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Geomorphology 71 (2005) 227–244

GEOMORPHOLOGY

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Stream ecosystem response to small dam removal: Lessons from the Heartland

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Received 6 December 2002; received in revised form 13 April 2004; accepted 14 April 2004
Available online 21 April 2005

Abstract

In this paper, we synthesize a series of small dam removal studies to examine how changes in channel form can affect riparian vegetation, fish, macroinvertebrates, mussels, and nutrient dynamics. Each of the ecosystem attributes responded to the disturbance of dam removal in different ways and recovered at very different rates, ranging from months to decades. Riparian vegetation appeared to require the greatest time for recovery, while macroinvertebrates had the least. Mussel communities were the most adversely affected group of species and showed no signs of recovery during the time period of the study. Based on these and other studies, we suggest that ecosystems may follow two trajectories of recovery following dam removal. First, ecosystems may fully recover to pre-dam conditions, although this may be unlikely in many cases. Even if full recovery occurs, the timescales over which different attributes recover will vary greatly and may be perceived by the public or management agencies as not recovering at all. Second, ecosystems may only partially recover to pre-dam conditions as the legacy of environmental damage of long-term dam presence may not be reversible or because other watershed changes inhibit full recovery. The potential for full or partial recovery is likely driven by the sensitivity of particular organisms, the characteristics of the dam removed, and the local geomorphic conditions of the watershed. Scientists and management agencies should assess the potential for full or partial recovery prior to dam removal and, in particular, should identify those species or groups of species that are likely to not recover to pre-dam conditions. Such information is critical in the decision of whether, or how, to remove a dam.

Keywords: Dam removal; Stream ecology; Disturbance; Recovery; Biogeomorphology; Ecohydrology

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doi:10.1016/j.geomorph.2004.04.011

1. Introduction

1.1. Biogeomorphology

Interest is rapidly growing in examining scientific problems that occur at the interface of disciplines. This trend represents not only a growing interest in how one discipline can inform another, but also how new questions are emerging that cannot be addressed within the confines of a single discipline. To this end, the Binghamton symposia have traditionally dealt with interfaces between geomorphology and some other scientific discipline. In 1995, geomorphologists turned their attention to "Biogeomorphology" (the relationships between biota and geomorphic forms and processes) and resultant papers (Hupp et al., 1995) considered how geomorphology affects biological processes, and vice versa. Examining the papers presented at the 1995 conference leads to an important question: what is "biology" to a geomorphologist? Sixteen of the 21 papers focus on vegetation, three on zoological factors (e.g., cows), one on the microbial dynamics of rock surface weathering, and one on food web dynamics on floodplains. This strong focus on vegetation indicates a bias toward examining biological factors already known to affect geomorphic processes and toward studies that are interested in the shifting geomorphic template as a means of describing changing habitat availability for large and conspicuous groups of organisms such as fish and riparian trees. Few studies have examined the role of geomorphic forms on ecological dynamics over a range of trophic levels or on biotic interactions between species (but see Power et al., 1995).

Beyond illustrating a potentially skewed research perspective, what geomorphologists consider to be "biology" also has ramifications for their input to ecosystem management or restoration schemes, like river restoration. If the presence of a particular species of fish is considered to indicate a healthy stream or river, then geomorphic design of a channel for restoration efforts will focus solely on creating forms and processes that facilitate survival and reproduction of that species. This is an inadequate approach, as managing or designing for restoration of the entire ecosystem recovery is a more desirable goal (Ward et al., 2001). Developing a more thorough understanding of how geomorphic forms and processes affect ecological dynamics is important beyond the pervasive habitat perspective.

1.2. Purpose and structure of paper

Our primary goal is to examine how geomorphic forms and processes affect stream ecosystems across a range of trophic levels. To address this goal, we synthesize a number of case studies of dam removal in the state of Wisconsin. Dam removals represent large-scale disturbances and are significant from a variety of perspectives (Heinz Center, 2002); observing how the coupled geo–eco systems recover following a common disturbance is instructive for both the individual and coupled systems. We have limited our review to Wisconsin because a large number of dams have already been removed in the state (Doyle et al., 2000), there are several completed and ongoing studies of dam removal within the state (reviewed below), and examining a single region limits variation because of physiographic factors.

We begin by briefly reviewing small dam removal in the U.S., summarizing our previous observations of how rivers geomorphically respond to dam removal, and describing the dominant geomorphic changes that can be expected at sites similar to those in Wisconsin. We then cover five attributes of stream ecosystems affected by dam removal: fish, vegetation, macroinvertebrates, unionid mussels, and nutrient dynamics. We have placed preference on using studies that have already been published or will be published, although we have also used general observations and modeling where empirical data are scarce. In each case, we briefly describe the site, study methods, and results, and then discuss the ecological response to dam removal and how geomorphic forms or processes were significant factors in controlling these responses.

2. Dams and geomorphology

2.1. Small dam removal

As is the case with most states in the U.S., dams dominate Wisconsin's riverways (Graf, 1999). The vast majority of these structures are characteristically small and abundant in small and mid-order channels.

Pervasive decline in the structural integrity of dams provided the inspiration for dam removal in Wisconsin as early as the 1960s. The initial wave of dam removal as a safety and management action drew little attention beyond the borders of the state. However, a second wave of removals in the 1990s has garnered substantial attention (e.g., Born et al., 1998; Johnson and Graber, 2002; Stanley and Doyle, 2002). Wisconsin's willingness to remove aging structures has led to multiple removals over the past decade and has made the state a laboratory for the political and scientific experiment of dam removal (Martini, 1998).

The recent attention given to removal of small dams in Wisconsin and elsewhere in the U.S. has revealed several trends. First, preliminary studies have highlighted a surprisingly limited understanding of the geomorphic and ecological effects of these structures (Hart et al., 2002; Stanley and Doyle, 2002). Second, awareness of the sheer abundance and structural and functional diversity of small dams has increased (Poff and Hart, 2002). Third, while debates about removal of very large dams are widespread, particularly in the western states, smaller dams are being extracted from rivers (Pohl, 2002; Heinz Center, 2002). Fourth, the pervasive assumption that small dams, and by extension their removal, have minimal impacts on channel form or ecological processes (e.g,. Graf, 1999) is not consistently supported by recent studies (e.g., Kanehl et al., 1997; Beasley and Hightower, 2000; Doyle et al., 2003a). In Wisconsin, the abundance of dams – most of which are classified as small structures – and their 100+ year residence in rivers combine to cause substantive impacts on the physical, chemical, and biological status of rivers and streams in Wisconsin (Gebken et al., 1995). Collectively, these trends indicate that there is still much to be learned about how the diversity of small dams may influence rivers and that removal of small dams can have substantive but as yet only sparsely studied effects on fluvial systems.

2.2. The geomorphic context of small dam removal

Despite the fact that numerous dams have been removed in the U.S. over the past few decades (Pohl, 2002), little information exists on how channels will respond to dam removal. The geomorphic impacts of dam construction and operation are fairly well understood, as these structures lead to sediment storage upstream and associated degradation downstream. In its most simple conceptual case, dam removal should reverse these geomorphic trends, leading to erosion of the sediment stored in the upstream reservoir, transport of this sediment to downstream reaches leading to subsequent aggradation of downstream reaches.

Geomorphic response to dam removal will be governed by the quantity of sediment stored in the reservoir and the ability of the fluvial system to adjust, with upstream erosion of reservoir sediment driving the rate and magnitude of downstream geomorphic response to dam removal. Presumably, systems with greater energy via higher discharge or higher slope that are able to erode sediment most efficiently will adjust more quickly than those in lower energy systems. Further, sediment texture should drive the potential timescales of response following dam removal in that fine sediment transport should occur at greater temporal rates than coarse sediment transport (Doyle and Harbor, 2003). Another important consideration is the spatial scale of geomorphic adjustments, i.e., how far upstream and downstream the impacts of dam removal are evident. Based on previous studies of geomorphic response to analogous disturbances (e.g., Simon, 1992), geomorphic response to disturbance should be most evident directly adjacent to the dam removal, and then decrease exponentially with both distance and time.

Unfortunately, there are few studies from which to base these qualitative predictions for the case of dam removal. Based on previous observations of dam removals, dam failures, and experimental sediment releases, it appears that the vast majority of geomorphic adjustments following dam removal (or similar event) occur within the first 1 to 5 years, and these timescales are in line with geomorphic recovery following similar disturbances of landslides, floods, and channelization (e.g., Simon, 1992). Further, the bulk of geomorphic changes appear to be localized to the reservoir itself and the reaches immediately below the reservoir (see summary Table 1 in Doyle et al., 2002). However, these previous studies represent a fairly limited range of dam sizes and channel types, and are particularly poorly representative of large dams with substantial sediment accumulation. Further, the pre-removal data for these previous studies are often lacking, and thus it is difficult to assess the quantity of sediment in the former reservoir, or how this sediment impacts downstream reaches.

For Wisconsin, impoundments have typically filled, at least partially, with sediment because of their age and history of upstream agricultural development. Removing these dams causes erosion of the impounded sediment, which is then transported and deposited downstream. Surprisingly little is known about the quantity of sediment that is eroded at these dam removal sites, the rate at which the erosion occurs, and how far downstream the sediment will be transported. In light of these uncertainties, recent papers have drawn on similar geomorphic research and have suggested geomorphic analogies for qualitatively predicting the geomorphic impacts of dam removal (Doyle et al., 2002; Pizzuto, 2002).

To test some of these general qualitative predictions, Doyle et al. (2003a) studied two small dam removals in Wisconsin and described the geomorphic response in terms of a channel evolution model. The model, based on earlier work on incised channels (Simon, 1989), describes the changes in geomorphology as six sequential stages and highlights the (i) similarities between adjustments associated with dam removal and other events that lower local channel baselevel, and (ii) the role of reservoir sediment characteristics (particle size, cohesion) in controlling the rates and mechanisms of sediment movement and channel adjustment (Fig. 1). At both study sites, channels developed in the reservoir sediment through bed degradation, channel widening, and aggradation. Upstream channel development and evolution were strongly controlled by the character of the reservoir sediment, in that a reservoir that was dewatered regularly and had relatively little consolidated or coarse sediment (Baraboo River) progressed rapidly through the evolution sequence, with erosion occurring throughout the reservoir immediately following dam removal. In contrast, a second site (Koshkonong

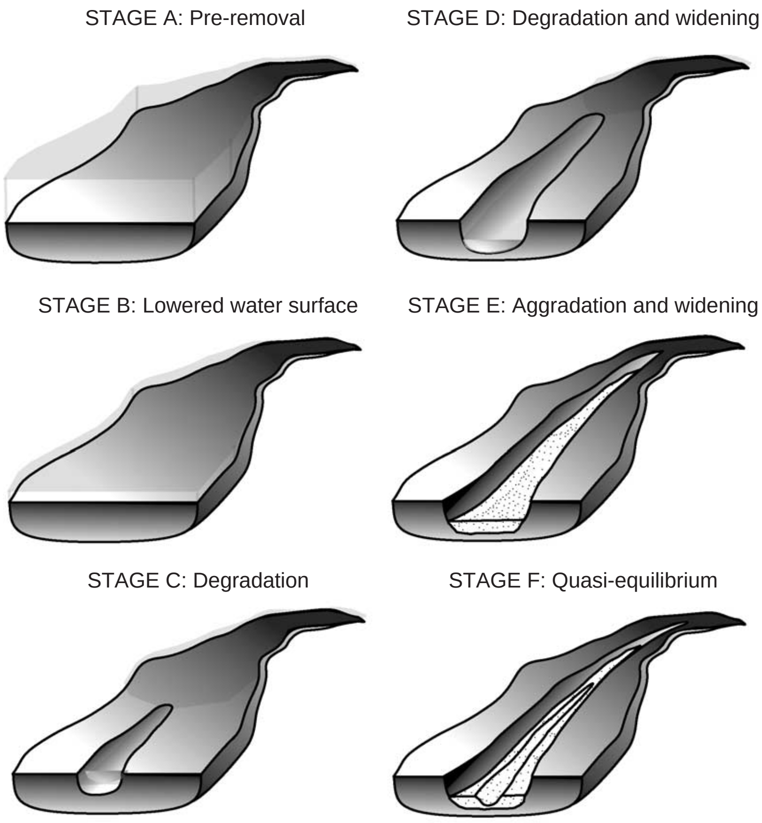

Fig. 1. Conceptual model of channel changes through time in reservoir following removal of a small dam (adapted from Doyle et al., 2003a).

River) with consolidated fine reservoir sediment progressed much more slowly through the stages because of the limited migration of a headcut, which controlled subsequent channel development.

At both sites, a large amount of fine sediment was exported from the reservoirs immediately following dam removal. But subsequent erosion of reservoir sediment, and thus subsequent downstream sedimentation, was strongly controlled by the rate and magnitude of channel development and evolution within the reservoir. At the site where erosion occurred along the entire length of the reservoir (Baraboo River), sand was transported through the reservoir and into downstream reaches. Downstream aggradation, however, was temporary. At the other site (Koshkonong River), little downstream sedimentation occurred through time because of the limited reservoir sediment erosion.

The results of this and other studies of small dam removals (Stanley et al., 2002) highlight the potential for widely varying rates of both upstream erosion and corresponding downstream sedimentation. Because upstream erosion and downstream sedimentation have impacts on ecosystem processes, there is also the potential for widely varying ecological changes immediately after the removal, as well as on the rate and trajectory of change in the weeks, months, and years after the dam has been removed. It is important to note that the dams studied in Wisconsin were run-of-river dams, and thus did not affect the downstream hydrologic regime. Potential impacts of such changes are beyond the scope of these studies, but are addressed elsewhere (Bednarek, 2001).

3. Ecological response to dam removal

3.1. Riparian vegetation

Dam removal exposes previously inundated reservoir sediment and forms new sediment surfaces downstream by sediment transport and deposition. Shafroth et al. (2002) suggested several scenarios of vegetation changes likely to occur upstream and downstream following dam removal. Initial vegetation in impoundments will tend to be dominated by weedy plants that grow quickly, have high seed production, and have effective propagule dispersal mechanisms. Eventually, colonizing species should give way to later successional species. However, like many aspects of dam removal, very little documentation exists describing vegetation colonization or succession following actual removals.

To examine the effects of dam removal on vegetation, Orr (2002) surveyed multiple sites from Wisconsin that represented a range of years since removal as a substitute for following a single site through time. Thirteen former impoundment sites were surveyed, from sites in which the dam had been removed as recently as 1 year ago, to others in which removal had occurred over 30 year ago. Orr (2002) found that vegetation established quickly following dam removal and that bare sediment was extremely rare (<1% of all sampled area), even on recent removal sites. Plant composition differed among recent and older sites as newer sites were dominated by a combination of grasses and small or early successional forbs, and riparian trees were common at sites over 30 year post-removal. Yet while older sites were different from younger ones, predictable patterns of replacement of one growth form by another were not apparent. Species diversity was also highly variable among sites within their first 10 year post-removal, with some sites being solely dominated by a few aggressive species while others also contained a variable number of additional species. Diversity was consistently high for the oldest dam removal sites.

Based on these results, Orr (2002) made several suggestions regarding vegetation following dam removal that have important geomorphic implications. First, persistence of exposed sediment for an extended period of time following dam removal is unlikely. This suggests a limited occurrence of overland sediment erosion following dam removal and that, in time, sediment erosion will likely be restricted to the channel bank and bed in association with channel adjustments. Second, plant communities are likely to continue to develop over time and not become arrested in an early successional stage. This finding is contrary to that of Lenhart (2000) who suggested that the combined effects of establishment of invasive species (e.g., reed canary grass, *Phalaris arundinace*) change in the historic water table height, and the accumulation of nutrient-rich sediment during dam closure could retard or even arrest plant succession.

More studies are needed to determine conditions controlling whether succession or persistence of invasive species dominates a given site.

The long-term vegetation community within former impoundments has important implications for channel stability, as there are large differences between the effects of grasses and trees for stream bank stabilization (Simon and Collison, 2002). If vegetation development proceeds to trees, then banks should be more stable than if vegetation communities remain dominated by grasses for extended time periods. Indeed, bank stability modeling results suggest that tree-vegetated channels could incise at least 20% deeper than unvegetated channels before banks become unstable and fail by mass wasting (Doyle et al., 2003b). Greater bank stabilization can reduce long-term channel erosion and migration and thus reduce sediment yield to downstream reaches.

3.2. Fish

Of all the attributes of stream ecology that are associated with dams and dam removal, fish are perhaps the hallmark. That dams affect fish distributions is well known (Kinsolving and Bain, 1993), and this is particularly true for anadromous fish. Enhancement or restoration of fish populations has been one of the most common arguments made in support of dam removal and anecdotal evidence of fish migration past former dam sites is widespread. For example, following removal of the Edwards Dam in Maine on the Kennebec River, presence of striped bass, alewife, shad, Atlantic salmon, and sturgeon upstream of the former dam site were indications to the local communities that removal had been an ecological success. However, despite the emphasis placed on fish, studies quantifying population- or community-level responses to dam removal remain extremely scarce. How quickly fish populations recover following dam removal and the efficacy of dam removal as a restoration tool for anadromous species remain largely unknown.

The response of fish communities to dam removal in Wisconsin has been documented following the extraction of the Woolen Mills dam on the Milwaukee River by Kanehl et al. (1997). The dam was ~106 km upstream from the mouth of the river and had been present since the 1800s, although the structure that was removed was completed in 1919. The dam was 4.3 m high, with an impoundment of 27 ha extending 2.3 km upstream. Removal occurred in 1988, although the impoundment was dewatered for long periods from 1979 to 1988. Sediment in the former impoundment was stabilized using vegetation and stone immediately after removal, and some of the channel was modified in 1989 to improve habitat quality for smallmouth bass.

Kanehl et al. (1997) established five study reaches around the Woolen Mills dam, with each reach being ~1.0 km in length. Reaches were (i) a 1.25-km reach immediately downstream of the dam, (ii) a 1.0-km reach immediately upstream of the dam (within the impoundment), (iii) a 1.3-km reach at the upstream end of the impoundment, (iv) a 1.0-km reach upstream of the impoundment, and (v) a 1.2-km reference reach on the nearby North Branch of the Milwaukee River. Each of the five reaches was sampled to estimate quantitative habitat characteristics (e.g., riffle occurrence, cover for fish, substrate type) and relative abundance and size structure of fish once per year. Sampling methods were used to estimate fish species presence and size and to quantify habitat quality, particularly for smallmouth bass. Smallmouth bass are a highly desirable species for anglers and also are indicative of good habitat and water quality. Using the fish assemblage data, biotic integrity of the site was estimated using a version of the Index of Biotic Integrity (IBI) developed for Wisconsin streams.

Removal of the Woolen Mills dam resulted in rapid geomorphic changes in the impoundment, including increases in sediment size, thalweg depth variability, and increased cover for fish (Kanehl et al., 1997). Cumulatively, these changes were reflected in increased habitat scores for the formerly impounded reaches and evident changes in fish assemblages following dam removal (Fig. 2). Carp, a ubiquitous and destructive non-native species, decreased in the impoundment site, while smallmouth bass increased. Interestingly, there appeared to be a ~3-year lag between dam removal and smallmouth bass recovery, whereas the effect of removal on carp was immediate. Cumulatively, IBI based on fish assemblage showed modest gains following dam removal, approaching but not reaching values for the reference reach (Fig. 2).

Recovery of fish species upstream of a dam removal is expected in part because of the removal

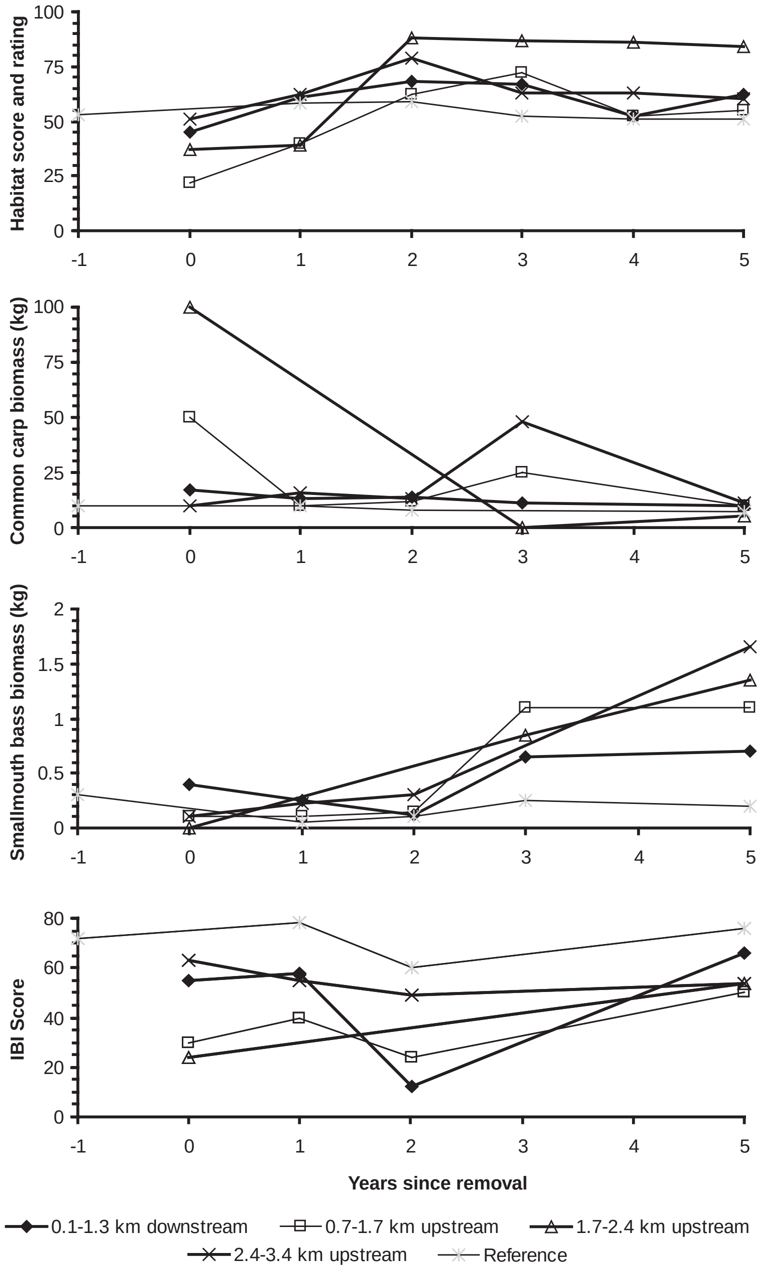

Fig. 2. Changes in habitat quality and fish assemblage characteristics following removal of the Linen Mills Dam on the Milwaukee River, WI (adapted from Kanehl et al., 1997). High values of habitat and IBI scores are associated with good habitat and good fish assemblages, respectively.

of a migration barrier. The effects of dams on migratory fish are well documented, and their removal has increased the use of upstream spawning habitats by some migratory species (Bowman and Hightower, 2001). In the case of the Woolen Mills dam, however, smallmouth bass were present upstream and downstream of the dam prior to removal, but not within the impoundment. That is, absence was due to habitat limitations rather than migration limitations. Recovery of smallmouth bass populations, then, required geomorphic changes (i.e., habitat changes) that may not have been needed for species restricted only by migration limitations. This may in part explain the time lag between dam removal and smallmouth bass recovery. In the Woolen Mills case, geomorphic changes occurred quickly and stand in contrast to other sites that, because of erosion-resistant reservoir sediment, required much longer periods of time to adjust to dam removal (Doyle et al., 2003a). Thus, geomorphic adjustments were necessary for fish community recovery, and so the rate of geomorphic recovery governs the potential rate of fish recovery.

In larger river systems, separating the effects of habitat recovery from barrier removal may be quite difficult. In modeling the Columbia-Snake River system, Kareiva et al. (2000) showed that dam removal alone would not necessarily restore chinook salmon populations. Rather, habitat restoration, including watershed restoration and channel restoration, would be needed as well. In all, recovery of pre-dam fish communities following dam removal may be strongly dependent upon whether fish are limited by migration or by habitat. If limited by habitat, then geomorphic processes will govern the rate of recovery. If limited by migration, then geomorphology will play a more limited role.

3.3. Macroinvertebrates

Macroinvertebrates have received substantial attention from researchers and managers because of their central role in stream food webs (e.g., Cummins and Klug, 1979) and because they provide an easy-to-collect, easy-to-assess indicator of water quality and habitat conditions. Their relative mobility and direct association with bed substrate mean that the composition of macroinvertebrate communities reflects local physical and chemical conditions in a stream integrated over several months. Stanley et al. (2002) examined responses of this group to the removal of two dams to consider the rate of change and the relationship of macroinvertebrate assemblage structure to habitat change in the Baraboo River, Wisconsin.

The Baraboo River is a low-gradient river (slope ~0.0002) draining ~1700 km^2 of south-central Wisconsin, and has a total altitude change of 46 m. Fourteen meters (~1/3) of this gradient occur within a 7-km reach historically known as the Baraboo Rapids, representing relatively unique habitat of high velocity and coarse substrate within the basin dominated by low velocity and fine substrate. Within this 7-km reach, three small dams were built by 1929, creating small (3–15 ha) impoundments. The three dams were removed between December 1997 and October 2001. Stanley et al. (2002) surveyed cross sections and collected benthic macroinvertebrate samples in 6 reaches before and after the removal of the second dam in January 2000: an upstream reference reach, reaches immediately above and below the dam that was removed, and sequential unimpounded and impounded reaches farther downstream.

Dam removal decreased cross-sectional area in the former impoundment as flow velocity increased and a channel incised into the reservoir sediment, although channel form in other reaches did not change. Fine, loose sediment was transported out of the impoundment reach and into downstream reaches. A flood in June 2000 (5 months post removal) further widened the channel through the former impoundment and transported sediment farther downstream out of the reach immediately downstream of the former dam site. One year after the removal, macroinvertebrate assemblages in formerly impounded reaches were indistinguishable from those in the upstream reference site and in downstream unimpounded reaches (Fig. 3). Regardless of their impoundment history, all unimpounded reaches had macroinvertebrate assemblages comparable to those in natural streams.

Similar to fish response in the study by Kanehl et al. (1997), macroinvertebrate assemblage structure in the Baraboo River study was determined by habitat availability. Given the relative mobility and short life cycle of macroinvertebrates, it is reasonable to expect that assemblages have the potential for rapid response to dam removal and that changes will be constrained by the rate of geomorphic adjustment following removal. Recovery within ≤1 year in the Baraboo River may in part be due to the limited geomorphic disturbance caused by the dam's presence and because the flood 5 months after removal increased the rate of geomorphic adjustment to dam removal, and presumably the rate of habitat recovery. It is worth noting that the time scale of this study was longer (5 years) than typical studies of natural disturbance, which often

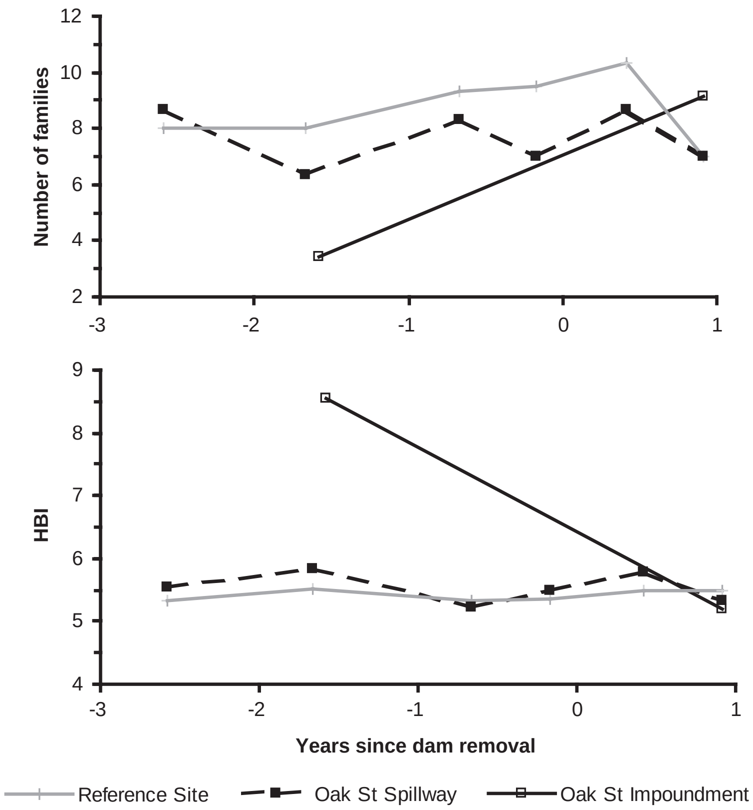

Fig. 3. Changes in macroinvertebrate assemblage characteristics through time following removal of the Oak Street Dam on the Baraboo River, WI (adapted from Stanley et al., 2002). The HBI is an indicator of habitat quality based on differences in invertebrate tolerances to organic pollution and uses genus-level macroinvertebrate abundance data. Low HBI values (HBI< 5.5) are associated with good habitat, and high values (HBI > 7.5) with poor habitat. Sites considered to have good water and habitat quality are typically characterized by high species diversity.

study invertebrate responses over a 1–2 year period (e.g., Collier and Quinn, 2003), and concomitantly lacked the temporal detail of such shorter term studies. However, the temporal scale of recovery of invertebrates following dam removal was consistent with recovery times in these previous studies.

3.4. Unionid mussels

Mussels are one of the most threatened groups of aquatic species in the United States and particularly in the Midwest. Of the 300 species native to North America, 70 are currently listed on the endangered species list. The negative impact of impoundments on mussel reproduction (Watters, 1995), community assemblages (Vaughn and Taylor, 1999), and survival (Parmalee and Hughes, 1993) has been well documented. As with anadromous fish populations, it seems logical that removing the cause of the problem (the dam) should improve conditions for mussels. Yet little empirical information exists on the effect of dam removal on mussels and their short- or long-term changes in response to changes in channel form.

In an effort to gain a preliminary understanding of potential effects of dam removal on mussels, Sethi et al. (2004) conducted a post-removal survey of mussels within the impoundment and downstream following the removal of the Rockdale dam on the Koshkonong River. Within the former reservoir, mortality rates of mussels following dam removal were extremely high (95%) due to desiccation and exposure. Mussel densities in a bed 0.5 km downstream from the dam declined from 3.80 ± 0.56 mussels/m^2 in Fall 2000 immediately after dam removal to 2.60 ± 0.48 mussels/

m^2 by summer 2003 (Fig. 4). One rare species, *Quadrula pustulosa*, was completely lost from community over the time of the study. Mortality of mussels buried in deposited silt was also observed at a site 1.7 km below the dam. Silt and sand substrate increased from 16.8% and 1.1% of total area sampled in fall 2000 to 30.4% and 15.9%, respectively in summer 2003. Total suspended sediment concentrations in the water column were always higher downstream from the reservoir than upstream. This transport and deposition of reservoir-born sediments likely contributed to downstream mussel mortality.

Overall, the physical changes caused by dam removal (lowered water surface, sediment transport to downstream) caused significant declines in mussel densities within the reservoir and downstream (Fig. 4). Further, the absence of mussels in the newly formed channel since dam removal emphasizes the slow recovery of this group compared to the rate of recovery of fish and macroinvertebrates. Establishment in this newly created habitat requires persistence of viable downstream or upstream populations that act as propagule sources, fish colonization (because mussel larvae disperse to new sites by piggy-backing on fish), development of suitable habitat for mussels, and time, as mussels are long-lived, slow growing organisms. Geomorphology thus plays multiple roles in governing mussel population dynamics following dam removal. If dam removal causes significant mussel mortality, then we expect that longer-term recovery may be slow and may be difficult to link to geomorphic adjustments.

3.5. Nutrient dynamics

At the most fundamental level of ecological change in rivers is the small but metabolically active periphyton community (algae, bacteria, and other associated microbes), whose growth can often be linked to nutrient retention in a stream reach (Kim et al., 1990). Periphyton is often responsible for a significant percent of nutrient uptake in streams

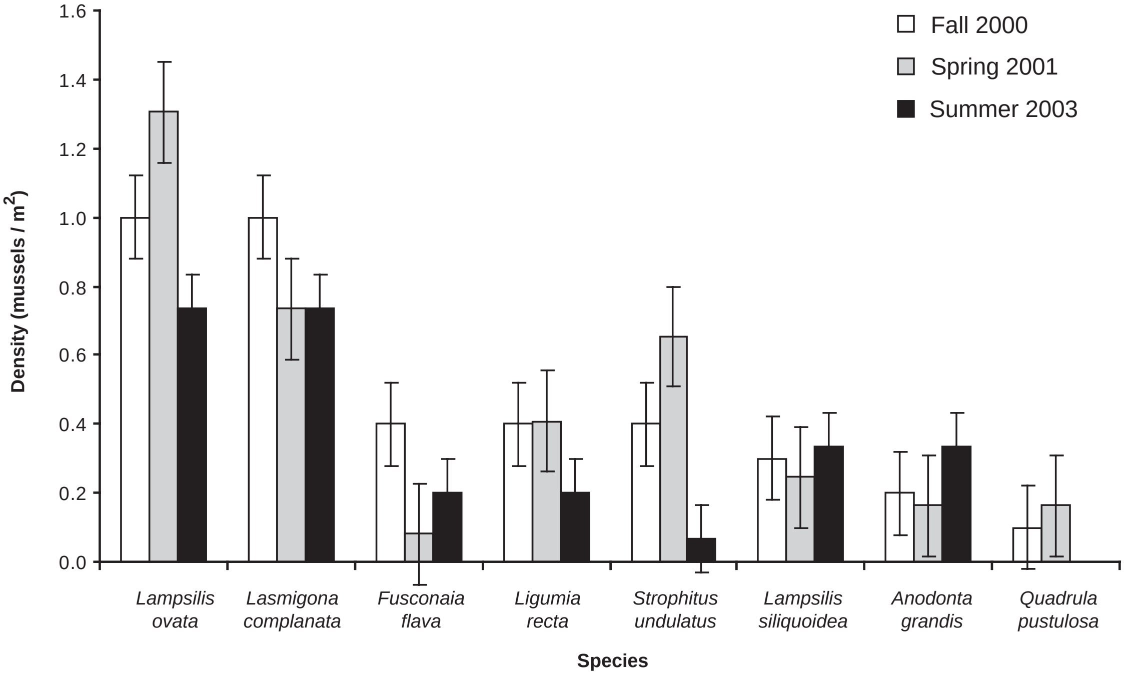

Fig. 4. Changes in mussel density 0.5 km downstream of the removal of the Rockdale Dam on the Koshkonong River (adapted from Sethi et al., 2004). Dam was removed in Fall of 2000, immediately prior to date of first data collection. Note that there are no *Q. pustulosa* in Summer 2003.

(e.g., Mulholland et al., 1983; Grimm, 1987) and is one of the basal energy sources that fuel many river food webs (Power and Dietrich, 2002). In addition to the importance of periphyton in stream ecosystems, nutrient retention in Wisconsin and other midwestern U.S. streams is a critical issue as these streams are often laden with nutrients, with profound impacts on both local freshwater ecology and marine systems downstream (Carpenter et al., 1998). Because of widespread implications of nutrient loading, how streams retain nutrients has received increased attention, and particularly, the potential role of geomorphology in stream nutrient retention (Alexander et al., 2000; Peterson et al., 2001).

Few data exist showing the effect of dynamic channel morphology on nutrient or periphyton dynamics in streams, as most existing studies have focused on dynamic hydrology or inter-site comparisons (see review by Marti and Sabater, 1996). Stanley and Doyle (2002) developed a conceptual framework for predicting nutrient export and retention associated with dam removal, although they did not give quantitative predictions.

To explore the potential linkages between dynamic channel morphology and nutrient retention, Doyle et al. (2003c) examined retention of soluble reactive phosphorus (SRP) through time at the Koshkonong River dam removal site (described above) using both pre- and post-removal data and simulation modeling. Five time periods representing five geomorphically different conditions were modeled assuming steady-state nutrient uptake parameters, an incoming nutrient concentration of 0.15 mg/L, and a discharge of 2.7 m^3/s, which approximates the conditions for SRP on 11 November, 2000. They also examined the effect of higher discharges by simulating retention at a discharge of 5.7 m^3/s.

Removal of the Rockdale Dam on the Koshkonong River caused upstream-progressing erosion in the form of a discrete headcut, and subsequent geomorphic adjustments well described by the conceptual model presented earlier (Doyle et al., 2003a). Changes in channel morphology were particularly pronounced downstream of the headcut as it migrated upstream. Eleven months after the removal, the headcut was located approximately 400 m upstream of the dam. Upstream of this point, the flow area was still relatively high, while downstream it was greatly reduced. Final equilibrium conditions had reduced flow area throughout the reservoir reach.

In the simulation results, pre-removal conditions represent the dam still in place, creating backwater conditions upstream (stage A in Fig. 1), while post-removal conditions represent the removal of the dam, but prior to any geomorphic adjustments within the reservoir (stage B). Eight months and eleven months after removal represent a transitional geomorphic condition when the reservoir is actively eroding reservoir sediment, and a channel is beginning to form in the downstream part of the reservoir (stages D and E). For estimating final, long-term equilibrium conditions (stage F), the channel geometry at an upstream channel cross section (4180 m upstream of the dam) was extrapolated through the reservoir at a uniform slope between that cross section and the base of the dam.

The simulated SRP concentration showed that the backwater conditions created by the dam greatly enhanced nutrient retention and thus as the free-flowing water progressed through the reservoir, there was a downstream reduction in nutrient concentration (Fig. 5). The greatest retention occurred in the final 500 m of the impoundment, where flow was the most stagnant and thus conducive to nutrient retention. Removal of the dam and formation of a narrow channel in the lower impoundment worked to greatly increase flow velocity, reducing the potential for nutrient retention. However, upstream of the headcut, the reservoir remained mostly unaffected by the dam removal, and so the nutrient retention trends are similar to when the dam was still in place. Final equilibrium conditions showed decreased, although still persistent nutrient retention. These simulation results suggest that changes in channel morphology following dam removal can cause large changes in nutrient retention patterns within a stream.

Other studies using empirical data (Wollheim et al., 2001) and alternative modeling approaches (Doyle and Stanley, submitted for publication) showed similar control of nutrient retention by geomorphology. This is significant from two perspectives. First, it shows that while dams are detrimental to many facets of stream ecosystems, they can create conditions conducive to nutrient retention (see also Stanley and Doyle, 2002). This is particularly important in Midwestern U.S. streams because of the enrichment by nitrogen and phosphorus. Second, while other studies have shown

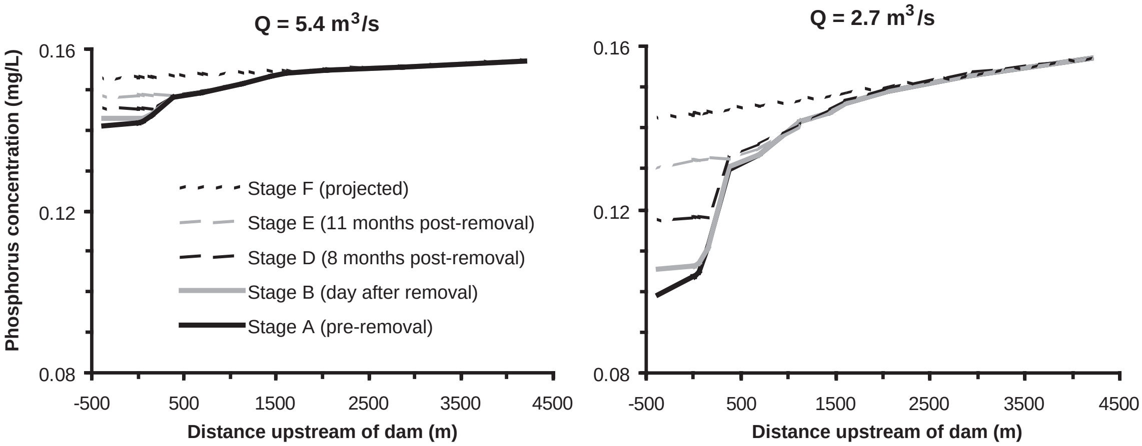

Fig. 5. Spatial and temporal changes in soluble reactive phosphorus concentration at the Koshkonong River following removal of the Rockdale Dam (adapted from Doyle et al., 2003c). Results are based on calibrated retention modeling assuming incoming phosphorus concentration of 0.15 mg/L and a constant benthic areal uptake rate. Steeper slopes indicate higher amounts of retention for a channel segment. Note: positive distances are upstream of the dam.

the importance of channel size in controlling nutrient retention (Alexander et al., 2000) and periphyton dynamics (Dent and Henry, 1999), the model results show that changes in channel shape can influence nutrient retention and thus stream ecosystem properties at the most fundamental trophic level. Many ecological models assume that the physical context for the model is temporally and spatially constant (Dent and Henry, 1999). Such model approaches are doubtlessly necessary to develop an understanding of the ecological processes at work, but by not incorporating the changes in physical context, vital connections between geomorphic and ecological processes may have been missed. Our results, and those of a similar modeling study of food-web dynamics on floodplains by Power et al. (1995), highlight the interconnectedness of geomorphology and ecology in controlling stream ecosystem processes and the need for explicit collaboration of ecologists and geomorphologists when examining stream ecosystems.

4. Discussion

4.1. Synthesis

In this review of case studies from Wisconsin, we show that dam removal can affect stream ecosystems in multiple trophic levels; and in each case, ecological changes could be related to geomorphic changes. By developing the ability to predict the mechanisms, rates, and magnitudes of geomorphic responses to dam removal, we will also begin to be able to predict ecological responses. At this point in time, however, we have only a cursory and qualitative understanding of the physical and ecological responses to dam removal.

Using the available geomorphic and ecological data presented above, a simplified conceptual model of ecosystem response to dam removal is suggested that considers the degree to which the river returns to a pre-dam state (Fig. 6). A single synthetic parameter is used to represent channel morphology and single parameters are also used for each of the ecological attributes examined earlier. We have assumed that both physical and ecological changes through time are asymptotic toward an equilibrium or steady state (Howard, 1982; Simon, 1992), although alternative recovery trajectories are possible (Stanley and Doyle, 2003). In our first scenario (Fig. 6A), we assume that both channel morphology and all components of the stream ecosystem will recover to a previous no-dam condition. In the second scenario (Fig. 6B), we assume full recovery of some components of the system, but only partial recovery or alternative states for other components.

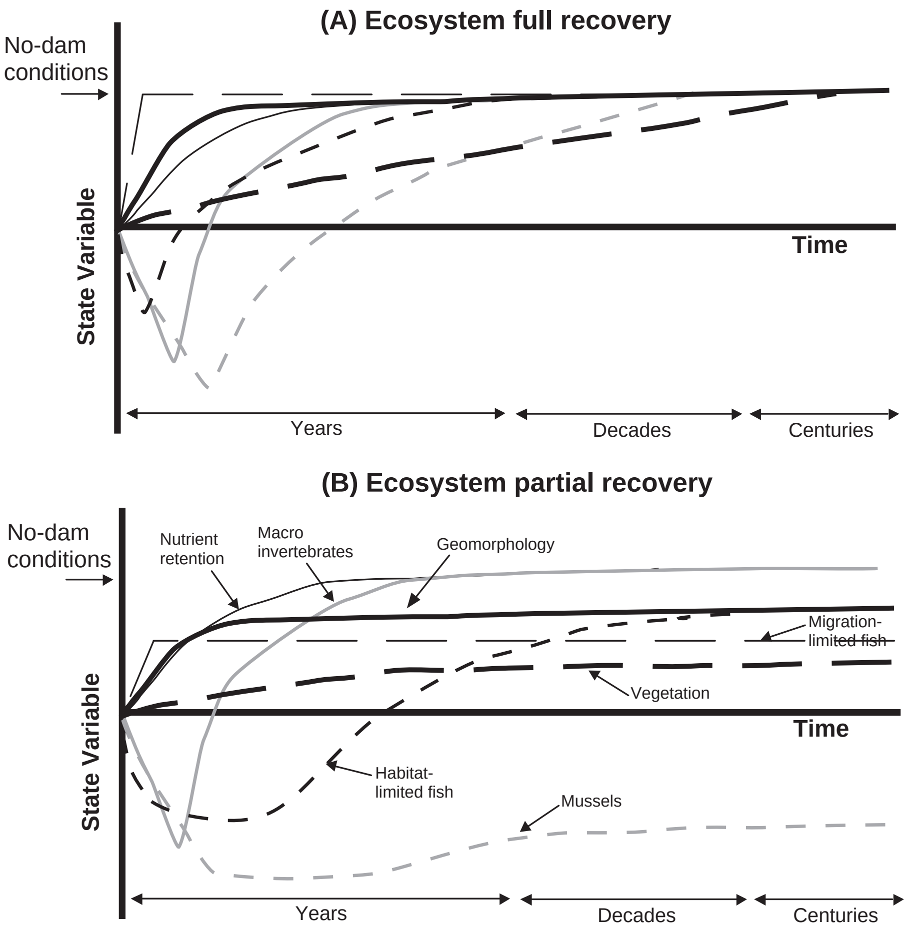

Fig. 6. Conceptual framework for ecosystem recovery following removal of a small dam. Full ecosystem recover assumes that all components of the stream ecosystem return to pre-dam conditions, but at variable rates of recovery. Partial ecosystem recover assumes that some components recover to pre-dam conditions, but that others only partially recover while still others are actually damaged by dam removal and not able to recover at all.

4.2. Conceptual framework A: ecosystem full recovery

An inherent assumption often exists that dam removal will result in the return to pre-dam conditions in many rivers. Even if all components fully recover following removal, recovery is likely to progress at disparate rates just as is the case for natural disturbances such as flooding (Fisher et al., 1998). Variability in response rates is important because if changes in a monitored species or taxa are particularly slow, then a dam removal project may be perceived an ecological failure simply because the benefits of removal have yet to be realized.

Because many organisms are limited by habitat availability, much of the ecological recovery should be controlled by the rate of geomorphic recovery as geomorphic recovery is a necessary precursor to the development of natural stream habitat. Our observations and those of others (see review by Doyle et al., 2002) suggest that the bulk of channel adjustments will occur within the first year after removal for small dams. The periphyton community, reflected by the nutrient retention modeling, is likely to recover rapidly following dam removal and should essentially move toward equilibrium at the same rate as channel morphology. Because nutrient retention was shown to be at least partly controlled by channel morphology, recovery rates cannot exceed that of the channel morphology recovery.

Both fish and benthic macroinvertebrate communities are expected to decline initially because of the disturbance of dam removal. Sediment movement in the former reservoir, downstream deposition, and elevated suspended loads should degrade habitat of fish and macroinvertebrates. While we did not examine short-term mortality from sediment movement at our sites, others have reported substantial fish and invertebrate mortality in such circumstances (Doeg and Koehn, 1994; Rathburn and Wohl, 2001). However, results from the Baraboo River for macroinvertebrates and the Milwaukee River for fish suggest that both fish and macroinvertebrates have the ability to recover to no-dam equilibrium conditions, provided suitable habitat is created by geomorphic adjustments. While recovery of fish and invertebrates will require recovery of vegetation, they will not require recovery of complete pre-dam vegetation conditions, but rather some vegetation that can provide habitat, shading, and organic matter inputs. Invertebrate recovery is likely to be slightly faster due to the shorter lifespan of these organisms—an expectation supported by the 3-year lag in recovery of smallmouth bass in the Milwaukee River study (Kanehl et al., 1997). Because of their habitat needs, fish and macroinvertebrate recovery rates should not exceed geomorphic recovery rates, but will follow closely behind. In the case of the Milwaukee River, geomorphic adjustment rates were increased by engineered channel modifications work, thus increasing the potential rate of fish recovery. In contrast, if fish communities are limited by the dam as a migratory barrier rather than as a habitat disturbance, the simple act of removing the dam, while initially detrimental, may be sufficient to restore upstream fish communities, and thus recovery will essentially be instant.

The two ecosystem components considered in our overview that are expected to require the greatest period of time to recover are vegetation and mussels. Vegetation showed surprisingly variable patterns with respect to time since dam removal, and apparently many decades may be required for the development of tree assemblages characteristic of riparian areas in Wisconsin. The rate of native vegetation establishment may be increased through active planting of the floodplain, although studies confirming this prediction have yet to be undertaken.

Very limited information is available on mussel responses to dam removal. Of all the ecosystem components, our observations suggested that mussel communities in midwestern streams were impacted most severely by dam removal and did not become established within the downstream channel within 3 years after dam removal. Because mussel reproduction and colonization are dependent on fish, at a minimum, mussel recovery requires the geomorphic adjustments necessary for fish recovery, as well as those needed for the mussels themselves. Further, should a situation exist in which downstream source populations are significantly reduced following removal, recovery could be delayed simply by reduction of source populations. Recent studies have suggested that mussels do recover following catastrophic disturbance, but recovery may be on the order of decades.

4.3. Conceptual framework B: ecosystem partial recovery and loss

Removing a dam cannot be assumed to completely return the local ecosystem to pre-dam conditions. Indeed, removing a dam may instead cause permanent ecological changes that are not reversible (Stanley and Doyle, 2003). Variable recovery scenarios are critical to consider because dam removals may be declared successful ecological restoration because of the return of a few notable large species or taxa (e.g., fish), while other less notable taxa do not recover. This necessitates careful consideration of how to define successes or failures in dam removal projects (Doyle et al., 2003d). Weighing such costs and benefits of dam removal is important prior to undertaking large-scale dam removal plans. Numerous alternative scenarios of partial ecosystem recovery exist, and only a few are presented here as possibilities.

In the second conceptual model scenario, we assume that nutrient retention and macroinvertebrate communities recover to pre-dam conditions due to the bulk of geomorphic adjustments allowing these parameters to approach pre-dam conditions (Fig. 6B). However, we also assume that channel morphology recovers toward pre-dam conditions, but morphologic conditions identical to pre-dam are not attainable. Such causes for this partial recovery could be that dam-induced incision is irreversible, or that upstream sediment loads are very different from pre-dam conditions due to land use changes and are sufficient to cause post-removal morphology to be substantially different from that prior to dam construction. Indeed, there is limited evidence that post-removal morphology may be different from pre-dam morphology (Lenhart, 2000). Due to this relatively low recovery of channel morphology in this scenario, habitat limited fish would not recover completely to pre-dam conditions.

Despite not being limited by habitat within the former reservoir, it is possible that migration-limited fish species travel upstream following dam removal only to find degraded habitat, poor water quality, or aggressive competitors and predators. Thus, the ability to migrate upstream will not necessarily restore pre-dam populations (Kareiva et al., 2000). For habitat-limited fish, downstream populations may be so heavily decimated by elevated suspended sediment loads immediately following dam removal that greater periods of time are needed before they are able to reproduce and establish viable populations. Alternatively, dam removal may result in hyper-recovery of some groups—that is, establishment of population densities that are significantly higher than are present in other adjacent areas. Such a scenario may develop when a dam is built in a geomorphically distinct area that may become a critical habitat once the dam is removed.

For vegetation, Orr (2002) suggested that initial conditions at the time of dam removal are critical in determining the trajectory of vegetation change through time. While occurrence of tree species increased through time, Orr noted that exotic species now common in the region were less prevalent at the time of removal for older sites, particularly reed canary grass (*P. arundinace*). Thus, succession of plant communities is currently occurring under very different conditions than existed at the time of dam construction. How the presence of aggressive exotic species alters rates and patterns of vegetative change at removal sites remains to be determined.

As with riparian plant communities, the long-term effect of dam removal on mussels in the midwestern U.S. is unknown. Mussels, or any other acutely sensitive group of species, may be vulnerable to any change in the river system attributes. That is, regardless of the long-term benefits, the drastic short-term changes may be sufficient so as to reduce local populations below a threshold, restricting further recovery, as may be the case for *Q. pustulosa* on the Koshkonong River (Fig. 4). If this scenario is correct, then dam removal poses a dilemma for management and recovery of mussel populations. Existence of dams is a major contributor to long-term declines in this group, but dam removal may push this weakened group over a threshold beyond which recovery of local populations is no longer possible.

4.4. Variability in ecosystem responses

In this review, we have examined only sites within Wisconsin, and so our results by no means represent all potential dam removal scenarios. Great regional variability is likely to exist in both the types of dams, their effects on local ecosystems, and thus the potential changes to local ecosystems caused by their removal. For instance, two concerns in Wisconsin (nutrient loading and mussel communities) may not be relevant in other areas that are nutrient limited, and thus would benefit greatly from dam removal, or in areas lacking downstream mussel populations. Further, areas with limited sediment loading to streams may have very little reservoir sediment accumulation, and thus removal would constitute a fairly insignificant disturbance. However, we expect that, in all cases, there will be some benefits and some ecological costs to removing a dam, and these should be explicitly identified for each case.

4.5. Management implications

Dam removal represents a very significant opportunity to restore geomorphic and ecological functioning in previously disturbed stream ecosystems. While certain aspects of stream ecosystems will undoubtedly return to pre-dam or near pre-dam conditions rapidly after dam removal (e.g., Stanley et al., 2002), the assumption that removing a dam will rapidly reverse the cumulative effect of years of environmental degradation caused by the dam's presence for all components of the stream ecosystem is unrealistic

(Stanley and Doyle, 2003). The very real possibility exists that environmental restoration associated with dam removal will not be evident for years, or decades, after a dam is removed and this will likely vary between components of the ecosystem. In fact, decision-makers must consider the potential for dam removal to cause irreversible degradation to specific ecosystem attributes. However, the benefits of dam removal are likely to be substantial, and thus dam removal represents a very powerful tool for restoring streams to more natural conditions.

The goal of management agencies responsible for removing dams should be to minimize the negative impacts of a removal as well as to maximize the rate of recovery of the physical and ecological systems. Thus, a primary goal should be to identify those species or taxa that are particularly sensitive to disturbance, and mitigate the potential impacts of dam removal. This will likely increase the cost of many small dam removals. Further, because channel morphology and channel adjustments control many of the subsequent attributes of the stream ecosystem, we suggest that management agencies focus on maximizing the rate of physical recovery following dam removal. This may involve channel manipulation, stabilization, or bioengineering. While currently there is very little basis from which to approach a channel design in a former impoundment, tools are available from which to begin such a project (ASCE, 1997).

Finally, management agencies should place great emphasis on developing realistic goals for dam removal. Given the current lack of thorough knowledge surrounding dam removal, not all dams should be considered for removal; and management agencies should develop strategies for targeting dam removals that minimize risks while maximizing the potential environmental restoration (Doyle et al., 2003d). This necessitates identifying species that may be particularly sensitive to dam removal and developing strategies for minimizing the potential damage to these species or groups of species.

Acknowledgements

This work would not have been possible without the extended cooperation by the Wisconsin Department of Natural Resources, particularly Sue Josheff and Meg Galloway, who aided us in identifying many of the dam removal sites for research opportunities. Many of the ideas presented here resulted from research supported by funding from several sources, including the Bradley Fund for the Environment, a Horton Grant from the American Geophysical Union, NSF grant DEB-0108619, the Showalter Fund, Fish America, the River Alliance of Wisconsin, Sigma Xi, and the Association of American Geographers. Reviews of an earlier version of this work by Andrew Marcus and Dick Marston greatly improved its clarity.

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