,substrate alterations, and non-native species introductions--driven by dams, altered flow regimes, and other human activities (Dudgeon et al., 2005; Schinegger et al., 2013; Hughes, 2015). Two major conceptual frameworks, the river continuum concept (Vannote et al.,1980) and the riverscape concept (Fausch et al., 2001) were developed to help explain how rivers change as they increase in size

and the importance of studying and managing entire riverscapes. Like large lakes, large rivers require considerable sampling effort for assessing their biota at both site (Bonar et al., 2009; Dunn &Paukert, 2020; Hughes et al., 2021) and riverscape extents (Smith & Jones, 2005, 2008; Hughes et al., 2012).

At continental and national spatial extents, the environmental predictor or driving variables for biotic responses differ amongst hydrologic units and ecoregions. In a study of 290 French river sites, Marzin et al. (2012) determined that fish, macroinvertebrate, macrophyte and diatom metrics responded differently to morphological and hydrological degradation. Studying 3105 European river and stream sites in 14 nations and16 ecoregions, Schinegger et al. (2013, 2016) reported that different fish metrics responded differently as a function of river type and anthropogenic pressure. Across the conterminous USA, Herlihy et al. (2020) found that the environmental factors and the strengths of the relationships varied among nine ecoregions and between fish and macroinvertebrate assemblages.Godoy et al.(In Review) also reported that the environmental drivers of macroinvertebrate assemblages in the USA differed by distance from the 689 sites and amongst the 30 ecoregions studied. After correcting for sampling effort in regions across the conterminous USA, Hughes et al. (In Review) determined that the environmental drivers for fish and macroinvertebrate taxa richness differed.

In the current study, we examined the patterns of fish and macroinvertebrate assemblages among and within seven large Pacific Northwest rivers (here, large is defined as raftable, boatable, nonwadeable or navigable; Hughes & Peck, 2008). We constructed site-to-site similarity matrices for each river for both biotic assemblages. We also constructed pairwise site similarity matrices for water chemistry, habitat structure, and river distance so that we

could analyze the relationships among these five components of riverine ecology. We hypothesized that (1) those patterns would differ more amongst rivers than within a river, (2) the fish and macroinvertebrate assemblage responses to environmental variables would differ among rivers, and (3) each river would show relatively clear upper river to lower river gradients in environmental conditions and assemblage composition. We expected greater differences among rivers than within rivers because of the great diversity of the landscapes through which the different Oregon and Washington rivers drain (Benke& Cushing, 2005), as well as their differing historical and present basin connections, especially for fish (Hocutt& Wiley, 1986). Likewise, we expected that the key predictor variables for fish and macroinvertebrate assemblages would differ among rivers because natural and anthropogenic predictor variables differed among rivers to differing degreesand because fish and macroinvertebrates respond somewhat differently to the same environmental conditions (Herlihy et al., 2020). In addition, we expected that in at least some of the rivers the fish or macroinvertebrate assemblages would differ simply because of distance between sites and possibly because of discontinuities in water quality or physical habitat structure driven by changes in ecoregion, riparian land uses, or channel slope.

2. Methods

2.1 Study Rivers and Site Selection

We chose seven rivers for longitudinal sampling to represent the range of river types across the Pacific Northwest states of Oregon and Washington (Figure 1). In particular we

selected rivers lacking mainstem storage reservoirs and that were of interest to state or tribal water agency managers. We sampled 20 sites on each river in between their mouth and the upper limits of sampling access by raft. For rivers flowing into estuaries, the downstream end of the river was defined by the head of tide. Sampling pointson each river were selected using a randomized, spatially balancedprobability design (Olsen & Peck, 2008) based on the river trace as represented digitally in the National Hydrography Dataset (USGS, 2013).

The seven study rivers range in watershed size from 3560-28,900 km^2 and 87-255 km of potential survey river length (Table 1). The basins of three rivers (Chehalis, Umpqua, Willamette) were mostly forested, but supported irrigated agriculture in their floodplains. The Chehalis River flowsbetween the Cascade and Coast Range mountains of western Washington before cutting through the Coast Range and entering the Pacific Ocean at Grays Harbor. The upper river drains an agricultural/urban valley with a number of dairies (USEPA 2011).The Umpqua River originates in the Cascades and Klamath Mountains of southern Oregon and then bisects the Coast Range on its way to the Pacific Ocean in Reedsport. Its floodplains support irrigated agriculture (Oregon Explorer 2021). The Willamette River flows northwards in northwestern Oregon through a heavily agricultural and urbanized valley lying between the Coast Range and Cascade Mountains before entering the Columbia River at Portland. The valley contains the majority of the population in Oregon (Hughes et al., 2019a).

The basins of the four other rivers (John Day, Malheur, Okanogan, Sprague) were mostly rangeland, but supported irrigated agriculture in their floodplains. The John Day River originates in the Blue Mountains of northeast Oregon and then flows through arid canyons of the Columbia Plateau before entering the Columbia River. It is the longest free-flowing river in

the conterminous U.S. (Benke,1990). Livestock grazing throughout the John Day basin and especially in its floodplains has fundamentally altered its riparian vegetation and flow regime (Wissmar et al., 1994). The Malheur River flows west to east through the high desert of Eastern Oregon before joining the Snake River at the Oregon/Idaho border. The lower Malheur floodplainis heavily used for irrigated agriculture because of naturally rich alluvial soils (Lovell 1980) and the river contains nine temporary irrigation dams/diversions. The Okanogan River originates in Okanagan Lake in Canada and flows southwards into the U.S. and then through the Columbia Plateau of north-central Washington into the Columbia River. Irrigated agriculture is the principal economic activity along the river floodplains (Wissmar et al., 1994). For logistical reasons, the upstream end of the Okanoganin our study was defined as the U.S./Canadian border. The Sprague River flows through an arid volcanic plateau region of the Eastern Cascade Mountains in south-central Oregon before entering the Klamath River system just north of Klamath Lake. Major land uses are livestock grazing, especially in its floodplains (Kondolf, 2012).

2.2 Field and Laboratory Sampling

Sites were sampled through use of two raftscarrying two people each. One crew sampled fish and macroinvertebrate assemblages while the other crew measuredphysical habitat structure and took water quality samples. Field protocols followed the methodology used by the U.S. EPA's National River and Stream Assessment (Hughes & Peck, 2008; USEPA, 2013). Each site was sampled over a length that was 50 times the mean wetted channel width ,

with the randomly selected point usually located near the middle of the site. Eleven equidistant transects were laid out along each of the sample sites (5 channel widths apart).

We sampled fish assemblages along the nearshore zone throughout each site through use of raft electrofishing (Hughes & Peck, 2008; USEPA, 2013). One netter collected fish as the rower maneuvered the raft. The DC electrical current was generated by a Smith-Root Model 2.5 GPP set at 30-60 pps and 400-1000 V depending on conductivity levels. Netted fish were identified to species and counted and returned to the river alive, except for voucher specimens preserved in formalin and stored in the Oregon State Ichthyology Collection.

Macroinvertebrate samples were collected nearshore at each of the 11 transects (30 seconds kick time)through use of a D-frame kick net (30 x 30 cm opening, 500 µm mesh) over an area of 0.09 m^2.Transect samples were composited in the field into a single sample per site, preserved in 95% ethanol (Hughes &Peck, 2008; USEPA, 2013), and taken to our Oregon State University laboratory for processing.In our lab, samples were randomly subsampled using a gridded sieve (Caton, 1991) with a count goal of 500 individuals. For identification, we examined specimens under a dissecting microscope with magnifications from 6-50X, but chironomid midge larvae were often slide-mounted and examined at higher magnifications using a compound microscope. We identified aquatic insects, crayfish, amphipods,isopods,and snails to the lowest practical taxon, usually genus.However, other non-insects were identified to varying taxonomic levels: cnidarians, free-living flatworms, nematodes, and tardigrades were identified to Phylum, copepods were identified to Order, and cladoceransand bivalve molluscswere identified to Family.Identifications were aided by taxonomic keys (Wiederholm,

1983; Thorp &Covich, 1991; Wiggins, 1996; Stewart & Stark, 2002; Rogers, 2005; Merritt et al., 2008).

River water was collected at the last transect and immediately placed in a cooler on ice. Water samples were kept cold until delivery to the Central Analytical Laboratory at Oregon State University. In the lab, water samples were analyzed for total nitrogen and phosphorus (persulfate digestion and colorimetry), sulfate, nitrate, and chloride (ion chromatography), turbidity (nephelometer), conductivity, and pH (multimeter).

Along each site, physical habitat measurements were made at each of the 11 transects and by rafting along the thalweg between transects (Hughes &Peck, 2008; USEPA, 2013). Thalweg depths, substrate, and habitat types were assessed at 10 equally spaced intervals betweenand at each of the transects. At each transect, measurements were made of riparian disturbance, canopy cover and density, fish cover, littoral substrate, shore substrate, and river width. Channel habitat metrics were calculated as the percentage of the 101 thalweg observations that were categorized as either fast water (riffle and rapid), glide, or pool. Littoral substrate metrics were chosen for our analyses as they were most closely associated with where the macroinvertebrate sampleswere collected. Substrate metrics were based on the littoral pebble count and calculated as the percentage cover in four combined classes, hard bottom (bedrock+hard pan), cobble+boulder, gravel, and sand+fines. Indices of riparian disturbance and natural fish cover were calculated as described in USEPA (2016a).

2.3 Data Analyses

The statistical analyses required the construction of site-to-site similarity matrices for fish, macroinvertebrates, water quality, physical habitat, and river distance. Fish and macroinvertebrate similarity matrices were calculated using assemblage data and Bray-Curtis similarity based on taxa proportionate abundances. Only fish (no amphibians), identified to species level, were used to calculate the fish matrix. The only exception were the juvenile lampreysthat we observed, which were potentially two different species, but were often impossible to differentiate, so they were analyzed together as just onelamprey taxon.To ensure comparability among macroinvertebrate samples, samples with more than 300 individuals were randomly rarified to a fixed 300 count and the lowest practical level of taxonomic resolution (typically genus) was used to define separate taxa. Ambiguous taxa (those not identified to our lowest levels) were removed before analysis.

We chose a representative set of water qualityand physical habitat measures (Table 2) to define their respective similarity matrices. Data were transformed to range between 0 and 1 to match biological similarity measures. Water chemistry variables (except for turbidity) were $\log_{10}$ transformed for normality and then expressed as a proportion of the maximum value observed on each river. For example, the maximum for turbidity in the Willamette was 3.2 NTU (Table 2). That site has a transformed value of 1 for turbidity and the site with the minimum value of 1.0 would have a transformed value of 0.313 (1.0/3.2) for calculating pairwise similarities. Most of our chosen habitat measures were percentage based so were easily converted to a 0-1 scale by dividing by 100. The exceptions were riparian disturbance and natural fish cover, which were transformed in the same manner as water chemistry based on the maximum value observed in the river. Similarity matrices for water quality and habitat

structure were calculated using Euclidean distance of the transformed values. We also measured the river distance (in km) upstream of the mouth for each of the 20 sample sites. That distance was used to calculate an additional similarity matrix for river distance using Euclidean distance.

To examine patterns of biological assemblage composition across all 7 rivers, we performed an ordination on all 140 sites using non-metric multidimensional scaling (NMS) in the PC-ORD software package (McCune &Mefford, 1999). NMS is a non-parametric ordination technique that is one of the most robust methods for exploring biological assemblage data (McCune, 1994).Within each river, correspondence between matrices was evaluated using a Mantel test conducted using the PRIMER version 6 package (Clarke &Gorley, 2006). The test statistic is the Spearman rank correlation coefficient of the pairwise similarities of the two matrices.

We used the BIOENV package in PRIMER to analyze which of the environmental variables (those in Table 2 plus upstream river distance) best explained the biotic structure of the fish and macroinvertebrate similarity matrices (Clarke &Ainsworth, 1993). We examined all possible 1, 2 and 3 environmental variable models to identify the subset with the highest Spearman rank correlation with each of the biotic similarity matrices. Significance of both the Mantel and BIOENV Spearman correlations was assessed using the PRIMER permutation procedure, in which the rows and columns of one of the matrices were subjected to random permutations 1000 times, with the correlation being recalculated after each permutation. The significance of the observed correlation, or rho statistic, is the percentage of such random

permutations that lead to a higher correlation coefficient than the observed. We considered a rho of <1% to be significant.

3. Results

3.1 Environmental Conditions

Geographically, the 7 rivers can be divided into semi-arid, higher-elevationEast-side (John Day, Malheur, Okanogan, Sprague) versus humid, lower-elevation West-side (Chehalis, Umpqua, and Willamette) by the north-south Cascade Mountain Range (Figure 1). West-side rivers have much higher precipitation and a milder climate because of their lower elevations and theprecipitation shadow effect that the Cascades have on the moisture flowing eastwards off the Pacific Ocean. Size-wise, the smaller Chehalis, Malheur and Sprague rivers have watershed areas <10,000 km2, mean wetted widths ranging from 15-65 m and mean thalweg depths of 0.54-4.8 m (Table 1). The larger watershed area rivers (John Day, Okanogan, Willamette) had widths ranging from 40-236 m and depths from 0.64-18 m. The Umpqua is intermediate in watershed area. Chemically, the ionic strength variables (conductivity, sulfate, chloride) did not vary much longitudinally along all the rivers except the Malheur which had significant increases in ionic strength and nutrients in the downstream sites (Table 2). The Malheur,overall, hadhigher nutrient and turbidity levels than the other six rivers. Physical habitat metrics were quite variable along all 7 rivers. For example, %sand+fine substrate varied over 70-80 percentage points in most rivers with the John Day having the smallest range of 0-

45% (Table 2). River habitat (pool/glide/fast water) was similarly variable; for example, the Willamette ranged from 0-100% glide amongst the 20 sample sites. Canopy density was always low in the John Day (all < 10% cover) but had very variable ranges in the other rivers (~10-60%).

3.2 Among-river Biotic Patterns

The NMS analysis of thefish assemblageat all 140 sites yielded a two-dimensional solution that accounted for 80% of the information in the original site similarity matrix with a stress of 15.3 (Figure 2). Overall, within-river variability was much lower than among-river variability. Sites within a river tended to occur very close together in ordination space. The Sprague sites were very distinct from those of the other rivers. Okanogan, John Day and Umpqua river sites were distinct but clustered together. Similarly, the Malheur, Chehalis and Willamette sites clustered together although the Willamette did have 3 sites that were similar to the Okanogan sites.

The Sprague River fish assemblage clearly separated from the other six rivers (Figure 2) in being dominated by five species (*Catostomus snyderi, Cottusklamathensis, Gila bicolor, Gila coerulea, Percaflavescens*) that were absent from the other rivers;four of thesespecies are Klamath basin endemics. Also, *Catostomus macrocheilus*, which has current or historical connections with the Columbia basin was a dominant species in the other rivers, but absent from the Sprague. The West-side Willamette River and the East-side Malheur River clustered together and shared two dominating species (*Catostomus platyrhynchus, Acrocheilusalutaceus*) that were absent from the others and which feed by scraping periphyton from coarse bottom

substrates. The West-side Chehalis River separated from the others because it was dominated by *Cottusgulosus*and also contained *Ambloplitesrupestris* and *Gasterosteus aculeatus*, which were absent from the other rivers. The latter species is most frequently associated with aquatic macrophytes, which were abundant in the upper Chehalis. A third West-side river, the Umpqua, separated from the others in hosting four species (*Ameiurus natalis, Cottusaleuticus, Ptyocheilusumpquae, Rhinichthysevermanni*) lacking in the other rivers; the latter two species are Umpqua endemics. The other two East-side rivers (John Day, Okanogan) contained markedly higher proportions of *Micropterus dolomieu* than the other rivers. It is important to note that four species that distinguish these seven rivers are non-native sportfish introduced by fishery agencies (*Ambloplitesrupestris*, *Ameiurus natalis, Micropterus dolomieu, Percaflavescens*).

The NMS analysis of the macroinvertebrate assemblages yielded a three-dimensional solution that accounted for 77% of the information in the original site similarity matrix with a stress of 15.7 (Figure 3). Because axis 3 explained the most variance (45%), we presentboth axis 3 vs. 2 and axis 3 vs 1 plots. Macroinvertebrate within-river variability in ordination space was much lower than among-river variability, though to a lesser degree than was evident for fish (Figure 2). East-side macroinvertebrate assemblages were distinguished from west-side assemblages, mostly along axis 3. Axis 1 separated the John Day from the Malheur whereas axis 2 separated out the Okanogan and Sprague. The west-side Willamette, Umpqua and Chehalis rivers cluster together in all three dimensions (Figure 3).

The macroinvertebrate assemblages indicated different patterns than the fish assemblages (Figure 3). The three West-side rivers all contained the endemic and generalist

foraging snail, *Juga*, as a dominant, but it was absent from the other four rivers. The Sprague was distinguished by the mayfly, *Caenis,* and three chironomid midges (*Cryptotendipes, Microtendipes,* and*Pseudochironomus*), all of which prefer slow flows and fine substrates. Two other East-side rivers (John Day, Malheur) have somewhat coarser substrates and were dominated by mayflies (*Asioplax, Baetis, Camelobaetidius*), as was the Okanogan, which was distinguished by two mayflies, *Apobaetis*and*Heterocloeon*.

3.3 Within-river Biotic Patterns

For fish assemblages, site-to-site similarity was strongly related to site-to-site river distance in the Willamette (r=0.61) but not significantly related to distance in the John Day or Okanogan (Table 3). Macroinvertebrate assemblages also showed different patterns but in different rivers. Site-to-site macroinvertebrate similarities were strongly related to site-to-site river distance in the Malheur (r=0. 60) and Willamette (r=0.52) but unrelated in the Umpqua. Plots of these biotic similarities to site distance similarities show that theywere strong for both fish and macroinvertebrates in the Willamette (Figure 4), and strong for fish but unrelated for macroinvertebrates in the Umpqua (Figure 5). In the John Day, longitudinal fish assemblage similaritywas unrelated to distance between sites (Figure 6), but macroinvertebrate assemblages were significantly, but weakly,correlated to site-to-site river distance (r=0.34).

We also examined the relationship of biotic assemblages to water quality and physical habitat similarity (Table 3). As with the relationship with river distance, there was no consistent pattern among rivers. Fish similarity was significantly related to water quality similarity in the

Malheur (r=0.48) and Chehalis (r=0.36) but not significantly related to water quality in the other 5 rivers. For macroinvertebrates, assemblage similarity was related to water quality similarity in the Chehalis, John Day, Malheur, and Willamette but not significantly related elsewhere. Fish versus physical habitat similarity was strongly related (r>0.5) in the Chehalis and Willamette and to a lesser extent in the Malheur (r=0.29) but insignificant in the other rivers (Table 3). Similarly, significant relationships for macroinvertebrates and physical habitat were observed in the Chehalis, John Day, and Sprague.

In addition, we examined other relationships among the various similarity matrices (Table 4). There was a consistent pattern among rivers in that water quality similarity was always more strongly related to similarity in river distance (r=0.4-0.6) than physical habitat was related to distance (r=0.1-0.4). Water quality similarity was only significantly related to habitat similarity in the Chehalis (r=0.38) but insignificant in all other rivers. For fish versus macroinvertebrate assemblage similarity, there were four rivers with significant relationships whereas in the other three rivers (John Day, Sprague, Umpqua) there was little or no relationship (Table 4).

3.4 Environmental Predictors of Assemblage Patterns

We used BIOENV to identify the optimal set of environmental variables that best explained both the fish and macroinvertebrate assemblage patterns (Table 5). We were able to identify significant relationships for macroinvertebrates in all rivers (r=0.46-0.65) and for all rivers but the John Day and Sprague for fish (r=0.37-0.65). The best set of environmental

predictors varied widely among rivers, between the two assemblage types, and between water quality versus physical habitat variables. However, all but four of the 14 models included both water quality and physical habitat variables.Along the rivers that we sampled, only the Willamette and Umpqua included large tributaries, but they did not appear to be major factors affecting longitudinal biotic patterns. Rather, channel slope change, as indicated by changes in substrate and habitat type (Table 5), was associated with longitudinal differences in fish and macroinvertebrate assemblages in the Willamette (Fig. 4). On the other hand, change in turbidity (Table 5) was most strongly associated with longitudinal change in fish assemblages in the Umpqua (Fig. 5).

4. Discussion

As a companion to this study, diatom assemblages were simultaneously collected in these 7 rivers at the same places. Pan et al. (2012) also saw that diatom among-river variability was usually greater than that within rivers. Within individual rivers, diatom assemblage patterns were strongly correlated with river distance to mouth in only two rivers (Malheur, Okanogan), and pollution-sensitive taxa decreased downriver in only three rivers (John Day, Malheur, Willamette). Bray-Curtis taxa dissimilarity as a function of distance among sites increased,and diatom assemblages were strongly linked with water quality only in the Malheur (Pan et al., 2012).

LaVigne et al. (2008) reported that declining fish assemblage condition in the Malheur was also associated with declining water quality, but Hughes and Gammon (1987) found

declining fish assemblage condition associated with declining water quality in the Willamette. Studying 30 sites along the Odelouca River in Portugal, Hughes et al. (2009) determined that bird and fish metrics were sensitive to riparian habitat fragmentation and channel and flow disruption whereas macrophytes and macroinvertebrates where more responsive to varying current velocity. Thus, rivers differ amongst themselves, and their assemblages respond differently to water quality and habitat structure gradients.

4.1 Environmental Gradients

Our hypothesis that there would be clear environmental gradients in the seven rivers was only partially confirmed. Water quality-distance relationships were relatively strong, buthabitat structure-distance relationships were usually weak or absent (Table 4).Also,water qualitysimilarity was not related to habitat structure similarity. This indicates that the natural and anthropogenic drivers for water quality differ from those for physical habitat structure, meaning that wecannot predict similar habitat structure based on water quality similarity and vice-versa.These resultsalso suggest that water quality is more controlled by basin-extent processes and sites are more directly linked by upstream flow inputs than is habitat structure, which is controlled more by local processes. Water quality in rivers tends to be mixed and smoothed with river distance, except near point sources; however, channel substrate and riparian conditions tend to be more patchily distributed at individual sites or reaches (Hughes & Gammon, 1987; Fausch et al., 2002; Hughes et al., 2009). As emphasized by Fausch et al.

(2002), such differences in the spatial patterns of environmental predictors necessitate assessing both chemical and physical habitats via an entire riverscape perspective.

4.2 Variability Patterns in Fish and Macroinvertebrate Assemblages

As hypothesized, among-river variability was much greater than within-river variability for both fish and macroinvertebrate assemblages (Figures 2 &3). Pan et al. (2012) reported the same for among-river diatom assemblages. Whittier et al. (1988) found distinct ecoregional differences in fish, macroinvertebrate, and periphyton assemblages amongst wadeable Oregon streams.Our results are not surprising, given that our seven study rivers cross11 markedly different Level-III ecoregions and 16 different Level-IV ecoregions (USEPA 2016c).However, ecoregions or other landscape classifications, if used alone to explain or predict, variations in biotic composition among individual sites will likely have limited use in aquatic bioassessments (Hawkins et al., 2000; Hughes et al., 2019b). For example, Van Sickle and Hughes (2000) reported that site proximity offered comparable site classification strength as ecoregion and twice as muchas hydrologic unit for western Oregon stream fish. Nonetheless landscape classificationscan provideuseful initial stratifications of sitelocations to ensure that different landscape features are adequately considered in sampling programs.

Contrary to our second hypothesis, our results indicatedquite variable patternsamong individual riversregarding the importance, or lack of importance, of distance, water quality and physical habitat structure similarities relative to fish and macroinvertebrate assemblage similarities (Table 3).The Malheur was the only river with largedownstream changes in water

quality. It was also the only one of our study rivers that had relatively high correlations for fish-water quality (0.482) and macroinvertebrate-water quality (0.478) similarities. Pan et al. (2012) also reported arelatively high correlation (0.69) for diatom assemblage similarity and river distance in the Malheur River.Two reasons that the Malheur appears more disturbed than the others is that its discharge is small relative to its floodplain agriculture and its landscape changes markedly from rangeland in the upper river to cropland in the lower river. However, all seven rivers are disturbed in their landscapes, hydromorphology, and local physical habitat structure, but to differing degrees. They differ because of their different natural landscapes and basin connections and because those different landscapes support different land uses. Farming (and higher conductivity, N, and P) occur where soils are rich. Livestock grazing occurs where the soils are poor and the vegetation is sparse. Therefore, the statistically significant predictors for fish and macroinvertebrate patterns differ by river and by assemblage (Table 5). Clearly, it is essential to assess entire riverscape stressor gradients to detect such patterns (Schweiger et al., 2016).

Also, the assemblage similarity responses differed for different rivers and for fish and macroinvertebrates within the same river (Figures 4-6). However, Pyron and Lauer (2004), using functional traits, determined upriver-downriver dissimilarities in fish assemblages in the Wabash River, Indiana. Nonetheless, unless there is a strong environmental gradient among sites in a river, one is unlikely to detect a strong biological-environment relationship. The same is true when assessing multiple sites across large spatial extents (Hughes et al., 2019b; Herlihy et al., 2020). Based on our sample of 7 rivers, patterns between environmental similarities and biological assemblage similarities aredifficult to generalize. However, if sevenPacific Northwest

rivers, five of which flow through only one or two ecoregions are that different, how different are those patterns in the many rivers inentire states, regions, or nations? Again, taking a riverscape approach for each river seems like a wise course for both river research and management (Fausch et al., 2002).

4.3 Environmental Predictors of Assemblage Patterns

Modeling the environmental variables that best explained the biotic structure of the fish and macroinvertebrate similarity matrices indicated significant relationships for macroinvertebrates in all rivers (r=0.46-0.65) and for all rivers but the John Day and Sprague for fish (Table 5). Fish assemblages were very similar across the whole John Day River so there was little signal to model. The best environmental variables varied widely among rivers, and among the two assemblage types. as predicted by our third hypothesis. Thus, it is difficult to generalize about a consistent set of major driver variables that are applicable to all seven rivers, although almost all models included both water quality and physical habitat variables. Hughes et al. (2009) reported that the predictor variables for fish assemblages differed from those for macroinvertebrate assemblages in a longitudinal study of a Portuguese river.Leitao et al. (2017) also found that the significant environmental predictors for Amazonian stream fish assemblage composition differed between regions. Likewise, Herlihy et al. (2020) reported that the significant environmental predictors for fish and macroinvertebrate multimetric index scores differed by assemblage and ecoregion. These results emphasize the need to measure both physical habitat and water quality variables, as well as both fish and macroinvertebrates,when

making rigorous ecological assessments. These are all important components of the European Union's Water Framework Directive and the USEPA's National Rivers and Streams Assessment (Feio et al., 2021).

4.4 Conclusions

By analyzing site-to-site similarity matrices for fish, macroinvertebrates, water quality, habitat structure, and river distance, we found that water quality-river distance relationships were relatively strong, but habitat structure-distance relationships were usually weak or absent. Water quality similarity was not related to habitat structure similarity. Among-river variability was much greater than within-river variability for both fish and macroinvertebrate assemblages. We observed very different patterns among the seven rivers regarding the importance of distance, water quality, and physical habitat similarities relative to fish and macroinvertebrate assemblage similarities. The best set of environmental variables for distinguishing biotic assemblage similarities varied widely among rivers, and among the two assemblage types.

Our research supports the value of implementing the riverscape concept in river monitoring, research, and management by sampling and analyzing data from a large number of sites selected randomly along a river, and therefore representative of each river. Doing otherwise is likely to produce unreliable results in all three applications because the biota in each river responded differently to candidate predictor variables. Furthermore, our results clearly indicate the value of rigorously sampling sets of both water quality and physical habitat structure variables as well as monitoring multiple biotic assemblages because fish and

macroinvertebrate results tell very different stories.The different variables and assemblages vary in their usefulness for assessing and interpreting ecological patterns and impacts—but it is difficult to predict which set of variables will be most useful in extensive monitoring and management programs.

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Table 1. Watershed area and river length containing the 20 sample sites and the range in wetted width and thalweg depth at the 20 sample sites in each of the seven study rivers.

River	Watershed Area (km^2)	River Length (km)	Wetted Width Range (m)	Thalweg Depth Range (m)
Chehalis	3560	87	30-65	0.88-4.8
John Day	17,800	190	42-72	0.96-2.0
Malheur	8830	122	19-47	0.54-1.3
Okanogan	21,100	109	40-104	0.64-2.7
Sprague	4170	108	15-55	0.64-2.5
Umpqua	10,500	209	33-134	0.63-4.0
Willamette	28,900	255	88-236	1.7-18.0

Table 2. Range in values (minimum-maximum) of the water quality and physical habitat variables analyzed in this study for the 20 sites in each river.

Variable	Chehalis	John Day	Malheur	Okanogan	Sprague	Umpqua	Willamette
Conductivity (µS)	92-115	150-220	131-595	236-332	101-132	67-173	43-79
Total P (ug//L)	48-113	23-37	223-458	19-52	53-118	21-168	45-104
Total N (µg/L)	240-920	180-260	270-3890	120-240	200-320	130-890	90-570
Sulfate (µeq/L)	50.6-88.7	84.8-140	159-1580	476-801	11.9-20.6	40.6-174	14.4-124
Chloride (µeq/L)	162-209	27.4-46.0	66.6-379	84.3-122	29.6-46.3	85.5-403	30.2-127
Turbidity (NTU)	0.7-1.9	0.3-0.7	9.9-29	0.4-1.4	1.2-6.0	0.3-0.8	1.0-3.2
%Littoral Sand+Fines	9.1-91	0-45	0-73	18-100	36-100	0-82	0-91
%Littoral Gravel	0-73	9.1-73	18-73	0-64	0-55	0-27	0-64
%Littoral Cobble+Boulder	0-46	0-64	0-55	0-46	0-38	0-64	0-36
%Littoral Hard Bottom	0-45	0-36	0-18	0-27	0-46	0-91	0-27
%Pool	0-27	0-49	0-1.0	0-3.0	0-28	0-76	0-100
%Glide	66-96	46-97	49-100	81-100	72-100	6.8-100	0-100
%Fast Water	0-22	3.0-33	0-51	0-19	0-8.0	0-33	0-31
Shoreline Canopy Density (%)	14-70	0.1-9.4	11-54	13-64	0-34	6.2-44	16-58
Natural Fish Cover Index	0.1-0.2	0-0.2	0-0.4	0.1-0.2	0-0.2	0-0.3	0.1-0.4
Riparian Disturbance Index	0.4-2.3	0.3-1.7	0.5-2.4	1.5-3.0	0.2-2.4	0.8-3.2	0.6-3.6

Table 3. Spearman rank correlation coefficients of biological assemblage similarity matrices versus distance, water quality (W. Qual.) and physical habitat structure (P. Hab,) similarity matrices in each study river.

River	Fish vs. Distance	Fish vs. W. Qual	Fish vs. P. Hab.	Macro vs. Distance	Macro vs. W. Qual.	Macro P. Hab.
Chehalis	0.274*	0.361*	0.503*	0.360*	0.524*	0.440*
John Day	-0.012	-0.005	0.179	0.335*	0.267*	0.300*
Malheur	0.615*	0.482*	0.289*	0.604*	0.478*	0.230
Okanogan	0.069	0.002	0.094	0.381*	0.126	0.127
Sprague	0.321*	0.153	0.141	0.326*	0.189	0.379*
Umpqua	0.400*	0.250	0.117	0.051	0.293	0.300
Willamette	0.612*	0.233	0.500*	0.517*	0.244*	0.269

* Rho (% of 1000 random permutations > maximum r^2) < 1%

Table 4. Spearman rank correlation coefficients comparing environmental and biological similarity matrices in each study river. W. Quality (water quality); P. Habitat (physical habitat structure).

River	W. Quality vs. Distance	P. Habitat vs. Distance	W. Quality vs. Habitat	Macroinvertebrate vs. Fish
Chehalis	0.482*	0.304*	0.383*	0.522*
John Day	0.429*	0.227*	0.045	0.246
Malheur	0.521*	0.272*	0.323	0.436*
Okanogan	0.597*	0.110	0.093	0.331*
Sprague	0.572*	0.147	-0.153	0.093
Umpqua	0.399*	0.295*	-0.06	0.181
Willamette	0.551*	0.402*	0.177	0.372*

* Rho (% of 1000 random permutations > maximum r^2) < 1%

Table 5. BIOENV model output relating the optimal subset of environmental variables that best explain the respective biological assemblage pattern for each study river. The maximum Spearman correlation coefficient for the best possible one, two or three variable model is shown along with the predictor variables.

River	Fish		Macroinvertebrates	
	Spearman r	Variables	Spearman r	Variables
Chehalis	0.608*	%Fast water Chloride	0.586*	Total nitrogen Chloride %Fast water
John Day	0.403	Riparian disturbance Total phosphorus	0.466*	%Pool Conductivity Total phosphorus
Malheur	0.648*	Conductivity Upstream distance Total phosphorus	0.650*	Chloride Upstream distance %Sand+Fines
Okanogan	0.392*	Chloride %Gravel Total phosphorus	0.557*	%Hard bottom Conductivity Total nitrogen
Sprague	0.368	Total Phosphorus %Cobble+Boulder %Hard Bottom	0.459*	%Pool Chloride Canopy Density
Umpqua	0.549*	Turbidity Upstream distance Riparian disturbance	0.529*	%Glide %Gravel Chloride
Willamette	0.650*	%Pool Upstream distance %Gravel	0.562*	%Cobble+Boulder Upstream distance %Fast water

* Rho (% of 1000 random permutations > maximum r^2) < 1%

Figure Legends

Figure 1. Map showing the location of the seven study rivers across in Oregon and Washington and the 20 sampling locations on each river. The number on the river is the river length (km) of the sample site upstream from the mouth.The Malheur dams are temporary irrigation diversions that are removed during the winter. The dam on the Willamette is a navigation lock around a waterfall. The Okanogan dam is outside our study reach. The Sprague dam had been breached to facilitate fish passage.

Figure 2. Fish assemblage NMS ordination plots for all 140 sample sites. A 2-D solution was optimal; axis 1 explained 54.9% and axis 2 explained 25.0% of the variability. Ellipses are drawn around each set of 20 river sites using a 0.5 confidence coefficient indicating that half the data assuming a bivariate normal distribution is contained within each ellipse. The plus sign in the middle shows the mean axis score for each river.

Figure 3. Macroinvertebrate assemblage NMS ordination plots for all 140 sample sites. A 3-D solution was optimal; axis 1 explained 12.6%, axis 2 explained 19.5%, and axis 3 explained 44.6% of the variability. Ellipses are drawn around each set of 20 river sites using a 0.5 confidence coefficient indicating that half the data assuming a bivariate normal distribution is contained within each ellipse. The plus sign in the middle shows the mean axis score for each river.

Figure 4. Pairwise Bray-Curtis similarity versus river distance between all possible pairs for both fish and macroinvertebrate assemblages in the Willamette River.

Figure 5. Pairwise Bray-Curtis similarity versus river distance between all possible pairs for both fish and macroinvertebrate assemblages in the Umpqua River.

Figure 6. Pairwise Bray-Curtis similarity versus river distance between all possible pairs for both fish and macroinvertebrate assemblages in the John Day River.

Fig. 1

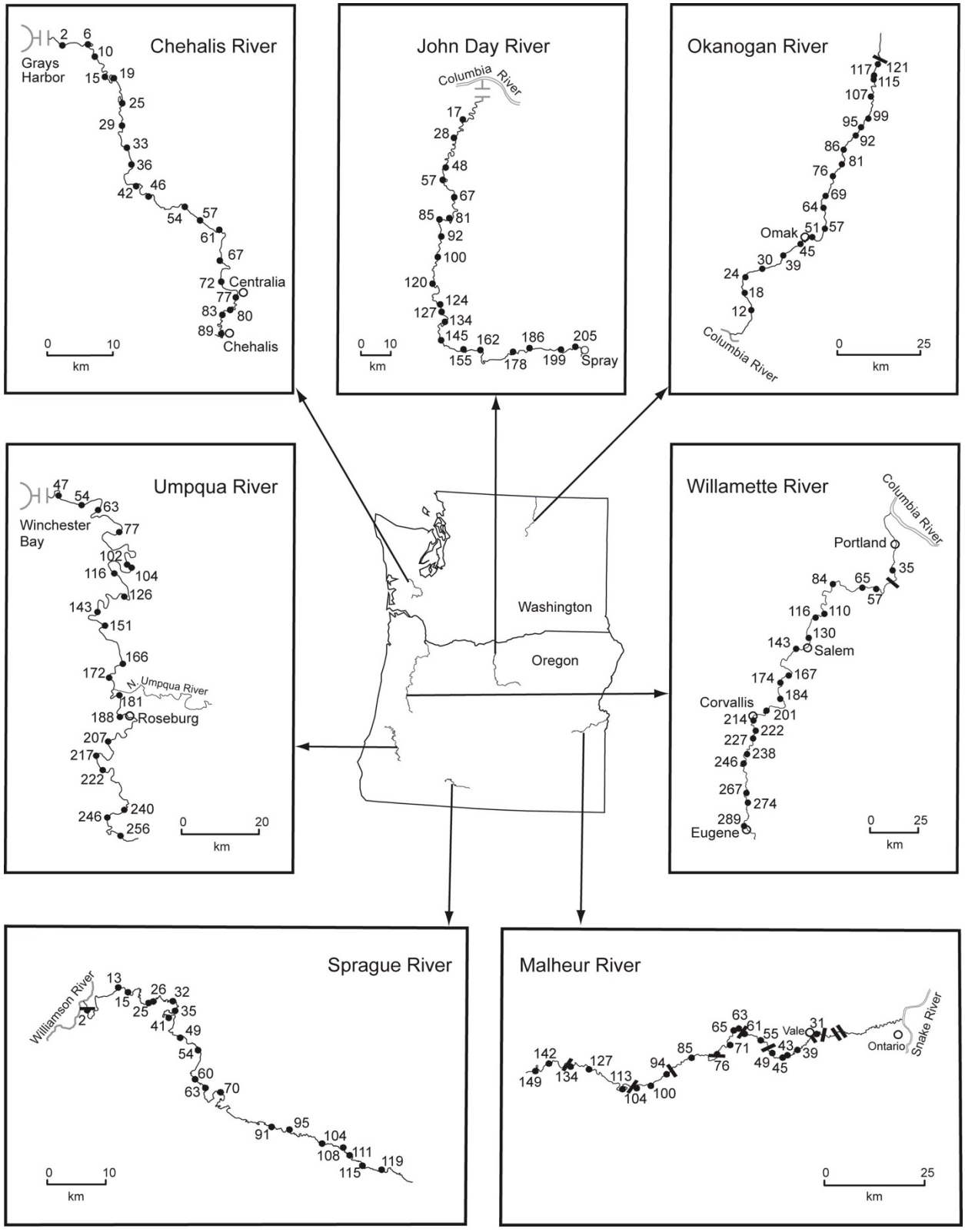

Fig. 2

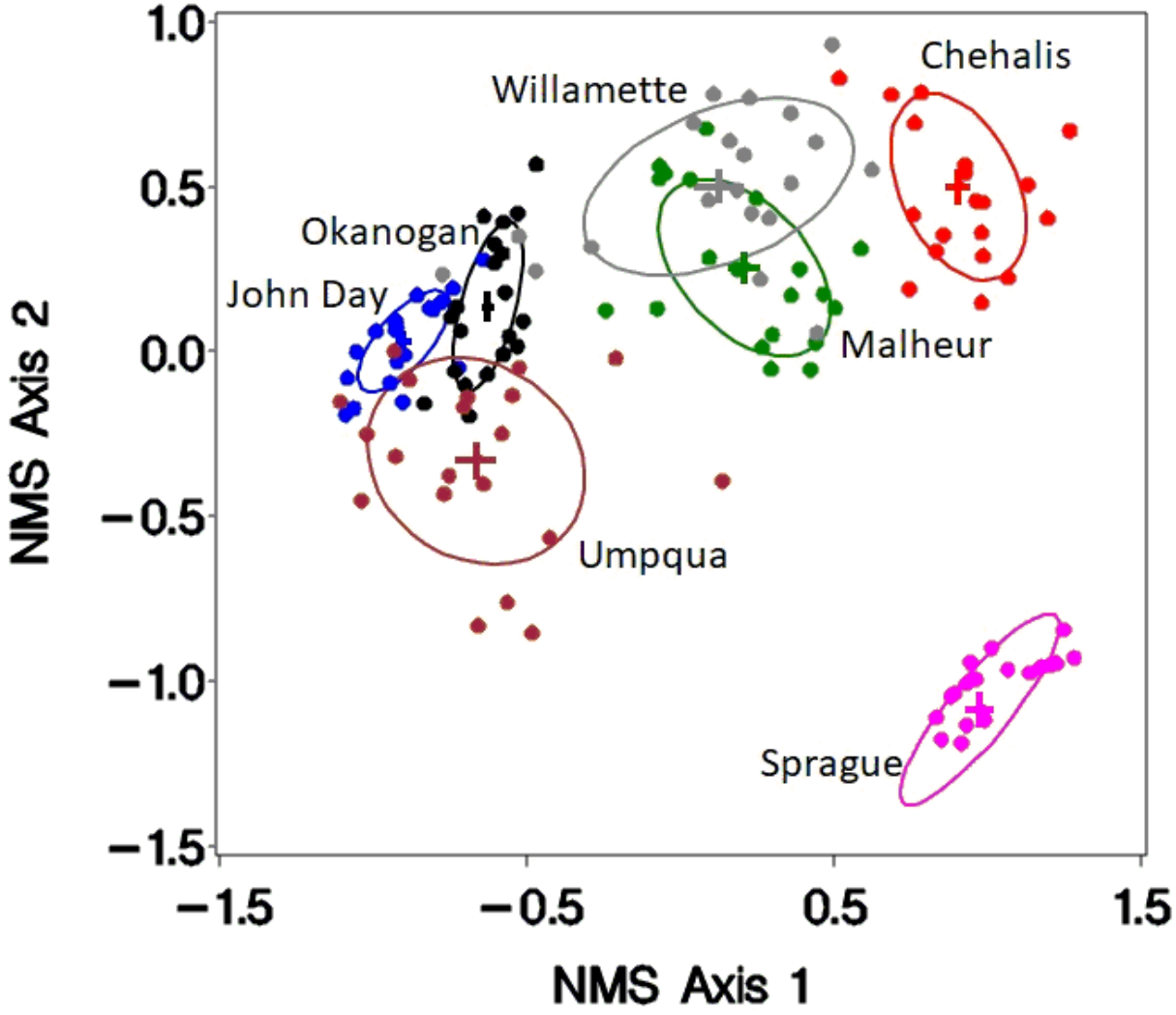

Figure 5

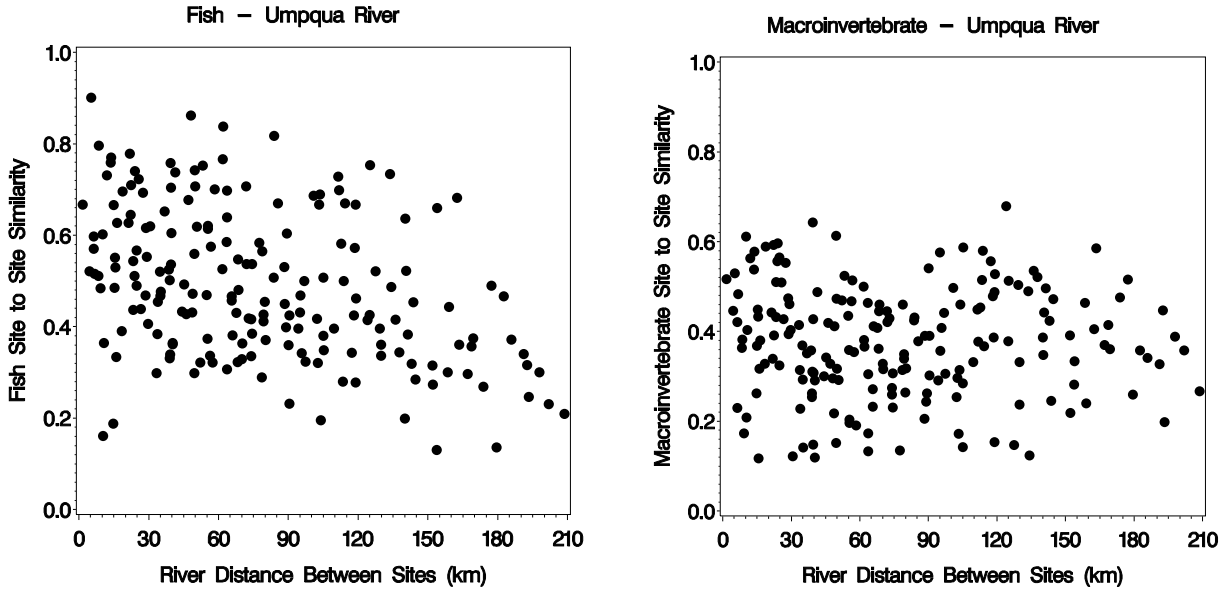

Figure 4

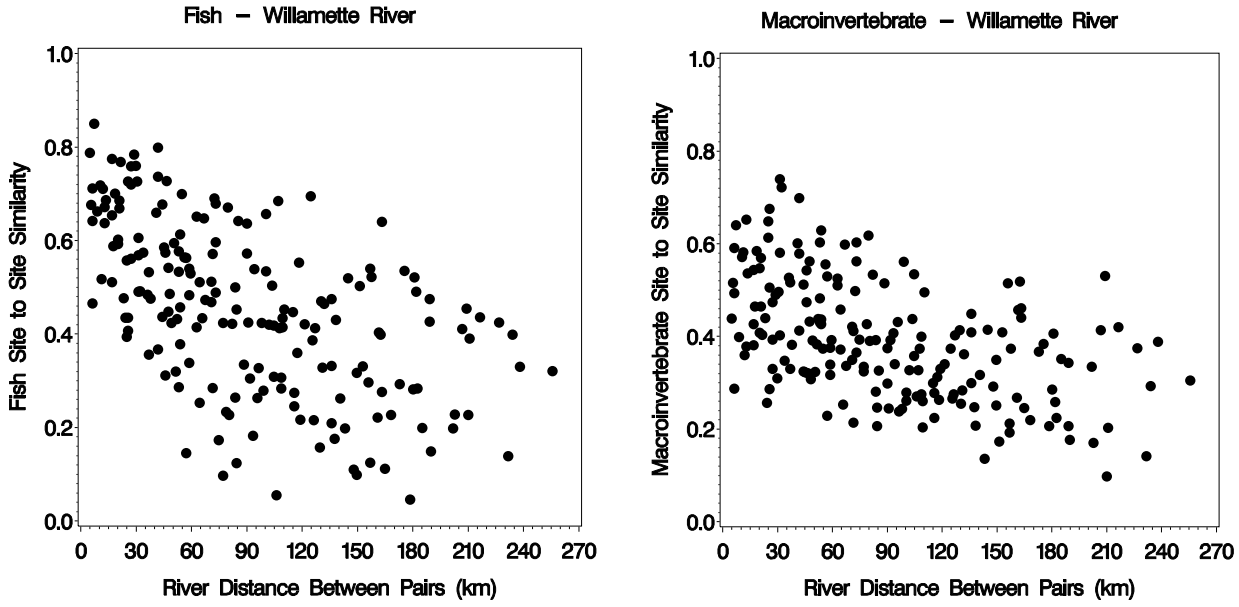

Figure 6

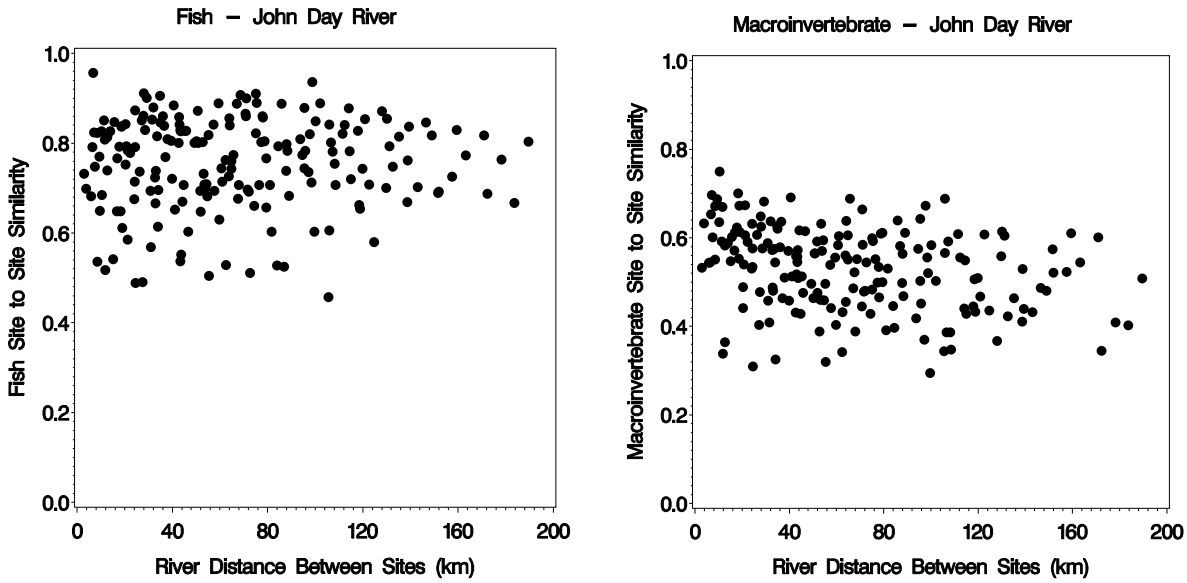

Figure 3