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Conceptualizing Ecological Responses to Dam Removal: If You Remove It, What’s to Come?


One of the desired outcomes of dam decommissioning and removal is the recovery of aquatic and riparian ecosystems. To investigate this common objective, we synthesized information from empirical studies and ecological theory into conceptual models that depict key physical and biological links driving ecological responses to removing dams. We define models for three distinct spatial domains: upstream of the former reservoir, within the reservoir, and downstream of the removed dam. Emerging from these models are response trajectories that clarify potential pathways of ecological transitions in each domain. We illustrate that the responses are controlled by multiple causal pathways and feedback loops among physical and biological components of the ecosystem, creating recovery trajectories that are dynamic and nonlinear. In most cases, short-term effects are typically followed by longer-term responses that bring ecosystems to new and frequently predictable ecological conditions, which may or may not be similar to what existed prior to impoundment.

Keywords: dam removal, river restoration, disturbance, conceptual models, ecological modeling

Once a river is dammed, is it damned forever? The purposeful removal of dams has accelerated in the last several decades. In the United States alone, over 1400 dams have been deliberately removed since the 1970s, and the pace of removal will likely continue as many dams approach the end of their engineered life expectancies (Doyle et al. 2008, O’Connor et al. 2015, American Rivers 2018). Although dams are removed for multiple reasons (e.g., safety, costs, loss of function), a common objective is the recovery of ecosystem function, often centered on species of economic and cultural importance (Bednarek 2001). But do ecosystems recover after dam removal? And do they recover to a condition similar to what existed prior to dam emplacement or have factors—both intrinsic and extrinsic—changed such that the newly undammed river enters a new ecological state? These questions are challenging, but understanding and predicting ecological responses to dam removal is crucial for prioritizing which dams to remove and how to remove them (Poff and Hart 2002), as well as for setting realistic expectations about the magnitude and timing of ecological recovery, which may lag far beyond dam removal.

A challenge in understanding and predicting recovery trajectories is that ecological responses vary spatially and temporally. The local and regional context of each dam is distinct, and therefore, the responses to removal are—more often than not—unique (Foley et al. 2017a). In addition, the size and purpose of a dam affects the method and pace of its removal and the magnitude and timing of potential ecological perturbations and recovery. And for rivers with multiple dams, the outcomes of any one dam removal depend on the watershed location (upstream or downstream) and context (e.g., purpose, management practices) of any remaining dams (Skalak et al. 2013, Foley et al. 2017a).

Despite the importance of the physical and ecological context of the specific dam and river, we suggest that ecological responses to dam removal are generally governed by shared sets of physical and biological links and feedbacks among the ecosystem’s components, creating recovery trajectories that are dynamic and nonlinear. In most cases, short-term effects are typically followed by longer-term responses that bring ecosystems to new and frequently predictable ecological conditions, which may or may not be similar to what existed prior to impoundment.
The ever-increasing number of empirical dam-removal studies provides the basis for understanding these links and feedback loops (Bellmore et al. 2017a). However, these empirical studies individually have limited inferential power (Hart et al. 2002). Most dam-removal studies are of short duration (1–2 years) and, therefore, provide only narrow windows onto the ecological response at a specific site (Bellmore et al. 2017a). Moreover, in many studies, responses are monitored only for specific species or trophic levels and, therefore, lack the ecological resolution necessary to mechanistically explain observed responses (Bellmore et al. 2017a). Nevertheless, we synthesize these studies by weaving together the threads of empirical information into a tapestry patterned with broader ecologic theory and knowledge. Empirical studies provide information on specific elements of the ecosystem, and conceptual models and theory guide predictions of how the different elements interact—the links and feedback loops that drive system behavior.

Using this approach, we develop conceptual ecological-response models for three distinct spatial domains affected by dam removal: upstream of the reservoir, within the former reservoir, and downstream of the removed dam (figure 1). We use these conceptual models to explore the ecological responses likely to emerge from the physical and ecological links in each spatial domain, and we illustrate how these models can be used to inform numerical modeling efforts. These models provide a needed systems approach to our conceptual understanding of the ecological responses to dam removal and build on recent syntheses of physical processes (Major et al. 2017), management concerns (Tulloch et al. 2016), and the landscape context of biophysical responses to dam removal (Foley et al. 2017a).

**Conceptual models of river ecosystem response: Assembling the pieces**

The conceptual models for each spatial domain (figures 2, 3, and 4) are framed as causal-loop diagrams depicting relations among key physical and biological components of the ecosystem. From these links, we postulate longer- and shorter-term ecological responses to dam removal in each domain as a function of overall watershed conditions and history (figure 5). Although some ecological responses to dam removal are conceptually and even quantitatively predictable, responses commonly follow a transient, nonlinear pathway. We refer to this as an ecological response trajectory. Although it is theoretically possible to duplicate a previously observed trajectory, variation in the local and regional context of each dam assures that most dam removals will have different ecological response trajectories, even if they follow similar generalized forms.

**Short and long term** are difficult to define precisely for these conceptual models, because events may occur relatively quickly (e.g., months) for some removals but much slower (e.g., decades) for others. Short-term responses are generally those directly associated with the removal sequence, such as reservoir sediment release and associated habitat and organismal impacts. Long-term responses are those associated with trajectories toward a new dynamic equilibrium, such as the reestablishment of organisms following the initial release of reservoir sediments. The duration of short- and long-term effects is governed by the specific controlling processes, the manner and rate of dam removal, and its overall watershed and ecological context. But in all cases, short-term refers to those physical and ecological responses that occur prior to long-term responses and vice versa.

We focus on the effects of dam removal on taxonomic groups of aquatic and riparian organisms (fishes, aquatic invertebrates, aquatic primary producers, and riparian vegetation). We intentionally omit the identity of specific
Recolonization is self-reinforced by feedback loops that promote productivity and diversity of upstream habitats. The shaded shapes indicate key ecological parameters. The arrows indicate the direction of influence, and the plus and minus signs indicate whether the influence is positive or negative. When they are positive, the variables change in the same direction (when causal variable increases the effected variable also increases or vice versa). When they are negative, the variables change in the opposite direction (when causal variable increases the effected variable decreases or vice versa). Causal links that control responses at short time scales (hours to years) and long time scales (years to decades) are shown in orange and yellow, respectively.

Upstream of the former reservoir: Going against the flow

Conceptual models of river ecosystems frequently emphasize downstream fluxes of nutrients, organic matter, and organisms (Vannote et al. 1980, Newbold et al. 1981, Humphries et al. 2014). However, upstream movement of organisms, such as fish, are also crucial to the function of river ecosystems (Pringle 1997). Dams can reduce biodiversity and productivity by severing these upstream flows (Pess et al. 2008). When dams are removed and longitudinal connectivity is restored, fishes, invertebrates, and commensal microorganisms living on or within these mobile species can recolonize (or initially colonize) upstream habitats. This upstream movement of organisms is a major driver of ecological responses above the former dam and reservoir (figure 2).

As is illustrated in the upstream causal-loop diagram in figure 2, reestablishment of longitudinal connectivity can increase species richness, life history diversity, and the delivery of nutrients and organic matter upstream of the former dam. For example, in the midwestern and eastern United States, low-head dam removals resulted in increased numbers of fish species upstream of the former dam sites (Burdick and Hightower 2006, Catalano et al. 2007, Burroughs et al. 2010, Magilligan et al. 2016). Upstream migration was evident within weeks or months of the dam removals, and up to 95% of all species found downstream of the dams migrated upstream within 1–3 years (Burdick and Hightower 2006, Catalano et al. 2007, Burroughs et al. 2010, Hitt et al. 2012). Colonizers deliver nutrients and organic matter sequestered in downstream habitats (including the ocean in coastal dam removals) that can be incorporated into aquatic and riparian food webs (Gende et al. 2002, Pess et al. 2014). Within a year following the removal of Elwha Dam (one of two large dams removed from the Elwha River, Washington), marine-derived nutrients from adult Pacific salmon were detected upstream of the former dam site in American dippers (Cinclus mexicanus)—an obligate aquatic songbird that feeds on aquatic invertebrates, small fish, and salmon eggs (Tonra et al. 2015).

Changes in life-history diversity above former dams are not as well documented as changes in species richness and nutrients. However, once-isolated fish populations can reexpress migratory life-history strategies once downstream connection is reestablished (Morita et al. 2000, Pascual et al. 2001, Quinn et al. 2017). For example, before the Elwha River was dammed, it had a high proportion of stream-type juvenile Chinook salmon that reared in freshwater for 1 year, relative to ocean-type fish that migrated to sea within months of emergence (Pess et al. 2008). The expression of the stream-type life history was generally confined to the
colder waters upstream of the former dams. After the Elwha was dammed, Chinook salmon were restricted to warmer reaches lower in the river, promoting an ocean-type life history strategy (Pess et al. 2008). Within the first 3 years after the dam removals, adult Chinook recolonized and began spawning upstream of the former dam sites, and some of these fishes began adopting a stream-type life history.

Following the necessary first step—removing a dam—the recovery process can be reinforced by positive ecological feedback loops (figure 2). These feedbacks likely operate at longer time scales of years to decades and are yet to be observed following dam removal but are nevertheless supported by the broader ecological literature. We note three example ecological feedback loops. First, nutrients and organic matter delivered by organisms colonizing upstream can enhance biological productivity or food availability for consumers in receiving waters. In turn, enhanced productivity may increase the rate of colonization and success of colonizers. This feedback may be particularly important when upstream habitats are recolonized by keystone species that strongly affect aquatic or riparian communities and food webs, such as anadromous salmonids (Gende et al. 2002, Morley et al. 2016) and amphidromous fishes and shrimp in tropical rivers (Pringle et al. 1999). Second, increased life-history diversity promotes species persistence and colonization. Species that exhibit a diversity of life histories are more resilient to environmental change, are less likely to experience local extirpation (Schindler et al. 2010), and are more likely to have migratory variants that can recolonize after disturbances (Waples et al. 2009). Third, having a greater number of species (species richness) may, in some cases, reduce extinction rates by stabilizing community dynamics, as has been postulated through theoretical and mathematical models, as well as observations that more diverse communities are more stable (McCann 2000). For instance, greater species richness is often associated with more complex food webs that have a higher proportion of weak predator–prey interactions that counteract the destabilizing effects of strong interactions (McCann 2000). Moreover, the reestablishment of organism movement across the river network could allow recoupling of previously isolated food webs (by movement among upstream, downstream and tributary habitats); these spatially structured meta food webs may also promote community stability and species persistence (Bellmore et al. 2015). As is indicated in figure 2, these feedback loops likely interact among each other to affect the overall ecological response.

On the basis of these hypothetical causal links and feedbacks, we expect the upstream ecological response trajectory following dam removal to be roughly sigmoidal in shape (figure 5). Responses can occur relatively quickly following dam removal and may be reinforced by positive feedback loops. However, overall ecosystem recovery is limited by the availability of colonizers. Therefore, the recovery process will slow as upstream species and life-history diversity approach the levels found in the downstream river network (Pess et al. 2012). Moreover, if some life-history variants or species have been extirpated while the dam was in place, a full recovery that approaches pre-dam conditions may not be possible without interventions, such as species reintroduction. Altered environmental conditions, particularly flow, sediment, and temperature, may limit the suitability of upstream habitats to possible colonizers (Anderson et al. 2014). In particular, the presence of other upstream dams may limit the spatial scope of recovery and the suitability of upstream habitats. Dam removal may also facilitate the spread of undesirable, nonnative, or highly invasive species upstream of the former dam site (Doyle et al. 2005, Kornis et al. 2015). In such cases, the response trajectory for native species may be negative, creating conflicting conservation outcomes (Fausch et al. 2009, Tullos et al. 2016).

Within the former reservoir: Ponds to rivers

The former reservoir can be the reach most altered physically and ecologically by both dam emplacement and dam removal. When a dam is constructed, the impounded reach is often converted from a flowing river (lotic) to a slower, lake-like (lentic) environment that stores sediment, organic matter, and nutrients and that favors organisms adapted to slower waters (Ward and Stanford 1983). Removing the dam starts a sequence of commonly rapid physical and hydrologic changes, whereby the reservoir reverts back to a flowing river. These profound physical changes trigger large ecological responses within the former reservoir (figure 3).

Conversion from a lentic to a lotic system following dam removal can drive fundamental shifts in community structure (figure 1). As the reservoir is drained, the water depth decreases, and the flow velocity increases. These hydraulic changes, in turn, adversely affect pelagic organisms, such as plankton and lentic-adapted fishes (Foley et al. 2017b). Plankton can be exported downstream, and aquatic vegetation growing in the littoral zone can be stranded on reservoir margins. At the same time, these new hydraulic conditions favor organisms adapted to flowing waters (e.g., Ephemeroptera, Plecoptera, Tricoptera [EPT]; Smokorowski et al. 2011), create better foraging conditions for lotic fish species, and allow more light to penetrate to the streambed, facilitating benthic primary production (Allen and Castillo 2007). The spatial and temporal trajectories of these processes, however, are strongly controlled by the size of the dam and reservoir, the rates and processes of reservoir sediment erosion, and the ensuing channel dynamics within the evolving reservoir reach. For instance, ecological transitions may occur quickly behind shallow run-of-the-river dams, where lotic species predominate before the dam is removed.

Dam removal typically causes erosion of the sediment accumulated in the former reservoir as the base level of the dam is lowered (Major et al. 2017). Dynamic channel processes erode and transport reservoir sediment downstream and can initially create bed conditions too transient to support benthic producers and consumers—particularly during and immediately after removal. However, as sequential
Figure 3. Causal-loop diagram depicting the cause-and-effect links and associated feedback loops influencing dam removal responses within the former reservoir. Sediment erosion and changes in channel hydraulics alter the environment from one that favors pelagic production and lentic fish assemblages to one that favors benthic production and lotic fish assemblages. The shaded shapes indicate key ecological parameters. The arrows indicate the direction of influence, and the plus and minus signs indicate whether the influence is positive or negative. When they are positive, the variables change in the same direction (when causal variable increases the effected variable also increases or vice versa). When they are negative, the variables change in the opposite direction (when causal variable increases the effected variable decreases or vice versa). Causal links that control responses at short time scales (hours to years) and long time scales (years to decades) are shown in orange and yellow, respectively.

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hydrologic events winnow these sediments, feedback processes can result in a more stable streambed (Collins et al. 2017). Rapid river incision into stored sediments commonly forms knickpoints (abrupt changes in riverbed slope) that migrate upstream of the former dam site (e.g., Randle et al. 2015, Major et al. 2012, 2017). Downstream of the knickpoint, bank failures and lateral channel migration accelerate overall reservoir erosion (Evans 2007). Reservoirs can lose 50% or more of their impounded sediment volumes within the first few weeks to months after dam removal (Wilcox et al. 2014, Warrick et al. 2015, Major et al. 2017). However, as sequential flows entrain the most mobile sediments, channels tend to stabilize (Collins et al. 2017), facilitating a shift from pelagic to benthic communities. Over years to decades, riparian vegetation can recolonize and further stabilize reservoir terraces and stream banks (Orr and Stanley 2006, Shafroth et al. 2002), although colonization by invasive vegetation species is a management concern (Tullos et al. 2016). Riparian vegetation that establishes after removal also contributes leaf litter and terrestrial invertebrates to the river—important allochthonous inputs providing energy for aquatic food webs (Wallace et al. 1999, Baxter et al. 2005).

Contrasting with upstream habitats, causal links and feedback loops operating in the former reservoir reach commonly produce a shorter-term (days to years) perturbation response to dam removal, largely driven by sediment erosion and dynamic channel processes. Over longer time scales (months to decades), this initial perturbation response will typically transition toward ecological recovery and a new equilibrium condition as reservoir sediment stabilizes and more natural flow, temperature, and sediment regimes are reestablished (figure 5). The strength and duration of the initial perturbation and subsequent geomorphic and ecological responses will vary according to the magnitude of change, which depends on physical aspects such as the dam's size, the reservoir's sediment volume and composition, the watershed area, and the overall sediment supply that accumulated during the dam's presence (Bednarek 2001). Studies of aquatic invertebrate and fish responses to dam removal generally support this trajectory (Bushaw-Newton et al. 2002, Stanley et al. 2002, Dorobek et al. 2015). In a meta-analysis of numerous dam removals, Carlson and colleagues (2018) found that lentic invertebrates first declined in density after dam removal but subsequently recovered within 15–20 months. During the recovery phase, lotic invertebrate taxa, such as EPT, tended to become more prevalent (Bushaw-Newton et al. 2002), attaining community assemblages similar to upstream free-flowing reference sites (e.g., Stanley et al. 2002). Shifts in the aquatic invertebrate community may not increase species richness or diversity, however, because similar numbers of taxa may be lost and gained in the shift from lentic to lotic conditions. Nevertheless, increases in invertebrate taxa richness, biomass, and density are evident in some former impoundments following dam removal (Thomson et al. 2005, Hansen and Hayes 2012, Carlson et al. 2018). In some settings, fish diversity has increased following dam removal, likely because of restored longitudinal connectivity and the development of more suitable habitats in the former reservoir (Catalano et al. 2007, Foley et al. 2017a, 2017b), such as the formation of riffles that are important habitats for many riverine fishes and invertebrates (Cook and Sullivan 2018). Changes in aquatic–terrestrial trophic
Ecological recovery may be rapid—months to years—particularly if the geomorphic response is swift. The long-term ecologic conditions, however, may or may not resemble the predam conditions (figure 5). Similar to the upstream domain, the former reservoir is more likely to trend toward its predam conditions if the species and life-history variants that existed prior to the dam's emplacement are still present and capable of colonizing. Similarly, the presence of nonnative species, incomplete export of sediment from the former reservoir (Tullos et al. 2016), contaminants (Magilligan et al. 2016), and other watershed-scale land-use changes, such as other dams or altered hydrology and water temperature, may prevent former reservoirs from attaining predam ecological conditions (e.g., Hobbs et al. 2009).

**Downstream of the dam: Here it comes!**

Dam-induced changes in natural flow, temperature, sediment, nutrient, and organic matter regimes (Ward and Stanford 1983, Humphries et al. 2014, Wohl et al. 2015) significantly alter the structure and function of downstream ecosystems. In reaches downstream of removed dams, the return of these “natural” regimes—to which many native organisms are adapted—provides an opportunity for ecological recovery (Bednarek 2001). But removing dams also releases decades or more of stored sediment, which affects habitat structure downstream for years or longer (Major et al. 2017). Ecological responses in the downstream domain are determined by the relative effects of initial fluxes of water, sediment, and organic materials from the reservoir reach in conjunction with the longer-term effects of reestablished river network connectivity (figure 4).

Short-term downstream ecological responses (days to years) for most dam removals owe chiefly to reservoir sediment erosion, which increases the downstream transport and deposition of sediment, nutrients, and organic matter and temporarily raises water turbidity (figure 4). The initial deposition of reservoir sediment, in turn, disturbs benthic organisms (algae, invertebrates, and fish eggs) by burial and suffocation (Sethi et al. 2004, Orr et al. 2006) and creates an unstable streambed not suitable for many species (Collier 2002). These effects can temporarily decrease the abundance and richness of downstream periphyton and invertebrate communities after the dam’s removal (Chiu et al. 2013, Carlson et al. 2018) and can shift invertebrate assemblages to more disturbance-oriented taxa (Renöfält et al. 2013). For instance, Orr and colleagues (2006) observed significant decreases in benthic chlorophyll a and invertebrate density associated with downstream sediment deposition at two small dam removals in Wisconsin. Increased water turbidity following a dam’s removal may also reduce primary production by limiting light penetration (Morley et al. 2008). High turbidity from suspended sediments can also negatively affect fish via reduced foraging efficiency, physical abrasion, clogging of gills, and interference with orientation (Kjelland...
et al. 2015). However, the greater mobility of fishes than
of invertebrates, as well as their adaptation to seasonally
high flows and sediment loads, may limit direct mortality.
Nonetheless, in some cases, lowered fish abundance after
a dam’s removal has persisted for as long as 15 years before
populations increased (Burroughs et al. 2010). These per-
turbations are likely to be strongest immediately below the
removed dam and to dissipate downstream with sediment
diffusion and tributary influences.

Nutrients and organic matter associated with reservoir
sediments may buffer aquatic organisms from some of
these negative impacts (figure 4). Although this effect has
not yet been empirically documented in dam removal stud-
ies, increased nutrient loads can result in increased aquatic
primary production where the bed is stable and light levels
are adequate (Allan and Castillo 2007). Moreover, organic
matter from the reservoir may provide food for heterotro-
phic microbes and invertebrates. This may stabilize higher
trophic level production during the initial sediment dis-
turbance by shifting the food web from reliance on green
(periphyton, macrophytes) to brown (detritus) sources
of energy (Wolkovich et al. 2014). Additional research
is needed to quantify the strength of these potentially
stabilizing links.

Although sediment deposition may initially perturb
aquatic organisms and riparian vegetation, it is also a
resource for ecological recovery. Sediment-starved river
channels downstream from dams can become incised,
armored, and disconnected from their floodplains (Ligon
et al. 1995). Deposition and subsequent redistribution of
reservoir sediments create new gravel bars, a more hetero-
genous streambed, and more suitable spawning habitats
for nest-building fishes (Kibler et al. 2011). Entrained res-
ervoir sediments can also aggrade downstream channels
and reconnect lateral floodplain habitats (East et al. 2015,
Magilligan et al. 2016). Increased channel migration, cre-
ation of new gravel bars, and sediment deposition on flood-
plains provide new surfaces for colonization by pioneer plant
species and potentially restore a shifting riparian habitat
mosaic (Shafroth et al. 2002, 2016). Moreover, reestablish-
ment of downstream transport of plant seeds from upstream
of the former dam may facilitate vegetation recovery on new
floodplain surfaces (Cubley and Brown 2016)

Over timescales of years to decades, physical and eco-
logical recovery are strongly controlled by the reestablishment
of natural flow, temperature, sediment, nutrient, and organic
matter regimes to which native organisms are adapted (Ward
and Stanford 1995). For example, the reestablishment of
more natural hydrologic and sediment regimes typically cre-
ates more dynamic river channels, promoting greater habitat
diversity for aquatic and riparian species (Poff et al. 1997,
Wohl et al. 2015). This is yet to be documented for many
recent dam removals, because many have been relatively
small, run-of-the-river dams that did not significantly alter
downstream material and energy fluxes. As larger dams are
removed, such as the Elwha River dams and the pending
removals of those on the Klamath River (California and
Oregon), physical and ecological recovery will depend on
the extent to which these natural regimes are restored.

Similar to those in the former reservoir, causal links and
feedback loops in the downstream domain are likely to
produce an initial perturbation response to dam removal—
primarily associated with transport and deposition of reser-
voir sediment—followed by evolution to new geomorphic
and ecological conditions associated with reestablishment
of unimpeded fluxes of water, energy, and materials from
the upper watershed (figure 5). The timing, magnitude, and
duration of the initial perturbation response to dam removal
depends on the amount and locations of sediment deposited
downstream (Orr et al. 2008, Chiu et al. 2013, Tullos et al.
2014, East et al. 2015), which are a function of the amount
of sediment stored in the former reservoir and the ability of
the river to mobilize this sediment (Major et al. 2017). Recovery
follows this initial perturbation as reservoir erosion slows
and the downstream sediment pulse disperses, but the over-
all magnitude of recovery may vary considerably, depending
upon local and regional conditions. Evolution of physical
and ecological conditions may tend toward a state similar to
the dammed condition, the predam condition, or some new
condition (figure 5), depending on a broad range of watersh-
shed and land-use factors (Foley et al. 2017a). For instance,
predam ecological conditions are unlikely if natural flow,
temperature, sediment, and nutrient regimes remain altered
by other dams, if reservoir sediment contains contaminants,
and if nonnative species are present.

**Interactions across spatial domains**

The river connects all three spatial domains as a corridor
for upstream and downstream fluxes of energy, materi-
als, and organisms. Therefore, dam-removal responses in
one domain can accelerate or attenuate the rate of change
and subsequent recovery in other domains. One obvious
interdomain interaction is reservoir sediment erosion and
downstream deposition. Prolonged erosion of sediment
from the former reservoir could slow downstream ecological
recovery. In turn, the rate of downstream ecological recovery
could influence the timing, composition, and magnitude of
upstream organism colonization. Understanding these links
may influence decisions on the rate and style of dam removal.
For situations in which voluminous or contaminated reser-
voir sediments are present, dam removal practitioners may
decide to remove or stabilize reservoir sediments as part
of the dam-removal process (e.g., Randle and Greimann
2006, Woelfle-Erskine et al. 2012) to protect downstream
communities. The condition of the river network upstream
of the dam and reservoir may also influence downstream
recovery. For example, ecological recovery in the reservoir
and downstream reaches depends in part on colonization
by organisms from upstream, such as aquatic invertebrates
that actively and passively drift downstream (Naman et al.
2016). Downstream recovery may be hampered if the diver-
sity and abundance of these potential colonizers has been
compromised by factors such as land use, other dams, and invasive species.

One frequently overlooked interaction is the influence of tributaries and floodplain channels on ecological recovery. Floodplain side channels and tributaries can serve as refuges during the initial downstream sediment disturbance and potentially provide important source populations for river network colonization, assuming they are not buried by sediment (Pess et al. 2008, Peters et al. 2017). For example, adult coho salmon in the Elwha River (Oncorhynchus kisutch) were actively relocated to tributaries upstream of the lower dam to accelerate recolonization early in the dam-removal process when suspended-sediment concentrations and potentially deleterious effects were greatest (Liermann et al. 2017). These transplanted coho salmon immediately spawned, which resulted in levels of smolt out-migrants that were comparable (per stream kilometer) with other established populations in the Pacific Northwest, even during high suspended-sediment levels in the mainstem Elwha River (Liermann et al. 2017).

**Quantitative modeling and prediction**

Although conceptual models are valuable for generating hypotheses, the many links and feedback loops in these models make it difficult to predict responses at a given location without quantifying the strength and character of these interactions. Our conceptual models provide blueprints for assembling quantitative models, whereby links between system elements are replaced with quantitative statements. The resulting models can be used to numerically model potential ecological responses to dam removal. In some circumstances, models may already exist and could be modified to represent processes in each spatial domain. For instance, population-dynamics models could be used to simulate species recolonization in the upstream domain (e.g., Pess et al. 2012). In former reservoir reaches, hydraulic and sediment-transport models could be linked to habitat-suitability models to explore how dam removal influences the quantity and quality of habitat available for benthic organisms and fishes (e.g., Gillenwater et al. 2006).

To illustrate how quantitative models can be used to explore ecological responses to dam removal, we simulated response trajectories for aquatic producers (periphyton) and consumers (fish and invertebrates) just downstream of a hypothetical dam removal using the aquatic trophic productivity (ATP) model (Bellmore et al. 2017b), a food-web model that includes many of the response variables of interest in dam removal (figure 6). The ATP model is a dynamic river food-web model (e.g., Power et al. 1995), whereby aquatic organisms—as well as dead organic matter—are compartmentalized into trophic groups that share similar predators and prey (figure 6). The biomass dynamics of this generalized food web and the success of specific trophic groups are linked in the ATP model to the physical, ecological condition.
We parameterized the model with idealized physical and chemical dam-removal response trajectories. These hypothetical trends indicate possible effects following a rapid dam removal (figure 6). We assumed that water turbidity and nutrient concentrations would peak quickly following dam removal and decay exponentially, that benthic substrate size would first decline with deposition of reservoir sediments but would later coarsen as finer sediments were exported and that bankfull depth would decline, bankfull width would increase, and channel gradient would decrease with deposition of reservoir sediments and reestablishment of natural flow and sediment regimes. In specific applications, these model inputs could be estimated prior to dam removal from physical and hydraulic models (e.g., Cui et al. 2017) or expert opinion. In the model, water turbidity and nutrient concentrations influence the amount of light and nutrients available to fuel periphyton at the base of the food web. Channel morphology (bankfull width, bankfull depth, and gradient) affects channel hydraulics, such as water depth, width, flow velocity, and shear stress acting on the streambed. In turn, water depth and turbidity influence light attenuation, channel width influences the wetted area available for biological production, and water velocity, shear stress, and benthic sediment size influence the mobilization, transport, and retention of benthic organisms and organic matter. For a full description of the ATP model, see Bellmore and colleagues (2017b). Once the ATP model was parameterized, we simulated ecological responses across three trophic levels: periphyton, aquatic invertebrates, and fish.

In the model simulation, the three trophic levels followed a similar response trajectory in the downstream domain: declines in biomass during the initial perturbation of the dam removal, followed by recovery to biomass levels that surpassed the preremoval conditions. The initial perturbation response was driven by two primary factors: high turbidity, which reduced available light for periphyton growth, and the deposition of fine-grained reservoir sediment, which created an unstable streambed that was not suitable for periphyton and aquatic invertebrates. But as turbidity declined and the streambed grain size coarsened, the biomass of each trophic level recovered. Final downstream biomasses exceeded preremoval conditions owing to higher assumed background nutrient concentrations (associated with reestablishment of nutrient transport from upstream) and a more biologically retentive channel that was wider and had a lower gradient. The timescale of the modeled response, however, varied among the trophic levels.
After nearly a century of impoundment, two dams on the Elwha River in northwestern Washington State were removed simultaneously, beginning in September 2011. The 32-m-tall Elwha Dam was built 8 kilometers (km) from the ocean in 1913, and the 64-m Glines Canyon Dam was built 14 km farther upstream in 1927. Both structures lacked fish passage, resulting in precipitous declines in anadromous salmon populations over the nearly 100 years of dam emplacement. Dam removal was intended to restore migratory access for seven species of Pacific salmon and steelhead—still present downstream of the lower dam—to pristine spawning and rearing habitats upstream in Olympic National Park. Phasing the removals over 1 and 3 years for Elwha and Glines Canyon Dams, respectively, helped control the release of ~30 metric tonnes of sediment accumulated in the reservoirs (Randle et al. 2015). This unprecedented release of sediment (65% of total in the first 5 years; Ritchie et al. 2018) resulted in modified channel morphology, fining of the downstream river bed, increased turbidity and a pulse of sediment and nutrients (East et al. 2015, Magirl et al. 2015, Warrick et al. 2015, Ritchie et al. 2018).

We used the ATP model (Bellmore et al. 2017b) to simulate downstream biomass responses for fish, aquatic invertebrates, periphyton and detritus (dead organic matter) following these dam removals. We parameterized the model with measured changes in channel morphology (East et al. 2018), turbidity (Magirl et al. 2015), nutrient concentrations (Washington Department of Ecology, Station 188070; figure 7), and other location-specific environmental information such as water temperature, discharge, and solar radiation.

Model simulations indicate that dam removal significantly affected trophic productivity (figure 7). In reaches just downstream from Elwha Dam, simulations showed an almost complete loss of fish, invertebrate and periphyton biomass coinciding with dam removal in late 2011. Modeled declines were largely due to the combined effects of high turbidity that limited light availability and periphyton growth and deposition of finer sediments that made benthic habitats unsuitable for periphyton and invertebrates. Biomass values remained low until mid-2014, at which point turbidity decreased to levels that allowed periphyton growth to rebound. Modeled detrital biomass was high during dam removal, reflecting the pulse of detritus from within stored sediments and restored longitudinal connectivity to the upstream river network. The availability of this low-quality detritus, however, was insufficient to offset the loss of high-quality periphyton as a food source for aquatic invertebrates. Although empirical data directly comparable to model simulations are currently limited, there is evidence to suggest that the downstream ecological community was indeed negatively affected. The density of benthic invertebrates, for instance, declined by almost two orders of magnitude relative to preremoval abundance. Simulations of ecological conditions for 2017–2021 indicated that fish, invertebrate, and periphyton biomass may increase further if turbidity continues to decline and the streambed continues to coarsen (figure 7).

Periphyton communities on the streambed were highly susceptible to the initial dam-removal disturbance but recovered more quickly because of higher turnover rates than those of invertebrates and fish.

Responses to real dam removals are more complex than the modeled responses presented in the present article (see box 1, figure 7); nonetheless, this simple example illustrates that such models may be able to predict realistic ecological response trajectories. Moreover, such analyses can explore potential responses before dams are removed (figures 6 and 7). For instance, different assumptions and removal strategies (e.g., instantaneous versus phased removal) could be simulated to identify approaches that reduce negative impacts and provide the best chance for long-term ecological recovery. Although simulations themselves are idealized, the process of organizing information into a quantitative framework can promote a greater understanding of the factors that control system dynamics. In the case of dam removal, making informed decisions with the aid of models is crucial, because once a dam is removed, there is no going back.

**Conclusions**

Empirical dam removal studies and ecological theory support our conceptual models defining the links and feedback loops affecting ecological responses to dam removal. These models define response trajectories that clarify pathways of ecological transitions upstream of the former reservoir, within the former reservoir, and downstream of the former reservoir. Within each spatial domain, these models illustrate that dam-removal responses are controlled by multiple causal pathways and interdomain links, which interact to strengthen or dampen responses. Together, these interconnections create dynamic, nonlinear responses, which are complex but can be predicted if the relative strengths of the dominant links and feedback loops—controlled by local and regional factors—are known.

Our conceptual models can be used in multiple ways to increase understanding of these interconnections. First, dam-removal practitioners can use these models to trace the important causal pathways likely to determine responses at specific locations. These qualitative exercises can improve decision-making and prediction by fostering a holistic understanding of the multiple pathways by which dam removal is likely to influence specific ecological communities. This qualitative understanding can be used to prioritize the physical and ecological variables that should be monitored following removal. Second, these models provide a template for more detailed conceptual models that account for location-specific processes, organisms, watershed context, and management scenarios. For instance, these models are being adapted to evaluate potential ecological responses to
We conclude by returning to the original question: When a river is dammed, is it damned forever? Our conceptual models and a growing number of empirical studies suggest that rivers, given the opportunity, can indeed recover substantially from having been dammed. But the structure and function of the ecosystem may not be the same or even similar to what existed prior to dam emplacement. Damming rivers causes changes in ecological communities by extirpation of native species and spread of nonnative and invasive species (Olden 2016). Therefore, the ecological communities that assemble following dam removal may be very different than those that existed before the dam was constructed. Moreover, baseline conditions of the watershed may have changed significantly while the dam was in place. Land use, pollution, the presence of other dams, sediment

Figure 7. Environmental data (a–g) used to parameterize the aquatic trophic productivity model for dam removal on the Elwha River (Washington state), and simulated outputs (h–k) for fish, invertebrate, periphyton and detritus biomass. Abbreviations: AFDM, ash-free dry mass; $D_{50}$, median particle size of benthic substrate; DIN, dissolved inorganic nitrogen; FNU, formazin nephelometric units; SRP, soluble reactive phosphorus

dam removals on the Klamath River in Northern California, where several dams are being removed in series. Finally, our models provide a foundation for constructing quantitative models, parameterized with relevant local and regional environmental information. Simulations from these models can provide alternate hypotheses, which can be tested with empirical data following removal. Although modeled results may not match actual outcomes, information gathered during postremoval monitoring can be used to refine model parameter values and model structure, as well as the underlying knowledge and assumptions on which the model is based. For instance, unanticipated results could help identify important feedback loops and local environmental conditions that may be important for predicting outcomes of future dam removals.
contamination, climate change, and numerous other factors will constrain the trajectory of both physical and ecological recovery (Foley et al. 2017a). The ability to go back to a predammed state will likely depend on how long the dam existed and the magnitude of its many-faceted effects on the ecosystem. Even if all elements of the ecosystem still exist, it is unlikely they will reassemble in the exact fashion that existed previously (Temperton et al. 2004).

But what is “damned forever”? The perception of ecological recovery following dam removal ultimately depends on societal expectations (Hobbs 2007). Recovery expectations may be high in settings in which vivid recollections of pristine predam conditions still exist. On the Elwha River, for example, a strong written and oral history of large Pacific salmon runs promoted expectations that dam removal would lead to recovery of historical populations. In contrast, dam removal expectations may be substantially different from predam conditions in locations in which these memories have been lost. Managers and practitioners can use models such as those presented in the present article to help stakeholders and community members understand the potential range of ecological responses to dam removal and the most likely trajectories and future conditions, thereby better shaping (and even guiding) more realistic expectations for ecological recovery as well as avoiding undesired outcomes.

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