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Aquatic Macroinvertebrates in the Colorado River Basin: Using Ecological Theory to Assess the Impacts of Large Dams

In their natural state, river systems can be considered as a continuum of physical, chemical, and biological features that interact across many scales of time and space (Vannote et al., 1980; Allan, 2004). By disrupting the connections inherent in this continuum, the damming of rivers has a substantial impact on the structure and function of riverine ecosystems (Vörösmarty et al., 2010). As one of the most hydrologically developed and dammed river systems on the planet, the Colorado River system exists as an alternating series of lentic and lotic habitats, contributing to its current state as a highly fractured and ecologically degraded system (Carpenter et al., 2010; Kennedy et al., 2014, 2016). Large dams not only disrupt longitudinal connections, but can be managed in ways that further degrade river conditions. This is particularly true for practices like hydropeaking in hydroelectric dams, where river flows are increased during the day when energy demand is higher (Kennedy et al., 2016). Aquatic macroinvertebrates play an integral part in riverine and even riparian food webs, and so understanding how aquatic macroinvertebrates respond to the disturbances presented by large dams is particularly important for assessing riverine function and stability (Moog et al., 1993).

This paper serves to explore how large dams in the Colorado River Basin (CRB) affect patterns of aquatic macroinvertebrate distribution and diversity. In the last 50 years, a significant body of ecological theory has developed around the structure and function of riverine systems, providing a useful lens through which we can understand impacts on aquatic macroinvertebrate communities in the CRB.

Why Aquatic Macroinvertebrates?

A key tool in measuring stream or river condition is biomonitoring: the use of biological variables to survey and assess an environment (Barbour et al., 1999; Bonada, 2006). Aquatic macroinvertebrates serve as unique tools for assessing the biological health of river systems because of (*a*) their intimate connection to the physical, chemical, and biological conditions of a river, (*b*) their often limited mobility within habitats, (*c*) their critical roles in riverine food webs, (*d*) their high levels of species diversity with different species offering different environmental responses to a variety of stressors, (*e*) their compatibility with simple, low-cost sampling techniques, (*f*) their documented pollution tolerances, and (*g*) their ubiquity across many habitats and regions (Rosenberg and Resh, 1993; Barbour et al., 1999; Karr and Chu, 1999; Usseglio-Polatera et al., 2000; Bonada, 2006). The macroinvertebrate taxa that are most intolerant of disturbances, and therefore most indicative of stream health, are the Ephemeroptera (Mayflies), Plecoptera (Stoneflies), and Trichoptera (Caddisflies), also known collectively as the EPT. Macroinvertebrate indices can reveal a longer time frame of disturbance history within a river system, whereas other physical and chemical measures may provide only a snapshot in time. However, the use of macroinvertebrates in any survey is still most informative when paired with other measures of habitat quality, hydrology, and chemistry (Rosenberg and Resh, 1993; Bonada, 2006).

In their larval stages, aquatic macroinvertebrates are essential to riverine food webs, generally occupying the middle levels of any freshwater trophic pyramid as primary or secondary consumers. While ecosystem outcome depends on any given river’s context, the placement of most macroinvertebrates at the middle of the trophic pyramid can confer influence over both primary productivity and predator communities like fish (Wesner, 2009). Many aquatic macroinvertebrates (particularly the insects) can also play important roles in terrestrial food webs when they emerge as winged adults that serve as prey items for terrestrial predators like birds, bats, or even other terrestrial macroinvertebrates (Nakano and Murakami, 2001; Paetzold et al., 2005). Accordingly, changes in macroinvertebrate communities can have multiple cascading effects both within riverine and riparian food webs (Nakano and Murakami, 2001; Paetzold et al., 2005; Epanchin et al., 2010). Studies on how diminished adult aquatic insect subsidies have affected terrestrial and riparian food webs are generally lacking in the CRB, but empirical evidence from other studies and relevant food web subsidy theory indicate that the effects are likely substantial for some terrestrial predators (Polis et al., 1997; Epanchin et al., 2010).

Using theory to understand dam disturbances on aquatic macroinvertebrates

Understanding how large dams and their management affects aquatic macroinvertebrates in the Colorado River Basin requires an understanding, at least at the broad scale, of ecological theory for riverine systems. To this end, what follows is an overview of some of the major conceptual breakthroughs, each building on the previous, that have advanced our understanding of riverine ecology across scales of time and space. Reviewing all of the literature relevant to the theoretical understanding of river systems is beyond the scope of this paper, but the theories chosen here have particular relevance for contextualizing the effects of large dams. Large dams alter the properties of riverine systems at multiple spatial and temporal scales, and so our theoretical understanding of rivers will also address these issues of scale.

In an early seminal study on nutrient processing within stream systems, Bormann and Likens (1967) considered watersheds using biogeochemical parameters, focusing primarily on external inputs from geological erosion, atmospheric gases, and precipitation, and their expected outputs downstream, rather than on internal exchanges within the system. This focus on measuring the inputs and outputs of a stream system is encapsulated in Bormann and Likens’ “small watershed concept” (SWC). The SWC primarily views stream systems from a mass-balance perspective, focusing on the inputs and outputs at different nodes along a stream or river network.

The River Continuum Concept (RCC; Figure 2) built on and further clarified the work of Bormann and Likens (1967; Vannote et al., 1980), focusing more on the internal nutrient processing and exchanges within riverine systems. One of the innovative core hypotheses of the RCC is that biological organization in rivers will conform structurally and functionally to the parameters of both the physical environment and its upstream biotic inhabitants. Specifically, the RCC predicts trends along a gradient from headwaters (more detrital inputs = net heterotrophy) to large rivers (more light inputs = net autrotrophy). Upstream communities should be optimized to capitalize on coarse detrital nutrient inputs, while downstream communities should be optimized to capitalize on the processing inefficiencies of upstream communities and increased light inputs. For example, aquatic insect and macroinvertebrate communities in headwater streams are expected to fill functional roles that correspond more to the shredding and processing of coarse detrital inputs (e.g. leaf inputs), while downstream communities are expected to fill functional roles that process the "leftover" inputs from upstream (e.g. fine particulate organic matter) and capitalize on grazing of primary producers (if light penetration is adequate; Vannote et al., 1980).

However, the RCC has its limitations. Spatially, rivers are assumed to only function linearly and somewhat homogeneously. The Serial Discontinuity Concept (SDC) adds other spatial components to the RCC by considering the role of floodplains and anthropogenic interruptions like dams on river systems (Figure 3; Ward and Stanford, 1983, 1995). When these lateral and discontinuous spatial components are included, species diversity patterns, temperature, and system stability can differ from the original predictions of the RCC. As one of the most heavily dammed river systems in the world, the SDC is particularly relevant for the CRB as it recognizes that river systems may not be free-flowing across their entire continuum and are instead, most frequently, relegated to alternations of lotic and lentic habitat (Ward and Stanford, 1983). The SDC partly contends that because the vast majority of river systems contain large impoundments like dams, our concept of how riverine systems operate has to inherently consider these modifications.

Temporally, the RCC does not account for seasonal or event-influenced differences that can play large roles in riverine systems. The pulse-shunt concept (PSC) adds a temporal dimension to the processing dynamics postulated by the RCC (Figure 4; Raymond et al., 2016). The PSC emphasizes the importance of infrequent hydrologic "pulse" events (e.g. storms or snowmelt events) that push large amounts of water and terrestrial-derived organic matter into headwater streams, but with a short enough residence time that nutrients are "shunted" from headwater communities before they can process them. Thus, these terrestrial inputs will bypass headwaters and may be processed downstream or exported entirely from the system. The RCC postulates that downstream communities are adapted to capitalize on the inefficiencies of organic matter processing by upstream communities, and that the diversity of compounds decreases with stream order due to the uptake of these inputs in low-order streams (Vannote et al., 1980). In the PSC, a diversity of upstream compounds are shunted into downstream communities that, according to the RCC, should only be equipped to process a narrow range of inputs (Raymond et al., 2016).

Ultimately, the original RCC was not necessarily incorrect but incomplete, and so remains a useful framework for understanding how inputs are processed in riverine networks, as well as how communities respond to the types of inputs they are receiving (Ward and Stanford, 1983, 1995; Raymond et al. 2016). The predictions of the RCC can be valid when tested in many boreal, temperate, and otherwise environmentally homogeneous watersheds, but lack as much predictive power in most other environments (e.g. Dudgeon, 1989). With the caveats and modifications of the SDC and the PSC, as well as the underpinnings of the SWC, the RCC is still useful when considered as a sort of null model to understand how large dams affect ecological processing, connectivity, and diversity across the CRB.

Applying theory to macroinvertebrate communities and dams in the Colorado River Basin

In the context of ecological theory for river systems, large dams in the CRB primarily alter macroinvertebrate communities by disrupting 1) upstream-downstream connections, 2) natural thermal regimes, and 3) natural flow regimes. In its most basic form, the RCC predicts that downstream communities are conditioned to capitalize on resources coming from upstream communities (Vannote et al., 1980). In particular, suspended organic particles coming from upstream may be utilized by macroinvertebrate collectors that utilize traps or specialized mouthpart filters (e.g. Hydropsychidae and Simuliidae). We would thus expect a loss of collector taxa immediately downstream of dams since reservoirs capture and store suspended organic particles that would otherwise remain suspended in lotic waters (Cross et al., 2013; Sabo et al., 2018). In this sense, lotic stretches of river downstream of dams are energetically isolated from upstream stretches, as is consistent within the framework of the SDC (Ward and Stanford, 1983).

Large dams in the CRB also inhibit the downstream transport of sediments, with the majority of annual sediment load trapped in the reservoirs of Lake Powell and Lake Mead. While pre-dam reference conditions are not available or incomplete, we can expect that macroinvertebrate communities were adapted and attuned to the suite of environmental conditions associated with increased sediment loads (Sabo et al., 2018). Two potential impacts of reduced sediment loads in Lower Basin are worth noting here: 1) increased availability of light for primary production, and 2) increased predation potential from visually-oriented predators like fish. River reaches downstream of dams in the CRB can thus be expected to show, if other conditions are adequate, higher levels of production from algae and other primary producers (Blinn et al., 1998), and thus higher abundances of grazer macroinvertebrates. We can also expect more efficient visually-oriented predation by fish on macroinvertebrates as waters become less turbid, particularly for macroinvertebrates that are conspicuous, large-bodied, and lacking refugia (evidence for this is lacking in the CRB, but has been demonstrated elsewhere: see Lunt and Smee, 2015). Higher predation efficiency in lower turbidity waters is likely to be particularly beneficial for introduced visual predators like rainbow trout (*Oncorhynchus mykiss*), unlike many of the Lower Basin's native fish that are adapted to chemosensory prey detection in more turbid waters (US Fish and Wildlife Service, 2018). While many of the direct and emergent effects of disrupted connections between upstream and downstream communities are often unclear and largely unstudied in the CRB for macroinvertebrate communities, the RCC and SDC provide a useful road map for expected outcomes.

Large dams can also transform the natural thermal regimes of rivers from heterogeneous and seasonally variable to generally homogeneous and cold (Ward and Stanford, 1983; Carpenter et al., 2011). In its most basic form, the RCC predicts that as stream order and channel width increase, water temperature will generally increase, primarily because of increasing inputs of light to widening and unshaded water surfaces (Vannote et al., 1980). Since large impoundments like Glen Canyon Dam and Hoover Dam are designed to release most water from near the bottom of their respective reservoirs, downstream reaches often have consistently colder and seasonally homogeneous thermal regimes (Mullan et al., 1976). In this sense, large dams transform higher order river reaches like the Colorado River mainstem into thermal and physical conditions that mimic lower order streams (Blinn et al., 1998), as would be predicted by the SDC (Ward and Stanford, 1983). A homogeneous thermal regime has many implications for aquatic macroinvertebrate populations, as most species have life-history traits that depend on thermal cues (Lehmkuhl, 1972). Populations lacking adequate thermal cues for emergence, hatching, or growth may experience a "life-history bottleneck" where recruitment is severely diminished in successive generations (Kennedy et al., 2016). In the Lower Basin of the CRB, life-history bottlenecks have been particularly pronounced for sensitive insect taxa like caddisflies and mayflies, whose populations are exceptionally low or entirely absent along stretches of the

Colorado River mainstem below Glen Canyon Dam and Hoover Dam (Kennedy et al., 2016; Metcalfe, 2018).

Large dams are perhaps most impactful on riverine ecosystems through their alteration of natural flow regimes (Vörösmarty et al., 2010). In river systems that naturally experience highly variable flows, macroinvertebrate communities may remain intact if flow regimes remain approximately natural (Mullan et al., 1976). In the PSC, high-flow events not only serve as potential disturbance events, but also as “pulses” that transport significant amounts of organic material directly from headwater streams to higher order streams and rivers. In the CRB prior to damming, high flows and pulses of organic matter into headwater streams were often seasonally induced by spring snowmelt in the mountainous Upper Basin. Due to high flows, a majority of this organic material would have foregone processing in headwaters and instead been “shunted” into higher order reaches and, eventually, the Colorado mainstem (Raymond et al., 2016). In its current form, the CRB’s reservoirs mostly attenuate the high flows and organic material transport of seasonal flow regimes (Sabo et al., 2018). In dispersing to new riverine habitats, macroinvertebrates typically move upstream as adults (typically via flying for winged adult insects) and drift downstream as larvae. High flow events often serve as cues for macroinvertebrate larvae to drift downstream (or during more extreme flow events, downstream drift may be “accidental”; Kennedy et al., 2014). When flow regimes are too artificial, macroinvertebrate communities often become dominated by fast-growing taxa (e.g. Dipterans like Chironomidae and Simuliidae) at the expense of slower-growing taxa (e.g. Amphipoda; Cross et al., 2011). In the tailwaters of the Glen Canyon dam, the fast-growing Chironomidae and Simuliidae taxa are the only insect taxa present, despite historical accounts (though they are largely anecdotal) of the presence of more sensitive EPT taxa (Kennedy et al., 2014).

In the CRB, one of the most notable and studied disruptions of natural flow regimes comes in the form of hydropeaking, or the practice of increasing river flows during the daytime when energy demand is higher and decreasing river flows at night when demand is lower (Kennedy et al., 2016). Discharge during hydropeaking can vary by a factor of 10 within one day, and the wave effects of these diel pulses can be observed up to 400 km downstream (Moog et al., 1993). Thus, hydropeaking creates artificial intertidal zones along the shorelines of rivers and has significant ecological consequences for macroinvertebrate communities. Artificial intertidal zones, much like homogeneous thermal regimes, can create life-history bottlenecks for macroinvertebrate populations (Kennedy et al., 2016). Most macroinvertebrate adults cement their eggs to submerged substrates like rocks along the river shoreline to avoid the higher flows near to the center of the channel (Kennedy et al., 2016; Metcalfe, 2018). When the artificial tide at night lowers the level of the river, it often exposes cemented eggs to desiccating air until the next day when the river level will again be raised for hydropower generation. Macroinvertebrate eggs that do not remain submerged will desiccate and become unviable after about one hour of air exposure. Recruitment is thereby lowered through acute egg mortality, and populations may become bottle-necked by their own life-history traits (Kennedy et al., 2016).

In the CRB, hydropeaking is a much more pronounced practice for dams in the Lower Basin than for dams in the Upper Basin. As such, there is a general gradient of decreasing macroinvertebrate diversity as one travels down the Colorado River mainstem. The RCC predicts significant species turnover in the transition from low order to high order streams, but does not predict a loss of diversity like is seen under the hydropeaking gradient of the CRB (Vannote et al., 1980; Kennedy et al., 2016). Both Glen Canyon Dam (an annual provider of ~5 billion kilowatt-hours of hydroelectric power to seven states) and Hoover Dam (an annual provider of

~4.5 billion kilowatt-hours to three states) drive extreme flow-fluctuations in their tailwaters and show exceptionally depleted macroinvertebrate diversity relative to other CRB dam tailwaters (Mullan et al., 1976; Moog et al., 1993; Kennedy et al., 2014, 2016). For the taxa that can tolerate tailwater conditions, population abundance is also remarkably depleted. In fact, abundance is consistently low enough that a lack of macroinvertebrate prey is listed as the main conservation concern for the federally endangered Humpback Chub (*Gila cypha*) in the Lower Basin, specifically in the tailwaters of Glen Canyon Dam in the Grand Canyon (US Fish and Wildlife Service, 2018). In response, management in the Lower Basin has begun implementing low "bug flow" experiments on select weekends during the summer as a means to give eggs laid on the weekends the chance to remain submerged until hatching (i.e. "give bugs the weekends off"). The preliminary results of the "bug flow" experiments have been promising for increasing midge populations (Chironomidae), while other more sensitive taxa like caddisflies (Trichoptera) are likely to require river restoration efforts at a holistic level beyond just hydropeaking attenuation (Kennedy et al., 2016; Metcalfe, 2018).

Conclusions

Ecological theory can be a useful tool for predicting ecosystem outcomes when empirical evidence is lacking, but applying ecological theory to any specific ecosystem comes with significant challenges of context, contingencies, and complexity. Additionally, while the theories outlined in this paper provide a useful heuristic framework for understanding how dams interrupt and transform riverine ecosystems, significant critiques and amendments exist for these theories (see Thorp et al., 2006). For example, even prior to the installment of large dams, theory like the RCC alone would likely be lacking in predictive power for the CRB because of the natural environmental gradient between the Upper and Lower Basins. Encompassing the western slope of the Rockies and the eastern slope of Utah ranges, the Upper Basin is densely packed with headwater streams fed by melting winter snowpack, while the Lower Basin is characterized by the much drier conditions and lower stream network density of the Sonoran and Mojave deserts (Figure 1; Metcalfe, 2018). Since river networks both reflect and transform the characteristics of their surrounding watersheds (Allan, 2004), the Upper and Lower Basins of the CRB could be expected to differ significantly in their stream and river characteristics. Adding to this complexity, the mainstem of the Colorado River in the Lower Basin, is still expected to be intimately tied to the suite of organic and inorganic inputs coming from the Upper Basin, as would be predicted by theory (Vannote et al., 1980).

The RCC, SDC, and PSC remain as useful models based on real-world phenomena, and so they retain high levels of internal validity relative to uncategorized observations and experiments (Naeem, 2001). In the CRB, the changes wrought by large dams and their management practices has led to many changes in aquatic macroinvertebrate communities. Understanding these changes, as well as finding solutions for management, is best done through the lens of ecological theory for riverine systems.

Works Cited

Allan, J. D. 2004. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 35: 257–284.

Barbour, M.T., J. Gerritsen, B.D. Snyder, & Stribling, J.B. 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency; Office of Water; Washington, D.C.

Bonada, N., Prat, N., Resh, V. H., & Statzner, B. 2006. Developments in Aquatic Insect Biomonitoring: A Comparative Analysis of Recent Approaches. *Annual Review of Entomology* 51: 495–523.

Bormann, F. H., & Likens, G. E. 1967. Nutrient cycling. *Science* 155(3761): 424-429.

Blinn, D. W., J. P. Shannon, P. L. Benenati, and K. P. Wilson. 1998. Algal Ecology In Tailwater Stream Communities: The Colorado River Below Glen Canyon Dam, Arizona. Journal of *Phycology* 34: 734–740.

Bond, N. R., and P. S. Lake. 2003. Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. *Ecological Management and Restoration* 4: 193–198.

Carpenter S.R., Stanley, E.H., Zanden, M.J.V.. 2011. State of the world's freshwater ecosystems: Physical, chemical, and biological changes. *Annual Review of the Environment and Resources* 36: 75–99.

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

Cross, W.F., C.V. Baxter, E.J. Rosi-Marshall, R.O. Hall, T.A. Kennedy, K.C. Donner, H.A. Wellard Kelly, S.E.Z. Seegert, K.E. Behn, and M.D. Yard. 2013. Food-web dynamics in a large river discontinuum. *Ecological Monographs* 83: 311–337.

Dudgeon, D. 1989. The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. *Hydrobiologia* 179(3): 183-194.

Ellis, L.E., and N.E. Jones. 2013. Longitudinal trends in regulated rivers: a review and synthesis within the context of the serial discontinuity concept. *Environmental Reviews* 21: 136–148.

Epanchin, P. N., Knapp, R.A., Lawler, S.P. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. *Ecology* 91: 2406–2415.

Kennedy, T.A., J.D. Muehlbauer, C.B. Yackulic, D.A. Lytle, S.W. Miller, K.L. Dibble, E.W. Kortenhoeven, A.N. Metcalfe, and C.V. Baxter. 2016. Flow Management for Hydropower Extirpates Aquatic Insects, Undermining River Food Webs. *BioScience* 66: 561–575.

Kennedy, T.A., C.B. Yackulic, W.F. Cross, P.E. Grams, M.D. Yard, and A.J. Copp. 2014. The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river. *Freshwater Biology* 59: 557–572.

Lehmkuhl, D.M., 1972. Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. *Journal of the Fisheries Board of Canada* 29(9):1329-1332.

Lunt, J., and D. L. Smee. 2015. Turbidity interferes with foraging success of visual but not chemosensory predators. PeerJ 3:e1212.

Metcalfe, A. N. 2018. Metcalfe, A. 2018. Aquatic Insect Distribution in the Colorado River Basin (Master's Thesis). Northern Arizona University, Flagstaff, AZ. 85 p.

Moog O. 1993. Quantification of daily peak hydropower effects on aquatic fauna and management to minimize environmental impacts. *Regulated Rivers: Research and Management* 8: 5–14.

Mullan, J.W., Starostka, V.J., Stone, J.L., Wiley, R.W., Wiltzius, W.J. 1976. Factors affecting Upper Colorado River reservoir tailwater trout fisheries. Pages 405-427 in Orsborn, J.F. and Allman, C.H., eds. Proceedings, symposium and specialty conference, instream flow needs, Vol. II, Am. Fish. Soc., Washington, D.C.

Naeem, S. 2001. Experimental validity and ecological scale as criteria for evaluating research programs. Scaling relations in experimental ecology. Columbia University Press, New York, 223-252.

Nakano, S., Murakami, M., 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98: 166–170.

Paetzold, A., Schubert, C.J. and Tockner, K. 2005. Aquatic Terrestrial Linkages Along a Braided-River: Riparian Arthropods Feeding on Aquatic Insects. *Ecosystems,* 8, 748–759.

Poff, N.L., Olden J.D., Merritt D.M., Pepin D.M. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences* 104: 5732–5737.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annual Review of Ecology and Systematics* 28:289–316.

Raymond, P. A., Saiers, J. E., & Sobczak, W. V. 2016. Hydrological and biogeochemical controls on watershed dissolved organic matter transport: Pulse-shunt concept. *Ecology* 97(1): 5-16.

Rosenberg, D.M. & Resh, V.H., eds. 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. New York: Chapman & Hall.

Sabo, J.L., M. Caron, R. Doucett, K.L. Dibble, A. Ruhi, J.C. Marks, B.A. Hungate, and T.A. Kennedy. 2018. Pulsed flows, tributary inputs and food-web structure in a highly regulated river. Journal of Applied Ecology 55: 1884–1895.

Statzner, B., and L. A. Bêche. 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshwater Biology 55: 80–119.

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

U.S. Fish and Wildlife Service, 2018. Species status assessment for the Humpback Chub (*Gila cypha*). U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver, CO.

Usseglio-Polatera, P., Bournaud, M., Richoux, P., & Tachet, H. (2000). Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology*, 43: 175-205.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C. E. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.

Vörösmarty C.J., et al. 2010. Global threats to human water security and river biodiversity. *Nature* 467: 555–561.

Ward, J.V., and J.A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. *Dynamics of Lotic Ecosystems* 10: 29–42.

Ward, J.V., and J.A. Stanford. 1995. The serial discontinuity concept: Extending the model to floodplain rivers. *River Research and Applications* 10: 159–168.

Wesner, J.S. 2009. Seasonal variation in the trophic structure of a spatial prey subsidy linking aquatic and terrestrial food webs: adult aquatic insects. *Oikos* 119(1): 170-178.

Figures

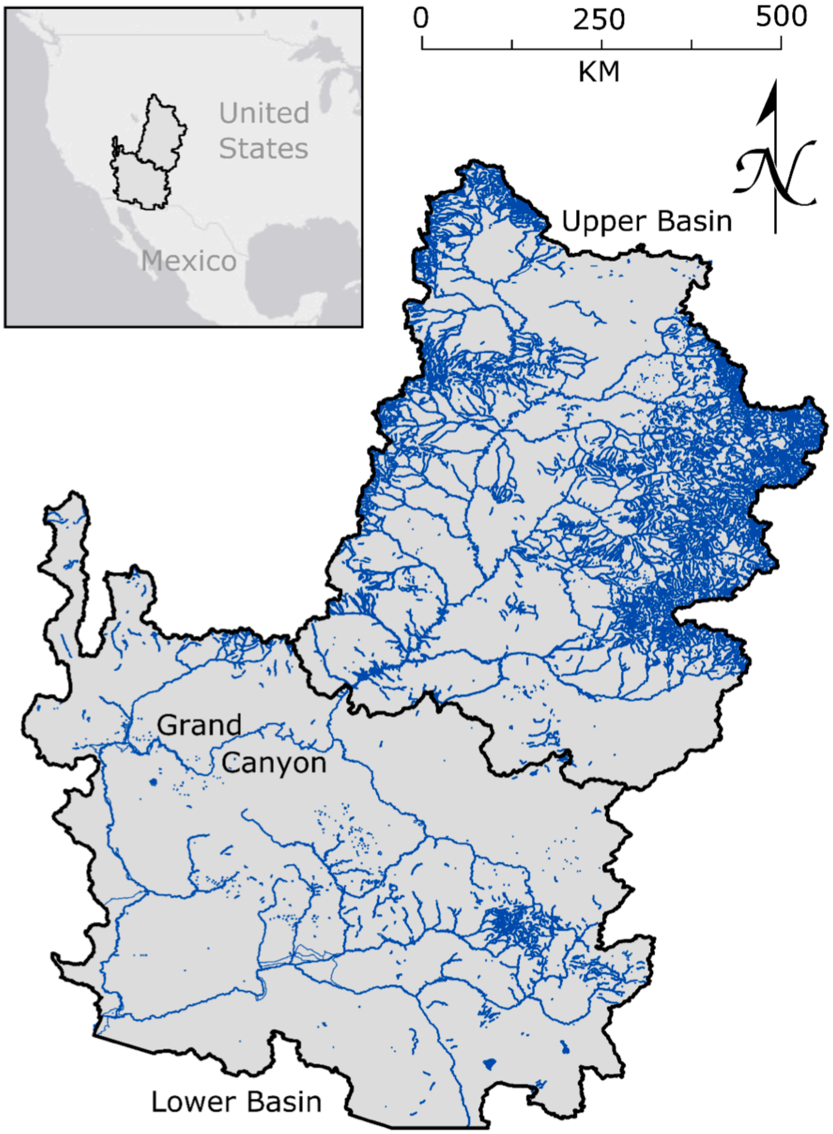

Figure 1. The Upper and Lower Basins of the Colorado River watershed within the United States, with blue lines representing streams and rivers. Notice the high density of stream networks in the Upper Basin relative to the Lower Basin. Adapted from Metcalfe, 2018.

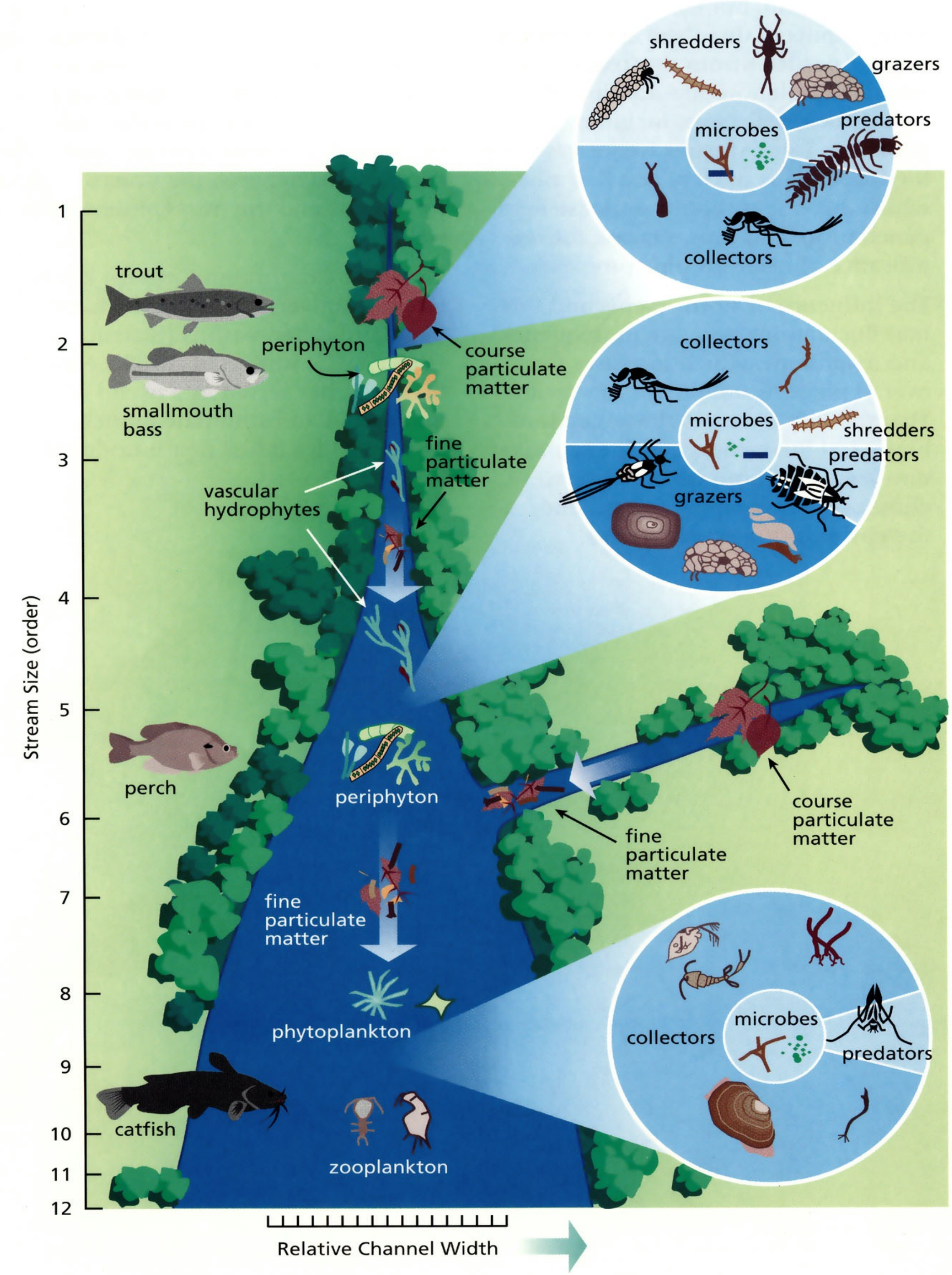

Figure 2. A conceptual schematic of the River Continuum Concept. Adapted from: Stream Corridor Restoration: Principles, Processes, and Practices, 10/98, by the Federal Interagency Stream Restoration Working Group (FISRWG).

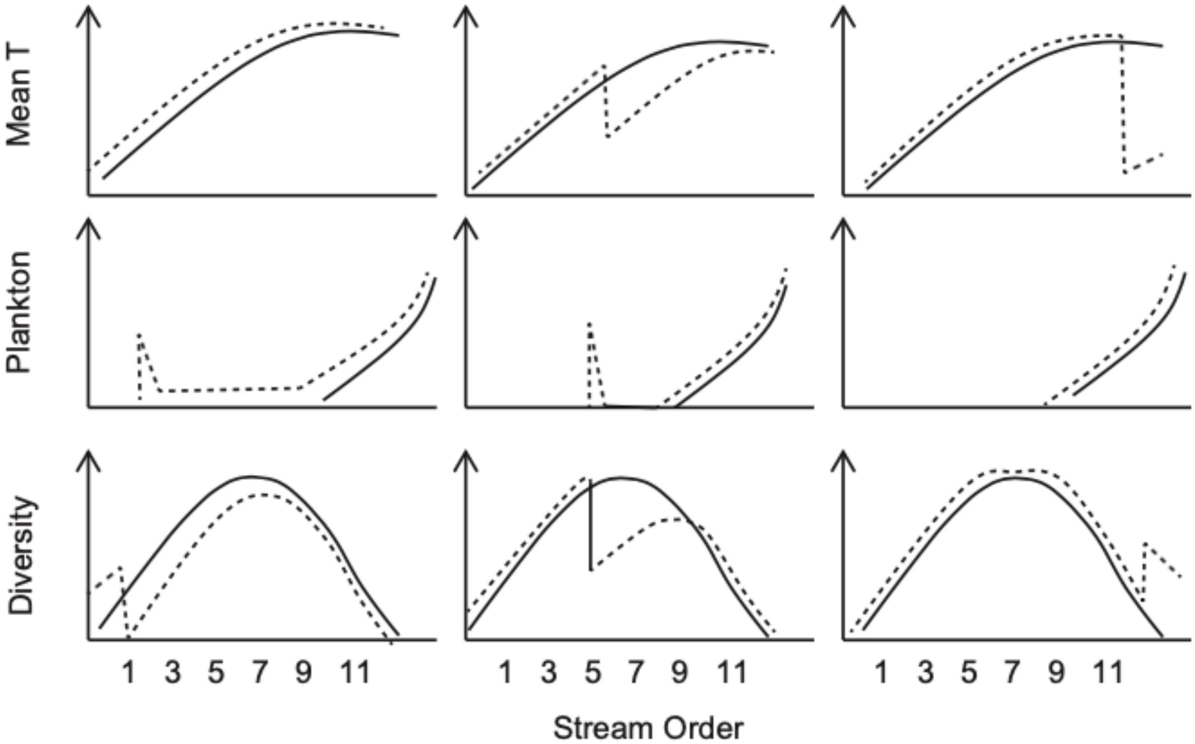

Figure 3. General predictions of the Serial Discontinuity Concept, as interpreted by Ellis and Jones (2013). Solid lines represent conditions under a natural river continuum, while dashed lines represent changes with the addition of an impoundment at the headwaters, middle reaches, or lower reaches of a river system. Mean T = Mean Temperature. Adapted from Ellis and Jones (2013).

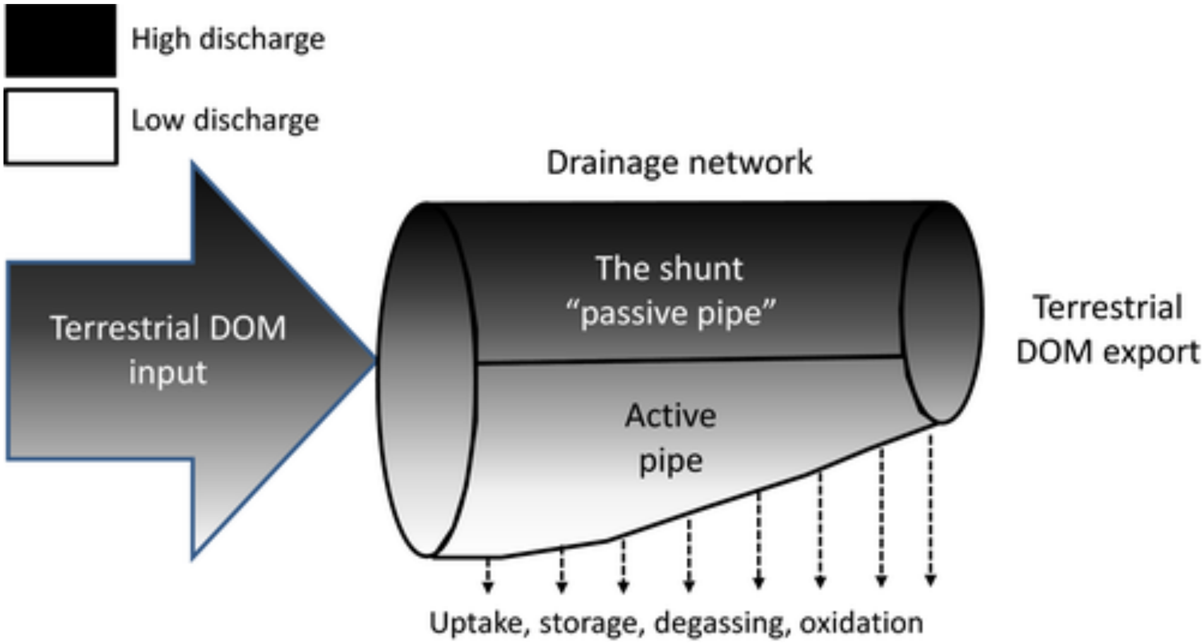

Figure 4. A conceptual schematic of the Pulse-Shunt Concept. DOM = Dissolved Organic Matter. Adapted from Raymond et al. (2016).