RUNNING HEAD: Subsurface biogeochemistry links ecology and hydrology

Subsurface biogeochemistry is a missing link between ecology and hydrology in dam-impacted river corridors

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Keywords: hyporheic zone, hydropeaking, organic matter, temperature, groundwater-surface water mixing, biogeochemical hotspot

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27147v1 | CC BY 4.0 Open Access | rec: 27 Aug 2018, publ: 27 Aug 2018

Abstract

Global investment in hydropower is rapidly increasing, fueled by a need to manage water availability and by incentives promoting renewable energy sources. This expansion poses unrecognized risks to the world's vulnerable freshwaters. In particular, subsurface processes are altered by dam operations and may influence river corridor ecosystem health in ways that remain poorly understood. We advocate for a better understanding of dam impacts on subsurface biogeochemical activity, its connection to hydrology, and follow-on trophic cascades within the broader river corridor. We delineate an integrated view of hydropower impacts in which dam-induced changes to surface water flow regimes generate changes in surface-subsurface hydrologic exchange flows (HEFs) that subsequently (1) regulate resource availability for benthic microorganisms at the base of aquatic food webs and (2) impose kinetic constraints on biogeochemical reactions and organismal growth across a range of trophic levels. These HEF-driven effects on river corridor food webs, as mediated by subsurface biogeochemistry, are a key knowledge gap in our assessment of hydropower sustainability and putatively combine with other, more well-known dam impacts to result in significant changes to river corridor health. We suggest targeted laboratory and field-based studies to link hydrobiogeochemical models used to predict heat transport, biogeochemical rates, and hydrologic flow with ecological models that incorporate biomass changes in specific categories of organisms. Doing so will enable predictions of feedbacks among hydrology, temperature, biogeochemical rates, organismal abundances, and resource transfer across trophic levels. An understanding of dam impacts on subsurface hydrobiogeochemistry and its connection to the broader aquatic food web is fundamental to enabling mechanism-based decision making for sustainable hydropower operations.

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Introduction

More than 50,800 large dams manage water and/or energy for municipalities and agriculture worldwide (Dams, 2016; Poff and Schmidt, 2016, Figure 1). Hydropower in particular accounts for 80% of renewable energy (Zarfl et al., 2015), and international investment in dams is booming (Edenhofer et al., 2011). Investments increased six fold during 2010–2012 compared to 2000–2010, with 3,700 new large (>1 MW) hydroelectric dams currently planned (Hermoso, 2017; Zarfl et al., 2015). Such investments are fostered by recent climate agreements that encourage a transition from coal- and natural gas-based power sources to renewable energy (e.g., Paris Agreement, Rio+20, 2030 Sustainable Development Goals promoted by United Nations, Hermoso, 2017). Yet despite the advantages of hydropower as a renewable power source, freshwater ecosystems are threatened by such developments and are already among the most vulnerable worldwide (Latrubesse et al., 2017; Vörösmarty et al., 2010). While recent integrative frameworks have advanced our understanding of the connections between hydrology and ecology in unregulated watersheds (Dollar et al., 2007; Fisher et al., 1998; Thorp et al., 2010), we lack an understanding of how dam-driven dynamics alters these connections and the follow-on impacts to ecosystem health. In particular, the impacts of hydropower on subsurface processes and how those impacts translate into shifts in river corridor ecology remain unknown, and we call for researchers to address this knowledge gap.

Individual components of dam impacts on river corridors have been studied extensively and provide a baseline for cross-disciplinary research. Hydrologically, dams transform landscapes by creating artificial lakes; fragmenting river networks; changing channel morphology; and distorting patterns of stream flow, sediment transport, and water temperatures (Poff et al., 1997; Sánchez-Zapata et al., 2016; Vörösmarty et al., 2010; Zhou et al., 2018). Both lateral and vertical connectivity between surface and subsurface waters are impacted by dam operation (Ward, 1989), and novel cycles of discharge, sedimentation, temperature, and chemistry impact downstream riparian vegetation, benthos, and fisheries (Arimitage, 1984; Gregory et al., 1991; Petts, 1984; Ward and Stanford, 1983; Ward and Stanford, 1979). Dams also impede upstream-downstream migration patterns, diminishing spawning habitat, and increasing nutrient concentration (Duncan et al., 2018; Maavara et al., 2015; Poff and Schmidt, 2016), coincident with disturbances to invertebrate populations that decrease overall biodiversity and ecosystem productivity (Kennedy et al., 2016). For instance, salmonids (Groot and Margolis, 1991) and large aquatic insects (Kennedy et al., 2016) lay their eggs in nearshore sediments or on rocks just below the water's surface. Sharp drops in water level expose developing eggs to the atmosphere, suppressing hatch rates. Salmonid embryo success is also tightly correlated to dissolved oxygen content, which is perturbed by changes to channel morphology and residence time distributions (Coble, 1961; McNeil, 1962) such as those induced by hydropower operation. Previous work has shown interdependence between these processes and broader ecosystem functioning, in particular demonstrating disturbances to riverine food webs that are critical to the ecological integrity of aquatic systems (Cross et al., 2013).

While recent frameworks link surface and subsurface connectivity in unregulated systems, we lack understanding of how flow regulation alters these linkages and their impacts on river corridor health. These frameworks underlie a central theme that hydrologic and geologic processes are the drivers of river corridor function (e.g., the river continuum and wave concepts and the flood-pulse concept) (Frissell et al., 1986; Hein et al., 2003; Humphries et al., 2014; Junk et al., 1989; Poff et al., 1997; Thorp and Delong, 1994; Thorp et al., 2010; Townsend and Hildrew, 1994; Vannote et al., 1980) and lead to hierarchical frameworks that attempt to integrate hydrologic and ecological disciplines (Dollar et al., 2007; Fisher et al., 1998; Thorp et al., 2010). For instance in an advanced conceptualization, Dollar et al. (2007) propose parallel hierarchies in geomorphology, hydrology, and ecology that both interlink and have multiple components operating at different spatiotemporal scales but do not explicitly include biogeochemistry. However, this framework is presented in the context of more stable natural systems and does not encompass the full heterogeneity operating within dam-impacted river corridors. A notable exception to frameworks conceptualized within unregulated ecosystems is the serial discontinuity concept (SDC). Ward and Stanford (1983; 1995) proposed and revised the SDC which suggests flow regulation interrupts river continua and resets conditions to those found in lower order streams. This generates recovery of large-order stream hydrology and ecology with increasing distance from dams. Ward and Stanford's revised framework incorporates both lateral and vertical exchange fluxes and their subsequent potential influence on river corridor health. Despite Ward and Stanford's seminal work and in part due to the enhanced complexity of ecosystems with high variability, most subsequent work has focused on a limited aspect of science or portion of the river corridor in its investigation of regulated river corridors. To facilitate a cohesive understanding of dam-impacted systems, we highlight the importance of understanding subsurface hydrologic impacts on biogeochemistry that spread through aquatic food webs to affect watershed ecology (Figure 2). Existing frameworks do not provide the foundation needed to address the full suite of possible ecosystem impacts from subsurface hydrology and our aim here is to discuss missing conceptual linkages between hydrologic exchange flows, subsurface biogeochemistry, and river corridor food webs in mediating ecosystem health.

Much of our discussion focuses on connections between subsurface hydrology, biogeochemistry, and ecology in the 'hyporheic zone' [the subsurface domain of groundwater-surface water mixing adjacent to the main stem of river corridors (Boulton et al., 1998; Findlay, 1995)] that influences the health of the broader river corridor. Hyporheic zones are characterized by spatiotemporally variable biogeochemical hotspots and hot moments and serve as a nexus of hydrologic mixing, enhanced biogeochemical reactions, and refugia for benthic organisms (Boulton et al., 1998; Harvey and Gooseff, 2015; Maazouzi et al., 2017; McClain et al., 2003; Palmer et al., 1992; Stubbington et al., 2011). These zones have been demonstrated to contribute up to 96% of respiration in headwater streams (Naegeli and Uehlinger, 1997) and are considered major players in the biogeochemical cycles of larger river corridors (Gomez-Velez et al., 2015; Huizenga et al., 2017; Stegen et al., 2016; Stern et al., 2017). As such, the interplay between subsurface hyporheic dynamics and surface water hydrology is both integral for understanding ecosystem impacts of hydropower and a natural intersection for hydrologic, biogeochemical and ecological domains of scientific research. While models can be used to predict heat transport, biogeochemical rates, hydrologic flow, and biomass changes in specific categories of organisms that span trophic groups (e.g., Diersch, 2013; Gomez-Velez and Harvey, 2014; Grandy et al., 2016; Song et al., 2018), we lack the predictivity capacity to consider all these components of ecosystem health simultaneously. Doing so will reflect connectivity in our emerging conceptual understanding and reduce uncertainty in model forecasts.

We begin this paper with independent summaries of hydropower impacts on subsurface hydrology and aquatic ecology associated with multiple components of the river corridor. We then demonstrate the interconnectivity of these system features via subsurface biogeochemistry in an expanded conceptualization of river corridor function. Using this new conceptual framework, we discuss how hydropower impacts cascade from hydrologic exchange flows to subsurface biogeochemistry to river corridor food webs and ecosystem health. We conclude with a call to the scientific community to place their work within the presented multidisciplinary conceptual framework.

Hydropower Impacts on River Corridor Hydrologic Exchange Flows

Exchanges of water and chemical constituents between river channels and their hyporheic zones (termed 'hydrologic exchange flows' or 'HEFs') are tightly coupled to changes in river surface elevation ('stage', Figure 3, Boulton, 1993; Cardenas, 2015; Harvey and Gooseff, 2015). Hydropower operations regulate river stage, which in turn has direct impacts on HEFs. Short-term, high-frequency variation in dam discharge ('hydropeaking') causes rapid changes in river stage that impact river corridors in three dimensions – longitudinally, laterally, and vertically -- and have wide ranging effects as a function of an area's position in the watershed (Ward, 1989; Ward and Stanford, 1995). In particular, research has highlighted the importance of vertical connectivity that promotes surface water (increased stage) or groundwater (decreased stage) intrusion into the hyporheic zone in response to high frequency fluctuations (Francis et al., 2010; Fritz and Arntzen, 2007; Greimel et al., 2016; Johnson et al., 2015; Lauters et al., 1996; Sawyer et al., 2009; Song et al., 2018; Ward and Stanford, 1995; Zhou et al., 2017). Additionally, hydropower infrastructure diminishes free-flowing stretches of open water and creates large reservoirs of low-velocity water bodies behind dams. This regulation changes nutrient concentrations in reservoirs and dampens the hydrologic influence of storm-driven and seasonal water cycles on river corridors, in part, by decreasing the intensity of HEFs and the connectivity between surface water and floodplains (Maavara et al., 2014; Maavara et al., 2017; Maavara et al., 2015; Wohl et al., 2017).

Hydrologic exchange flows modulate river corridor biogeochemistry through direct effects on the supply and residence time of substrates involved in biogeochemical cycles and through indirect temperature effects on the kinetic reaction rates of these processes. Hotspots and hot moments of biogeochemical reactions in the hyporheic zone are generated by the mixing of waters with differing chemical composition that relieves nutrient limitation and by the exposure of surface water to mineral surfaces and benthic organisms in the subsurface environment that mediate biogeochemistry (Krause et al., 2017; McClain et al., 2003). Moreover, HEFs influence river bed, hyporheic zone, and surface water temperatures through (1) mixing of groundwater and surface water masses that are often at different temperatures (Johnson et al., 2015) and (2) by exposing surface water to subsurface sediments that are buffered against seasonal temperature changes (Song et al., 2018). For instance, when groundwater and surface water mix in the hyporheic zone, the temperature of the intruded surface water mass is mediated by the more stable thermal regimes in groundwater and by sediments that change in temperature more slowly than water (Boano et al., 2014). As this mixed water body returns to the main channel (via HEFs), riverbed sediment and surface water temperatures change in accordance with the temperature of the mixed water body (Bhaskar et al., 2012; Boano et al., 2014; Burkholder et al., 2008).

Despite the role of HEFs in regulating biogeochemistry and thermal regimes in dam-regulated river corridors, impacts of dam-altered hydrologic processes on river corridor biogeochemical function are highly uncertain. Most studies have examined HEFs and associated biogeochemistry in systems with relatively consistent hydrologic flow where steady-state assumptions conditions can be made (Trauth et al., 2015; Wondzell et al., 2009; Zarnetske et al., 2015; Zarnetske et al., 2012); however, a small number of studies link HEFs to biogeochemical function in dynamic systems such as those influenced by hydropower. Gu et al. (2012), for example, found variable river stage to increase groundwater-surface water exchange within hyporheic zones, leading to periods with elevated denitrification. Similarly, Trauth and Fleckenstein (2017) also demonstrate positive effects of hydropeaking on biogeochemical process rates, showing that extreme changes in river stage enhance the cycling of carbon and nitrogen, while Goldman et al. (2017) demonstrated decreased metabolism in the parafluvial zone in response to re-inundation.

Yet, this research is nascent and many possible outcomes of dynamic flows on biogeochemistry are left unexplored. Long-term dampening of HEFs that would otherwise be driven by storm-driven and seasonal water cycles and decreased connectivity between main river stems and their floodplains, for example, could suppress hyporheic zone hotspots and hot moments due to diminished groundwater-surface water exchange. It has been demonstrated that long-term drought alters hyporheic zone function, groundwater contribution to surface flows, and nutrient, carbon, and metabolism levels of surface water (Dahm et al., 2003; Valett et al., 1994; Wroblicky et al., 1998). Similar linkages between hyporheic zone function and surface water chemistry may result from extended low-flow periods associated with flow regulation. On the other hand, high-frequency HEFs may provide an opportunity for increased groundwater-surface water mixing from hydropeaking (enhancing biogeochemical cycling in the hyporheic zone) or conversely impede flow through the subsurface through colmation (Francis et al., 2010; Fritz and Arntzen, 2007; Greimel et al., 2016; Johnson et al., 2015; Lauters et al., 1996; Sawyer et al., 2009; Ward and Stanford, 1995; Waters, 1995; Zhou et al., 2017), with follow-on effects on river corridor function. Coupling HEFs driven by dam operations to associated changes in river corridor biogeochemistry through space and time is therefore a budding research frontier for understanding ecosystem impacts of hydropower.

Hydropower Impacts on Aquatic Ecology

In addition to impacting hydrobiogeochemistry (i.e. feedback among hydrology, geochemistry, and the biological agents that drive biogeochemical transformations), dam operations also significantly alter aquatic ecology. In ecology, individual species populations respond to specific stressors in ways that propagate across food webs. Food webs exchange matter and energy among organisms and across trophic levels (DeAngelis, 2016) and are a central concept in ecology, dating back to Darwin's description of a 'tangled bank' of interrelating organisms (Darwin, 1859) . They also provide a conceptual tool for linking organisms with biogeochemistry (de Vries et al., 2013; Neutel and Thorne, 2014; Rousk, 2016) and represent a popular avenue of research for linking ecosystem structure with function (Rousk, 2016).

Recent work has revealed large effects of dam-driven stage fluctuations on benthic food webs (Cross et al., 2013; Kennedy et al., 2016), but linkages to subsurface biogeochemistry and to river corridor ecosystem function are lacking. Investigated impacts of managed discharge are largely restricted to fish (Lagarrigue et al., 2002; Liebig et al., 1999), riparian vegetation and periphyton (Algarte and Rodrigues, 2013; Bejarano et al., 2017; Benenati et al., 1998), and invertebrate ecology (Céréghino and Lavandier, 1998; Cortes et al., 2002; Kennedy et al., 2016). Distance from dams, flow regulations patterns, and temperature effects all impact aquatic food webs at these broad trophic levels (Arimitage, 1984; Blinn et al., 1995; Gore and Petts, 1989;

Gregory et al., 1991; Lake et al., 2000; Petts, 1984; Poff et al., 1997; Stevens et al., 1997; Vinson, 2001; Ward and Stanford, 1983; Ward and Stanford, 1979). For example, Vinson (2001) showed in his seminal work that reduced peak-to-base flow variation, nutrient enrichment, channel morphology, and altered temperature regimes associated with flow regulation altered invertebrate community structure below dams. Blinn et al. (1995) and Grimm (1993) both suggest pronounced disturbance effects on biota due to atmospheric exposure in the parafluvial zone, with Blinn et al. (1995) demonstrating that benthos can require up to 4 months of recovery after two periods of 12-h exposure to the atmosphere. Cross et al. (2013) extend these analyses to show that food webs close to dams are less efficient and more sensitive to disturbance than those further downstream. In a recent study on population responses to variable discharge, Kennedy *et al.* (2016) showed that the number of biological species found in benthic invertebrate communities declined precipitously beyond a threshold of dam-induced discharge variation. Bejarano et al. (2017) note that changes in dispersal patterns due to hydropower infrastructure may cause aquatic vegetation species distributions to shift towards the upper boundaries of regulated rivers. Periphyton distributions also change in response to variable discharge because periphyton detach from substrates when shear stress thresholds are exceeded and desiccate under low stage (Benenati et al., 1998; Blinn et al., 1995; Larned, 2010; McKinney et al., 1999). Change in the abundances of these species in food webs, in turn, may impact biogeochemical function of the river corridor through associated changes in organic matter production, composition, breakdown, and delivery to the subsurface environment driven by HEFs. Although Grimm and Fisher (1984) first noted the large contribution of hyporheic zones to whole ecosystem function, hyporheic zone dynamics are often ignored or studied independently of each other when considering dam-regulated river corridors. Despite a strong history of research of the ecological impacts of surface flows in response to regulation, we lack knowledge on how changes to organismal and population ecology cascade across aquatic food webs (Humphries et al., 2014). This is particularly true when considering connections between surface and subsurface domains.

Microbial ecology and biogeochemistry have been incorporated within food web frameworks (Zou et al., 2016), but these inclusive conceptualizations of aquatic ecology have yet to be applied in dam-impacted systems. Given recent work relating river stage fluctuations to HEF-driven biogeochemistry in the subsurface and the dependencies of aquatic food webs on resources generated by biogeochemical cycling, a promising avenue of research lies in using subsurface biogeochemistry as a linkage between hydrology and aquatic ecology for a greater understanding of river corridor function in dam-impacted systems. In the following section, we detail an expanded framework describing how subsurface dynamics may propagate to have ecosystem-wide implications in dammed river corridors, and we argue that this integrated view is both a natural intersection of disciplines and essential for sustainable hydropower.

An Expanded Framework: Interconnectivity of Subsurface Hydrobiogeochemistry and Aquatic Ecology in Hydropower-Impacted River Corridors

While hydrology, biogeochemistry, and aquatic ecology are each experiencing significant advances with respect to the impacts of hydropower, integrative frameworks developed in unregulated systems (Dollar et al., 2007; Fisher et al., 1998; Thorp et al., 2010) cannot be directly applied to dam-impacted systems. We assert that a central knowledge gap in sustainably managing these systems is understanding relationships between HEFs, subsurface biogeochemistry, and ecology. We highlight that subsurface biogeochemistry is strongly influenced by HEFs and, in turn, influences resource availability to the base of food webs, thereby mediating dam-impacted connections between HEFs and ecology. These connections also involve feedbacks among all components and may amplify to influence river corridor ecosystem function and health. More specifically, HEFs transport organic compounds that are the product of primary production and the energy source for biogeochemical cycles into the subsurface. HEFs also influence concentrations of complementary resources that accelerate organic matter decomposition, further influencing resource availability for aquatic organisms. Lastly, biogeochemistry and ecology are moderated by thermal regimes, which regulate reaction rates and organismal growth through kinetic mechanisms. Below we detail the nexus of hydrology and aquatic ecology in hydropower-impacted systems through subsurface biogeochemical cycling, focusing on (1) resource supply and (2) kinetics that cascade into whole-ecosystem effects (Figure 4).

Resource Supply Cascades

Organic matter (OM) is a dominant energy source for biogeochemical cycling and a basal energy source for food webs in river corridors. The size and chemical composition of surface and subsurface OM pools are related to river hydrology and can be altered by dam operations (Chen et al., 2016; Hur et al., 2014; Maavara et al., 2017; Oliver et al., 2016; Wohl et al., 2017). Further, because the OM content of groundwater and surface water is often distinct (Graham et al., 2017; Stegen et al., 2018; Stegen et al., 2016) and HEFs mix these water bodies in the subsurface, hydropeaking causes a rapid rise or fall in OM content in surface waters through changes in stage and in subsurface hyporheic zones via HEF-driven mixing of discrete pools. Additionally, connectivity of rivers with their floodplains delivers essential resources to river corridors (Atkinson et al., 2009) and is altered by managed flow regulation. High flow scenarios, which may occur during hydropeaking, deliver high-quality terrestrial OM to rivers by washing material along shorelines into the surface water (Atkinson et al., 2009; Golladay et al., 2000; Meyer and Edwards, 1990), changing the ratio of terrestrial-to-aquatic material directly in surface water OM pools and indirectly within the subsurface. Conversely, low flows decrease surface water OM content and generate patchy nutrient inputs associated with groundwater contribution to surface water (Dahm et al., 2003; Dent and Grimm, 1999). Such events replace natural seasonal changes in OM quality and nutrient availability with pulse-driven nutrient availability (Junk et al., 1989; Ward, 1989). Longer-term changes in flow regimes due to dam operations also redefine the distribution of aquatic primary producers and riparian vegetation which supply OM to the river corridor (Bejarano et al., 2017; Boulton, 1993; Coleman and Dahm, 1990; New and Xie, 2008; Nilsson and Berggren, 2000; Zeug and Winemiller, 2008). Nearshore surface and subsurface zones are therefore a critical linkage for OM and biogeochemical cycles in river corridors (Dahm et al., 2003; Fisher et al., 1998; Grimm and Fisher, 1984). Interactions between short- and long-term implications of dam operations on surface OM content as well as delivery to and cycling within the subsurface is critical for comprehending hydropower impacts within the broader river corridor.

While dam operations can alter subsurface OM pool size and composition, subsequent energy flow through the benthic food web into broader river corridor ecology are not well-understood. Research focused on surface waters has highlighted a linkage between hydrology, OM pools, and food web ecology. For instance, Angradi (1994) describes particulate OM as a driver of aquatic community structure in response to flow variation below the Glen Canyon Dam on the Colorado River (in particular, connections between detritivores and predators). Others note that interactions between invertebrate communities and consumption of different surface water OM pools vary according to position or hydrologic stage within dammed river corridors (Roach and Winemiller, 2015; Short and Ward, 1980), and that hydrologic disturbances impacting vegetation can influence the diversity of sediment biota with follow-on impacts on biogeochemical cycles (Lake et al., 2000). Despite the connectivity between surface and subsurface OM pools via HEFs, our current understanding of trophic cascades induced by shifts in OM does not extend into subsurface domains.

Organic matter directly corresponds to heterotrophic microbial activities that catalyze a suite of biogeochemical processes, and alterations to microbial activity have demonstrated consequences for whole-ecosystem health (Cotner and Biddanda, 2002). Fluctuations in OM pool size have been shown to shift the balance of heterotrophic-to-autotrophic biogeochemical processes (Àvila et al., 2016). Dahm et al. (2003) note that decreases in organic carbon, organic nitrogen, and organic phosphorous are associated with increased microbial autotrophy, an effect that is most pronounced during low-flow periods that increase groundwater discharge. Since OM is a primary energy source for benthic microorganisms, OM pool size and composition putatively correlate to microbial biomass dynamics in the subsurface, subsequently influencing resource availability for river corridor food webs (Figure 4). In particular, increases in autotrophic organisms (e.g., ammonia oxidizers) that result from a decrease in OM content or shift in OM pool composition should alter the availability of inorganic nitrogen to primary producers. Subsurface OM pools therefore not only provide energy for heterotrophs but also have the potential to influence an expansive range of biogeochemical processes that interact with hydrology to determine resources available to benthic food webs. These processes then interact with the broader river corridor through HEFs that transport resources to and from surface waters, magnifying the impact of processes occurring in the subsurface at an ecosystem level.

To the best of our knowledge, no research has attempted to integrate HEF-driven OM cycling in the subsurface and aquatic ecology in dam-impacted river corridors. Dam-associated changes in HEFs that increase the extent of biogeochemical hotspots or hot moments are virtually certain to change OM availability. High-frequency stage variations generated by hydropower have been shown to expand the spatial domain of hyporheic zones by generating larger HEFs [but see (Siergieiev et al., 2014)]. These stage fluctuations can also increase the frequency of hot moments by facilitating fleeting periods of mixing. Theoretically, enhanced hotspots and moments should generate quicker biogeochemical cycles and/or pulsating resource availability that facilitate increased biomass of lower trophic levels (microorganisms and invertebrates). Such a connection would cascade through food web connections in the broader river corridor and indicates a need to incorporate hydrobiogeochemistry within food web models. Subsurface linkages between hydrology and aquatic ecology also combine with changes in resource availability from dam-driven saturation/desaturation dynamics along river shorelines to collectively yield whole-ecosystem impacts (McIntosh et al., 2017). Alterations to resource availability due to hydroelectric dam operations therefore interact with the effects of saturation/desaturation dynamics, potentially increasing invertebrate and embryo mortality rates (Richter and Kolmes, 2005). There are myriad possible alternative scenarios and follow-on effects of dam-driven shifts in OM supply that remain unexplored. Knowledge regarding the OM dynamics that regulate connections between hydrologic and ecological processes would constitute a major step towards more accurate predictions of hydropower impacts.

A number of quantitative tools exist within hydrology, biogeochemistry and ecology that can improve our scientific understanding of hydropower-impacted river corridors. With particular relevance to dam operations, available methods can (1) map OM/nutrient transport and reactivity through watersheds (e.g., reactive transport models, Bisht et al., 2017; Li et al., 2017; Steefel et al., 2015; Steefel et al., 2005), (2) trace resources through aquatic food webs (e.g., stable isotope tracers, Melville and Connolly, 2003; Michener and Kaufman, 2007; Peterson, 1999), and (3) decipher linkages among organisms that are mediated by specific resources (e.g., network and food web analysis, Carlier et al., 2007; Dunne et al., 2002; Krause et al., 2003; Milo et al., 2002; Williams and Martinez, 2000). These methods are commonly used but rarely together and to our knowledge, never in dam-impacted river corridors. In regulated rivers in particular, Angradi (1994) suggested that stable isotopes are effective tools for examining organic matter cycles in relation to food webs due to more exaggerated changes in organic matter composition along dammed river corridors than natural rivers. The application of stable isotopes within biogeochemistry and aquatic ecology could be integrated with hydrologic reactive transport models using an iterative model-experiment approach (ModEx). Additionally, network-based analyses are common in both environmental microbiology (Berry and Widder, 2014; Faust and Raes, 2012) and aquatic ecology (Krause et al., 2003; Milo et al., 2002). They can be employed in combination with isotope tracers and reactive transport models to identify ecologically-important organisms and to elucidate the whole-ecosystem impacts of hydropower operations. Fine tuning these methods for multidisciplinary applications within dammed river corridors would provide an ability to trace hydropower effects on resource availability from the onset of hydrologic disturbance through watersheds and across trophic levels for a broader view of ecosystem health than is currently feasible.

Kinetic Cascades

In addition to changes in resource availability, HEFs also alter temperatures of surface and subsurface environments, consequently regulating biogeochemical and organismal growth rates. Both short- (e.g., hydropeaking) and long-term (e.g., mean stage) hydropower-influenced stage fluctuations alter water and sediment temperatures. As well as discharge frequency, the vertical domain of dam reservoirs that is discharged also has a pronounced effect on surface water temperatures. The cumulative effects of dam releases on surface and subsurface temperatures are dependent on myriad factors, including the magnitude, depth, and purpose of the release (Clarke et al., 2008 and citations therein). Hypolimnetic draws, i.e. releases from deep in the reservoir generally create a summer-cold warm-winter temperature regime, whereby comparatively stable reservoir temperatures mediate seasonal temperature extremes in surface water (Arimitage, 1984; reviewed in Clarke et al., 2008; Edwards, 1978; Paller and Saul, 1996; Preece and Jones, 2002; Ward and Stanford, 1995; Ward, 1974). Conversely, epilimnetic draws from near the reservoir surface may have minimal impact on downstream temperatures or may elevate temperature during the summer months (reviewed in Clarke et al., 2008; Horne et al., 2004; Lessard and Hayes, 2003; Zhong and Power, 1996). While hydropeaking events can cause large daily fluctuations in temperatures, more stable releases can moderate surface water temperature fluctuations and delay spring warming and fall cooling events (Crisp, 1977; Jaske and Goebel, 1967; Ward and Stanford, 1979; Webb and Walling, 1988; Webb and Walling, 1993; Webb and Walling, 1996). Finally, decreased discharge generally impedes a river's capacity for heat assimilation, leading to elevated summer or colder winter temperatures (Gu et al., 1998; Poole and Berman, 2001; Sinokrot and Gulliver, 2000). All these effects also compound with river stage and time of day and/or year, further complicating dynamics.

While surface water temperature effects of flow regulation are well-documented, the extension of this research into subsurface domains that are critical for river corridor health are much sparser. In general when mean surface water elevation is increased, more intrusion of surface water into the subsurface is expected, increasing hyporheic zone temperatures in the summer and decreasing them in the winter, effects that interact with changes in surface water temperature from flow regulation. Under low mean stage, expectations are for increased groundwater discharge, with the hyporheic zone aligning more strongly with temporally-consistent groundwater temperatures. Further, hydropeaking impacts on HEFs drive surface water into the subsurface with temperature effects that are dependent on the relative temperatures of groundwater and surface water at that point in time (Bhaskar et al., 2012; Boano et al., 2014; Burkholder et al., 2008; Francis et al., 2010; Fritz and Arntzen, 2007; Johnson et al., 2015; Sawyer et al., 2009; Zhou et al., 2017). Changes to mean stage also interact with hydropeaking to influence surface water intrusion into the hyporheic zone. Song *et al.* (2018) have recently shown that high-frequency stage fluctuations drive more water into the subsurface than expected when mean stage is low, while hydropeaking under high mean stage has minimal effects on HEFs. The associated temperature changes persist for long periods of time (on the order of many weeks to months) when mean stage is low (Song *et al.* (2018)).

Given temperature-dependencies in biogeochemical rates and organismal ecology, there is potential for thermal impacts of dam operations to intensify through river corridor ecosystems. For example, Lessard and Hayes (2003) demonstrated that epilimnetic draws increased surface water temperature and corresponded to decreases in the abundance of cold-water fish species and changes in macroinvertebrate community composition. Elevated temperature in the hyporheic zone due to summer-time hydropeaking may accelerate organic matter decomposition and thus the supply of inorganic nutrients to primary producers that are key elements of the broader food web (Figure 4). Spillage of warm reservoir surface water due to reduced power demand and/or increased precipitation is likely to have a similar effect. Conversely, hydropeaking during winter or dam discharge from the bottom of reservoirs, should drive cold water into the hyporheic zone and suppress ecosystem functioning through kinetic constraints on biogeochemistry and organismal growth.

While temperature impacts are well-studied in hydrobiogeochemistry (Arora et al., 2016; Dinsmore et al., 2013) and aquatic ecology (Lefebure et al., 2013; Zander et al., 2017), there has been little integration across these domains despite their natural connectivity. To reveal how thermal impacts of dam operations circulate through river corridors, we propose integration of reactive transport and river routing models with food web modelling. Specifically, existing hydrobiogeochemical models used to predict heat transport and biogeochemical rates (e.g., Diersch, 2013; Song et al., 2018) and hydrologic flow (e.g., Gomez-Velez and Harvey, 2014) could be coupled to ecological models (e.g., Buchkowski et al., 2017) incorporating biomass changes in specific categories of organisms that span trophic groups (e.g., Grandy et al., 2016). Manipulative laboratory-based experiments and continuous field-based measurements of thermal and hydrologic properties can further enhance and evaluate computational outcomes. This approach will enable predictions of feedbacks among hydrology, temperature, biogeochemical rates, organismal abundances, and resource transfer across trophic levels. Such an effort will require close collaboration between aquatic ecologists that specialize in quantifying food web structure and hydrobiogeochemists that routinely quantify temperature-dependent reaction rates and apply reactive transport models. By expanding reactive transport and river routing models to encompass aquatic ecology, we can gain knowledge on whole-ecosystem effects of hydropower operations that can be used to inform sustainable operation of hydropower infrastructure.

Conclusion

Our understanding of the cumulative effects of dam operations on the interactions among HEFs, subsurface biogeochemistry, and ecology in river corridors is in its infancy. It is essential to understand these influences across both surface and subsurface domains and to provide comprehensive science to stakeholders responsible for dam operations and maintaining ecosystem health. In addition, to enable robust predictions under future environmental conditions, it is important to elucidate general principles that apply across systems and environmental contexts. This can be achieved through efforts that use consistent observational, experimental, and/or modeling approaches across a broad range of field systems. There are an increasing number of such efforts, but none that specifically focus on the connections among river corridor food webs and subsurface hydrobiogeochemistry in dam-impacted systems. Related efforts do exist, however, that could be leveraged. For example, the Worldwide Hydrobiogeochemistry Observation Network for Dynamic River Systems (WHONDRS) uses a distributed science approach to study the biogeochemistry, microbiology, and hydrology of dynamic river corridors, including dam-impacted systems (Stegen and Goldman, in review). The '1000 intermittent rivers project' is another example of a distributed science approach with an emphasis on the functioning of dynamic river corridors (Datry et al., 2018). In principle, the system-by-system biogeochemical and hydrologic context provided by both of these efforts could be leveraged by an additional distributed science effort focused on river corridor food webs. Explicitly linking efforts in this way would provide novel opportunities to work towards truly integrated understanding of the interactions among physical, chemical, and biological features of dam-impacted river corridor ecosystems.

Elucidating general principles that connect food webs with subsurface hydrobiogeochemistry across dam-impacted systems has far-reaching societal implications given that dammed river corridors regulate energy and/or water availability to almost 500 million people globally and are expanding rapidly (Richter et al., 2010). In this paper, we articulate the interconnectivity of hydrology and aquatic ecology through HEFs and subsurface biogeochemical cycling that mediate resource availability and thermal properties. We view an integrated approach to investigating these systems that includes a greater understanding of linkages between surface and subsurface processes as imperative given the ability we have to mitigate harmful impacts of hydropower through management practices (Kiernan et al., 2012). We advocate the extension of cross-disciplinary concepts to advance knowledge on the ecosystem-wide ramifications of hydropower operations, and we encourage the broader scientific community to place their research within the context of multidisciplinary river corridor science for sustainable management of hydropower projects.

Acknowledgements

This research was supported by the US Department of Energy (DOE), Office of Biological and Environmental Research (BER), as part of Subsurface Biogeochemical Research Program's Scientific Focus Area (SFA) at Pacific Northwest National Laboratory (PNNL). PNNL is operated for DOE by Battelle under contract

DE-AC06-76RLO 1830. This paper is part of the Worldwide Hydrobiogeochemical Observation Network for Dynamic River Systems collaborative project (WHONDRS, https://sbrsfa.pnnl.gov/whondrs.stm), an international investigation of hydrobiogeochemistry in dynamic river corridors. We thank the rest of the PNNL-SBR project members for conceptual guidance and Jeff Holmes and Andrew Pitman for assistance in text editing.

Figures

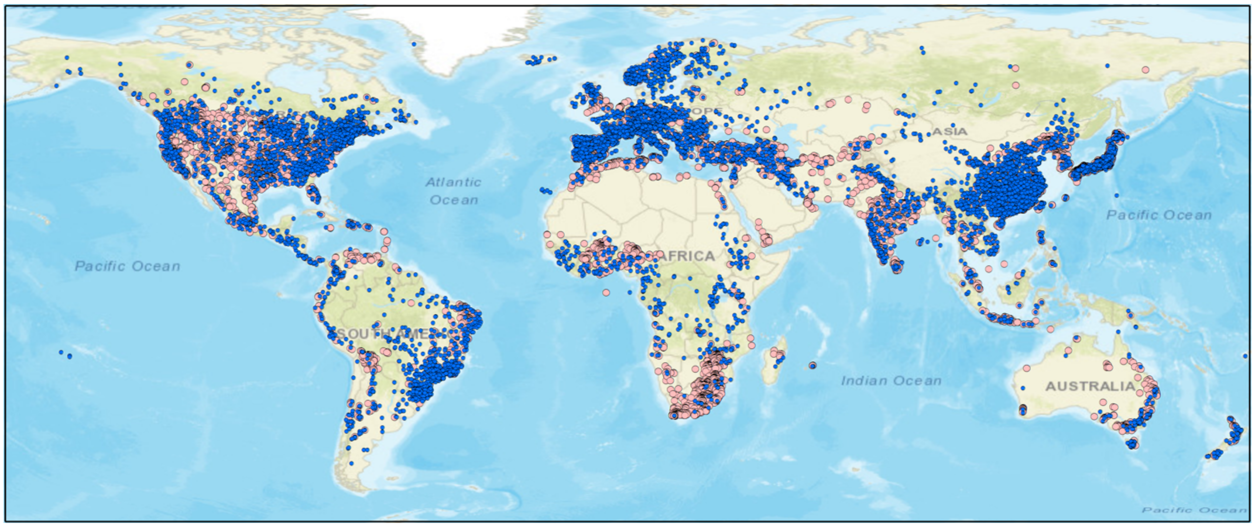

Figure 1. Global distribution of large dams. Blue dots represent dams with hydropower capacity and pink dots represent dams without hydropower. Data were obtained in November 2017 from three online databases: International Commission On Large Dams (ICOLD, http://www.icold-cigb.org), Global Reservoir and Dam Database (GRanD, http://www.gwsp.org/), and United Nations Food and Agriculture Organization AQUASTAT Database (http://www.fao.org/nr/water/aquastat/).

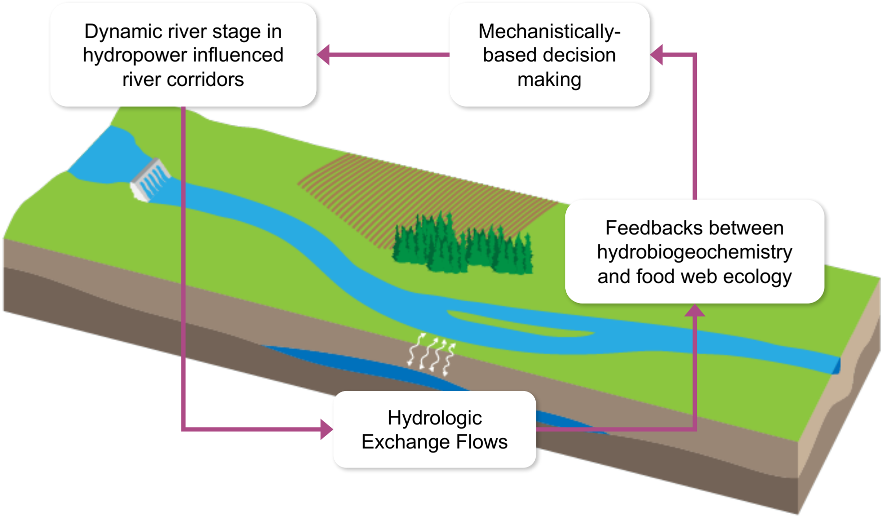

Figure 2. Simplified schematic of HEF-driven ecosystem functioning in hydropower systems. Hydropower generates dynamic river stages which in turn modify hydrologic exchange of surface water and groundwater through hyporheic zones adjacent to river channels. These altered-HEFs impact biogeochemical reaction rates via resource availability and thermal changes, effects that subsequently cascade through aquatic food webs. Integrating knowledge from hydrology (HEFs) and aquatic ecology (food webs) via biogeochemistry allows for management of dam operations that considers the full suite of mechanisms driving ecosystem health. Improved management practices can optimize river stage fluctuations to minimize harmful ecological impacts of hydropower (Bruder et al., 2016; Harnish, 2017; Jones, 2014; Richter and Thomas, 2007).

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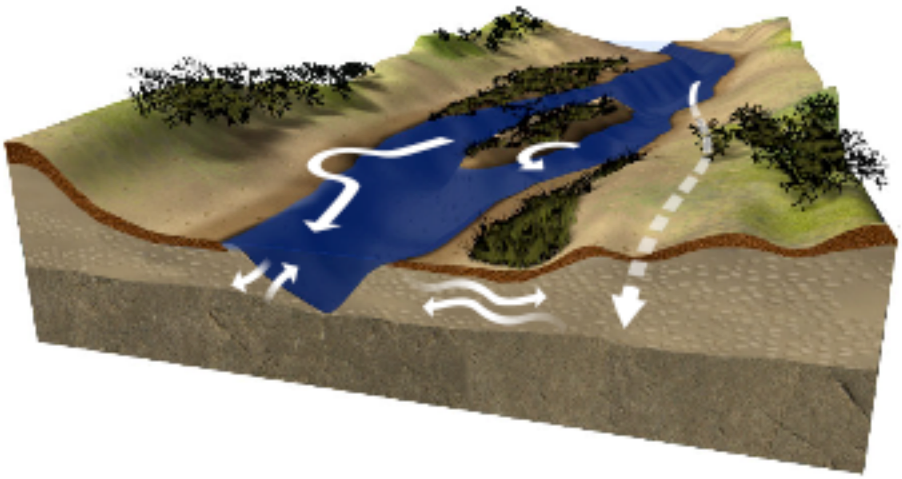

Figure 3. Depiction of hydrologic exchange flows (HEFs) in a river corridor. Hydrologic exchange flows (HEFs) exchange water and their associated thermal and chemical properties between surface water and groundwater. Examples of HEFs are shown by white arrows. Because the magnitude and directionality of HEFs are tightly correlated to river stage, hydropower-impacted systems experience dynamic HEFs that impact river corridor biogeochemistry and ecosystem health.

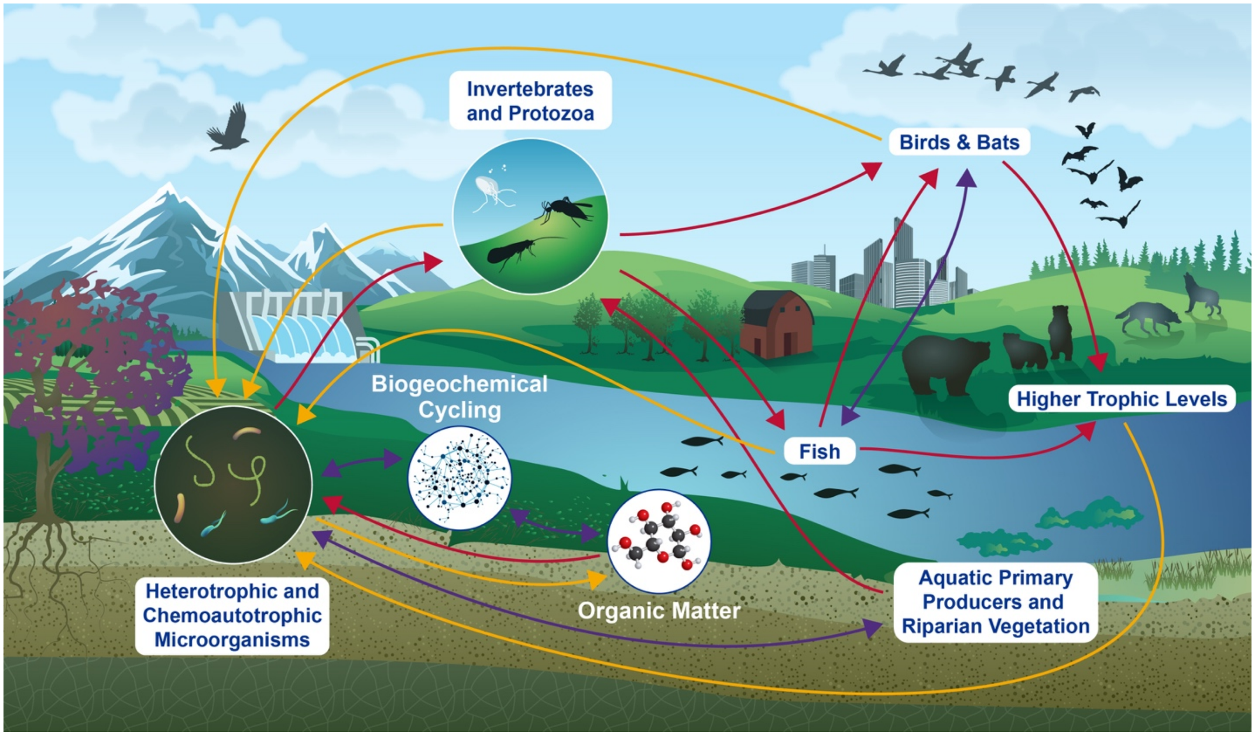

Figure 4. Simplified conceptualization of integrative hydrobiogeochemistry and aquatic ecology for sustainable hydropower. Hydrology and aquatic ecology in dam-driven systems are inherently linked through biogeochemistry, which is strongly impacted by dynamic hydrologic exchange flows (HEFs) and lies at the base of aquatic food webs. HEF-driven biogeochemistry controls resource availability and kinetic constraints on aquatic ecology through chemical and thermal processes. Flows of matter and energy in the expanded hydrobiogeochemical-ecological framework are shown within a simplified aquatic food web. Although myriad connections exist within food webs, we depict a simplified web for clarity in visualizing the dependency of aquatic food webs on hydrobiogeochemistry. Red arrows show energy flow up trophic levels via consumptive processes. Yellow arrows show decay from higher trophic levels into OM pools via microbial processes that drive the aquatic food web. Purple arrows show competition and bidirectional influences between organisms and/or chemical pools. Biogeochemistry, and OM in particular, are regulated by hydrologic processes associated with

groundwater-surface water mixing. The influences of these processes propagate through aquatic food webs, as depicted by the arrows, to impact whole-ecosystem health. Incorporating this expanded conceptualization for a holistic understanding of the linkages between hydrology and ecology is vital for managing dam operation to minimize harmful ecological impacts in dynamic hydropower-influenced river corridors.

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