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LONG-TERM IMPLICATIONS OF DAM REMOVAL FOR
MESOHABITAT AND MACROINVERTEBRATE
COMMUNITIES IN MICHIGAN AND WISCONSIN RIVERS

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LONG-TERM IMPLICATIONS OF DAM REMOVAL FOR MESOHABITAT AND MACROINVERTEBRATE COMMUNITIES IN MICHIGAN AND WISCONSIN RIVERS

By

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ABSTRACT

LONG-TERM IMPLICATIONS OF DAM REMOVAL FOR MESOHABITAT AND MACROINVERTEBRATE COMMUNITIES IN MICHIGAN AND WISCONSIN RIVERS

By

Jonathan Ford Hansen

The removal of the numerous aging dams in the United States has recently been a highly sought after stream restoration technique. The extent to which the damage done to streams by dams is reversed upon removal is unknown, especially on decadal time scales. The objectives of this study were to determine if mesohabitat heterogeneity and macroinvertebrate assemblages within rivers recover following the removal of a dam, and to estimate the time needed for recovery. A space-for-time substitution study was employed on 8 rivers in various stages of recovery following a dam removal, ranging from <1 - 40 years post-removal. Within each river, mesohabitat was mapped and macroinvertebrates sampled in a zone unaffected by the dam removal and two zones impacted by the dam removal (former impoundment and downstream zone), and compared to evaluate the extent of recovery. Mesohabitat recovery was variable, with some rivers recovering substantial heterogeneity within 7 years of removal while others exhibited much lower levels than the reference zone even after 40 years following dam removal. Generally, the macroinvertebrate community recovered 3 - 7 years following removal both in terms of taxonomic similarity and richness, although densities took decades to recover. Dam removal poses as a beneficial restoration technique yet the recovery of important stream components can be variable and may take longer than previous research has suggested.

This thesis is dedicated to my parents, Sandra Helpsmeet and David Hansen, who showed me how to love the natural world.

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The opportunity to tackle this graduate school endeavor was provided by Dan Hayes, who guided my development as a student and a professional while simultaneously providing a thoroughly enjoyable work environment. My thanks are extended to my committee members, Michael Wagner and Rich Merritt. Bryan Burroughs provided further guidance and is responsible for much of the formulation of the original ideas behind this project.

I have to thank my lab comrades, especially Tracy Kolb and Amy Schueller, who kept me sane, answered endless questions, and generated indispensable laughter. Thanks go out to all the friends I've encountered over the last three years; you made the time enjoyable. My heartfelt thanks and love go out to my family-no explanation needed. Lastly, I express my gratitude and love for my wife, Gretchen, who is to owe for all that is good in my life; you are my rock.

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INTRODUCTION

Dams provide numerous societal benefits including hydroelectric power generation, agricultural irrigation, flood control, and creation of recreational activities. Despite the many benefits dams have provided society, they have come at a cost to natural resources. The effects of dams have been thoroughly studied and research has highlighted a plethora of detrimental impacts to the ecological integrity of dammed rivers (Baxter 1977; Petts 1980; Ward and Stanford 1987; Ligon et al. 1995; Waters 1995; Kondolf 1997; Graf 1999; Grubbs and Taylor 2004). With an estimated 2.5 million dams in the United States (National Resource Council 1992), these detrimental effects are widespread.

Dams disrupt the flow of rivers and alter physical attributes of the channel, the thermal regime, and sediment transport (Heinz Center 2002; Poff and Hart 2002). Impoundments formed by dams act as basins, filling in and restricting sediment and nutrient cycling downstream (Waters 1995). Above the dam, impoundments transform the physical habitat, shifting the system from an erosional, lotic environment to a depositional, lentic environment. Downstream of a dam, the river becomes sediment starved due to the reduced sediment load thus increasing the erosive power and leading to disproportionate hardening of the substrate (Ligon et al. 1995). Dams warm impounded reaches and, depending on the type of reservoir release, may substantially alter the thermal regime, either warming or cooling downstream reaches. Thermal alterations associated with dams can negatively impact downstream fish and macroinvertebrate communities, especially in coldwater streams (Lessard and Hayes 2003).

The physical modifications associated with dams have significant implications for biotic communities as well. A free flowing river has many characteristics associated with its geomorphology that create a heterogenous and dynamic environment. An unregulated river tends to exhibit a longitudinal profile characterized by a sequence of alternating pools, riffles, and runs collectively referred to as mesohabitat. Mesohabitat (i.e. pool-riffle-run sequence) heterogeneity regulates the energy expenditure of rivers (Gordon et al. 2004). This diversity of habitat is also important in maintaining the biological integrity of a stream and can strongly affect macroinvertebrate assemblage distributions (Pardo and Armitage 1997; Beisel et al. 1998; Rabeni 2000). Once impounded, a stream shifts from a varying sequence of pool, riffle, run to primarily pool and run habitat within the impoundment, which will subsequently alter the associated macroinvertebrate community. Shifts from lotic to lentic systems associated with the impoundment can cause changes in the fish and macroinvertebrate communities favoring more tolerant organisms and reducing species richness (Tieman et al. 2004; Santucci et al. 2005), mostly due to habitat transformation. The creation of an impoundment favors fish and macroinvertebrates that prefer slower moving, warmer water. Modifications of the macroinvertebrate community can alter various components of stream functioning, including the aquatic and terrestrial vertebrate organisms which rely on aquatic invertebrates for food.

Beyond their role in stream foodwebs, aquatic macroinvertebrates serve as effective indicators of stream quality. Macroinvertebrates are widespread in all stream habitats, show a gradient of responses to disturbance, and are easily sampled; therefore, they have been widely used in biomonitoring efforts for nearly a century (Rosenberg and

Resh 1993). Numerous metrics have been developed to facilitate the analysis and interpretation of biomonitoring studies. One of the most widely used classifications of macroinvertebrates includes the designation of functional feeding groups (FFG) (Cummins and Klug 1979; Merritt and Cummins 2006). Functional feeding groups are categories of invertebrates based on their morphological attributes associated with resource acquisition. The river continuum concept (Vannote et al. 1980) suggests that the distribution and ratios of FFGs varies predictably along the longitudinal gradient of rivers. Thus, shifts in FFG composition are indicative of changes to the ecological functioning of streams.

The disruption of stream functioning from dams coupled with the aging state of dams in the United States has facilitated a recent movement supporting dam removal. Dams generally have a life expectancy of 50 years, and current estimates predict that more than 80% of the documented dams in the United States will exceed this age by 2020 (USACE 1996). Given these estimates, the fate of many dams will soon be in question. To date, removal is an extremely popular option with an estimated 654 dams removed from the nation's rivers (American Rivers 2007). Overall, dam removal appears to be a promising restoration technique beneficial to the integrity of aquatic systems. Yet, as with any restoration technique, the scientific community needs to evaluate all potential effects of dam removal, both negative and positive. By assessing the effects of dam removals on stream geomorphology and biota, restoration efforts can be more efficiently and effectively administered to maximize ecological benefits.

A dam removal can be viewed as a significant ecological disturbance and therefore presents a unique experimental research opportunity. Recently, this opportunity has been recognized and a surge of research has been conducted on the ecological effects of dam removal (e.g. Kanehl et al. 1997; Stanley et al. 2002; Doyle et al. 2003; Pollard and Reed 2004; Doyle et al. 2005; Thomson et al. 2005; Stanley et al. 2007; Cattalano et al. 2007), yet the body of technical literature demonstrating the effectiveness of removal as a restoration technique is still relatively small. Most studies have focused on short-term (<5 years) changes in the river geomorphology (Doyle et al. 2003; Stanley et al. 2002), macroinvertebrate response (Stanley et al. 2002; Pollard and Reed 2004; Thomson et al. 2005), and fish response (Kanehl et al. 1997). Stanley et al. (2002) observed significant erosion and sediment transport in the former impoundment, resulting in rapid channel development close to equilibrium. Sedimentation was observed downstream but was characterized as small and transient. Bushaw-Newton et al. (2002) discovered similar erosion in the former impoundment, yet ten months following removal, coherent riffle-pool formation had failed to emerge. Additionally, they observed downstream aggradation covering coarse cobble dominated riffles. Kanehl et al. (1997) found improved habitat, abundance, and recruitment of desirable fish species following the removal of a dam on the Milwakee River, Wisconsin.

Studies focused on the response of macroinvertebrate communities following dam removals have yielded mixed results. Bushaw-Newton et al. (2002) noted a shift in macroinvertebrate taxa from lentic to lotic in the former impoundment, and seemingly transient declines in sensitive taxa following a Pennsylvania dam removal. Within one year of dam removal, Stanley et al. (2002) found macroinvertebrate communities in both the former impoundment and downstream similar to an upstream reference site. Pollard and Reed (2004) found varying responses in the upstream reference and limited taxonomic changes near the dam and downstream sites. Downstream of dam removal, Thomson et al. (2005) observed no changes in macroinvertebrate assemblage structure and declines in density yet suggest that the negative impacts are relatively minor and temporary.

One recurring message throughout the peer-reviewed and gray literature is the need to evaluate long-term consequences of dam removal (e.g. Bednarek 2001; The Heinz Center 2002; Stanley and Doyle 2003). Few published studies have examined impacts beyond three years, with the exception of Cattalano et al. (2007) and Burroughs (2007) which focused on fish and fluvial geomorphological changes. Despite this acknowledged gap in understanding, some literature on dam removals has suggested time frames for some of these responses (Hart et al. 2002; Doyle et al. 2005). Major geomorphic adjustments including the sediment regime and channel form are suggested to take the longest to return to pre-dam condition. Conversely, many believe that macroinvertebrates will quickly respond to any newly available habitat and recolonize the impacted areas, due to their mobility and short life-cycles. However, studied responses of macroinvertebrate communities to dam are somewhat inconclusive and any observed decline in macroinvertebrate community metrics has been attributed to transient processes and suggested to be short-term. Before this study, no research has been conducted focused on evaluating the long-term effects of dam removal on macroinvertebrate communities.

Connections between macroinvertebrate community composition and mesohabitat (i.e. pool-riffle-run sequence) (Pardo and Armitage 1997; Beisel et al. 1998; Rabeni 2000) suggest that a dearth in available heterogenous pool-riffle-run habitat will have significant implications for macroinvertebrates. Considering the predicted and observed long time frame needed for recovery of key physical attributes such as mesohabitat (Bushaw-Newton et al. 2002) following dam removal, the recovery of the macroinvertebrate community could take more time than previous researchers have predicted. The goal of this study was to evaluate the long-term restorative capacity of dam removal. My objectives were to determine if mesohabitat heterogeneity and macroinvertebrate assemblages within rivers recover following the removal of a dam, and to estimate the time needed for recovery. This research serves as a valuable tool for managers when faced with questions regarding the long-term capabilities of dam removal as a restorative technique. Understanding long-term responses of community and physical dynamics of a river following dam removal helps to clarify expectations, determe reasonable objectives, and thus, paramount in conducting effective and responsible stream restoration.

STUDY AREA

I used a space-for-time substitution approach to quantify changes in mesohabitat and macroinvertebrate communities following the removal of dams from eight rivers in Michigan and Wisconsin (Figure 1.1a). Considering the lack of long-term datasets on dam removal, this approach addresses long-term questions by incorporating rivers in various stages of recovery following dam removal. Wadable rivers were selected from lists of all documented dam removals in Michigan and Wisconsin (Table 1.1; RAW 2005; Hanshue 2006) to maximize the temporal range of time since removal. Time since removal ranged from less than 1 year to 40 years, mean width ranged from 9.0 m to 28.2 m, and dam height ranged from 1.4 m to 5.2 m.

Table 1.1. Streams sampled and some key characteristics. Year removed and dam height information from RAW 2005 and Hanshue 2006.

River	County, State	Dam Name	Year	Dam	Study zone	Mean width (m)
Hersey River	Osceola, MI	Hersey	2006	3.35	5625	14.4
Pine River	Manistee, MI	Stronach	2003[1]	3.7	7475	20.3
Turtle Creek	Rock, WI	Shopiere	2000	3.7	7475	28.2
Au Sable River	Crawford, MI	Salling	1992	5.2	8650	13.3
Kickapoo River	Vernon, WI	Ontario	1992	4.3	6900	13.4
Tomorrow River	Portage, WI	Nelsonville	1987	4.3	5725	9.0
Flat River	Ionia, MI	Smyrna	1973	unknown	6575	42.9
Looking Glass River	Clinton, MI	Wacousta	1966	1.4	8050	21.3

[1] Indicates gradual removal beginning in 1997 and completed in 2003.

METHODS

Each study river was divided into three roughly equivalent sized zones relative to the location of the former dam: a reference zone assumed to not be impacted by the dam or subsequent dam removal (reference), the formerly impounded area immediately upstream of the former dam (impoundment), and a zone downstream of the dam site (downstream) (Figure 1.1b). Study zone lengths ranged from 5625 m to 8650 m, and were constrained by the estimated size of the impoundment and logistical constraints such as stream confluences and downstream impoundments. Within each stream, I compared the response variables in zones affected dam removal (impoundment and downstream) to those in the zone not impacted by dam removal (reference).

Mesohabitat

Mesohabitat was mapped for each river following the general guidelines of Hicks and Watson (1985), where visual assessment while walking the entire study section was used to differentiate between habitat types. The extent of the stream was categorized into a minimum of 25 m units each assigned one the following habitat categories: pool, riffle, run, rapids, or complex. Pools were slower, deeper (> 1 m) sections of the river in which water velocity was obviously reduced. Riffles were higher gradient, shallow (< 1 m) sections which displayed water surface disruption. Runs varied from shallow (< 1 m) to deep (> 1.5 m), and exhibited an undisturbed water surface while maintaining steady water velocities. Rapids were marked by sudden increases in gradient resulting in high water velocity usually displaying some form of "whitewater." Complexes consisted of more than one habitat type.

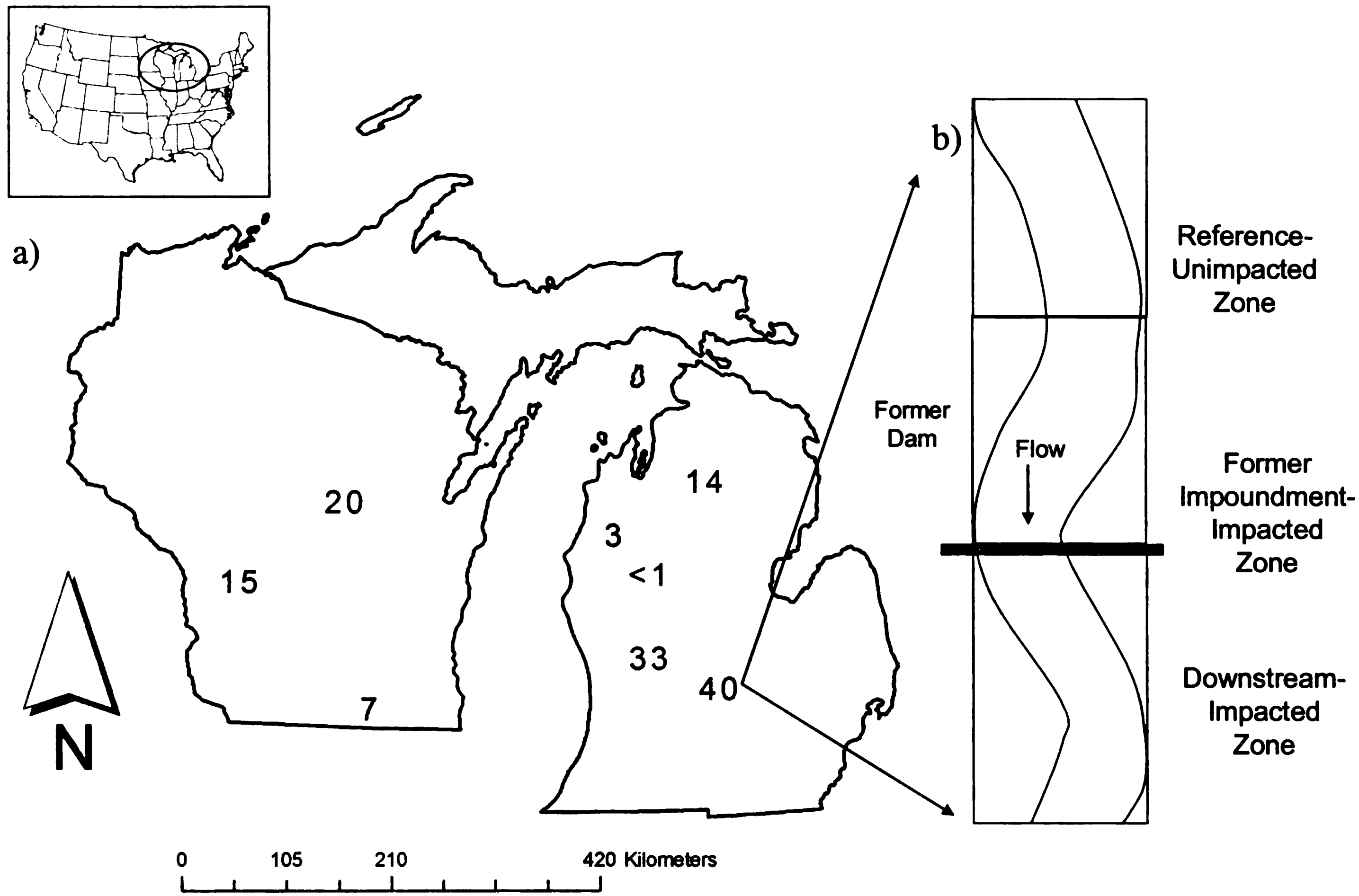


Figure 1.1. a) Map of study streams within Michigan and Wisconsin. Numbers placed approximately in location of former dam and indicate the number of years since removal. b) Location of three zones within each study river.

At the upstream extent of each habitat type unit (i.e. pool, riffle, etc…) the length and width of each unit were measured using a Nikon® laser rangefinder (+/- 0.5 m accuracy). Substrate composition within each habitat type was assessed visually and percentages were qualitatively assigned to each substrate type (clay, silt, sand, gravel, cobble, boulder, or vegetation). Mesohabitat mapping occurred between June 2005 and October 2007 (Table 1.2).

Table 1.2. Sampling dates for each study streams. Number in parentheses indicates number of years since removal at time of sampling.

River	Mesohabitat	Macroinvertebrates
Hersey River	6/20/2007 (<1)	6/21/2007 (<1)
Pine River	6/18/2007 (4)	7/7/2006 (3)
Turtle Creek	5/30/2007 (7)	5/31/2007 (7)
Au Sable River	7/5-6/2006 (14)	7/6/2006 (14)
Kickapoo River	6/2/2007 (15)	6/3/2007 (15)
Tomorrow River	6/5/2007 (20)	6/6/2007 (20)
Flat River	6/7/2005 (32)	6/28/2006 (33)
Looking Glass River	10/30-31/2007 (41)	6/23/2006 (40)

Macroinvertebrates

A stratified random sampling approach was used to characterize the macroinvertebrate assemblages (Cummins 1962). Sample sites were selected following the mesohabitat mapping by randomly selecting three riffles and three runs in each zone. Within each riffle and run a random distance from the upstream extent of the habitat unit and a random distance from shore were selected. Riffle sampling was conducted with a modified Hess sampler (0.086 m^2 area, 500 μm mesh) and run sampling was conducted using one minute timed intervals with a triangular dip net (500 μm mesh) (Merritt and Cummins 1996). At both run and riffle sample sites, if the depth was greater than the sampling equipment allowed, the sample was moved laterally until an adequately shallow depth was encountered. Macroinvertebrate sampling occurred in June and July 2006 and May and June 2007 (Table 1.2).

Macroinvertebrate samples were preserved in 80% ethanol and separated from the sediment in the laboratory via a sucrose floating method (Anderson 1959). Samples estimated to contain more than 400 individuals, based on preliminary sorting, were subsampled using a plankton splitter and taxa counts were multiplied according to the number of times the sample had been split (i.e. split once = N * 2, split twice = N * 4). Insects were identified to the family level and placed into functional feeding groups according to Bouchard Jr. (2004) and Merritt and Cummins (2006), while non-insects were identified to the lowest practical taxonomic level. Insects in the family Chironomidae were divided between the FFG collector-gatherer and predator, 90% and 10% respectively (R. W. Merritt, Michigan State University, personal communication).

Data Analysis

Patterns in mesohabitat changes over time since dam removal were evaluated multiple ways. Meshohabitat maps for each river were visually examined for spatial patterns. Trends in time following dam removal were evaluated by looking for differences in habitat heterogeneity or homogeneity between the reference zones and the two impacted zones (impoundment and downstream). Due to variations in field determinations I combined rapids with riffles and complexes with pools. Mesohabitat diversity (H) was determined using the Shannon diversity index (Krebs 1999) as:

$$H = \sum_{i=1}^{S} p_i \log_2 p_i$$

where s is the number of habitat types and p_i is the proportion of total sample belonging to the ith habitat type. Percent differences in mesohabitat diversity (PD_A) between the reference zone and the impacted zones were calculated as:

$$PD_A = \left(\frac{(D_i - D_r)}{D_r} \right) \times 100$$

where D_i is the diversity in the impacted zone i, and D_r is the diversity in the reference zone r. The amount of run habitat was expected to dominate zones impacted recently by a dam removal, therefore differences in percent run between the reference zone and the impacted zones were examined.

Responses of substrate were evaluated using the qualitative assessments within each zone. Percentage of gravel was used to indicate the extent of substrate coarsening, operating under the assumption that the amount of gravel will increase in impacted zones with time since removal. The percentage of gravel was averaged over all habitat types for each zone and the differences between the reference zones and the impacted zones were calculated. Patterns in differences in mesohabitat diversity, percent run habitat, and mean percent gravel between both the impoundment and downstream zones and the reference zones were examined for trends over time since dam removal using linear regression.

Responses of macroinvertebrate communities over time following dam removal were evaluated using multivariate based comparisons of similarities and other metrics plotted over time since dam removal including functional feeding group proportions, percent Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa, and percent differences in densities. Multivariate approaches included initial exploration of between zone and river similarities using classification and ordination techniques based on Bray-Curtis similarities (Bray and Curtis 1957) using the software package PRIMER (Clarke and Warwick 1994). Given the dominance in abundance of a few families, a one was added to all macroinvertebrate data which were then $\log_e$ transformed. The CLUSTER routine within PRIMER classified samples based on their Bray-Curtis similarities and produced a dendrogram illustrating the grouping of certain samples and their associated levels of similarity. Non-metric multidimensional scaling (NMDS) was also used to portray the grouping of samples in ecological space. Non-metric multidimensional scaling addresses the inherent non-normal distribution of macroinvertebrate count data and ordinates samples based on the ranking of Bray-Curtis similarities and plots them according to those ranks. A stress value is calculated with NMDS which measures the level of agreement between the rank order of distances calculated from the data versus the rank order of distances from the ordination, thus indicating the degree of true representation of the ordination. Typically, a stress level <0.20 is considered acceptable (Clarke and Warwick 1994).

Trends in macroinvertebrate similarity of the impacted zones to the reference over time since removal were evaluated using linear regression. Using the Bray-Curtis similarities generated from PRIMER, I plotted similarities of the macroinvertebrate community in riffles and runs in the impoundment zone and downstream zone to the associated reference habitat types and zones, which then created a temporal pattern of change in similarity. Similarities based on family taxa and FFGs were both evaluated to determine if taxonomic structure responded differently than function. Habitats and zones of rivers which were markedly dissimilar to the reference were further examined to determine which functional feeding groups were driving the differences. The highest contributing functional feeding groups were determined using the SIMPER routine in PRIMER which identifies the percent contribution of each taxonomic group to the average dissimilarity between samples.

General linear models were used to evaluate differences in percents of the collector-gatherer and scraper FFGs, percent differences in taxa richness, differences in percent EPT taxa, and percent differences in densities, all of which were differences relative to the reference zone. Each model followed the design of:

$$y = t + h + t{*}h + e$$

where y was the parameter of interest, t was a continuous variable representing the effect of time since removal, h was a categorical variable indicating the effect of habitat (riffle or run), $t{*}h$ was the interaction between time and habitat, and e was the error term. Separate models were run for each parameter of interest and each zone. General linear models were run using SAS (version 9.1, SAS Institute, Inc., Cary, North Carolina).

RESULTS

Mesohabitat

Visual examination of mesohabitat maps revealed mixed and variable results (Appendix A). Obvious differences in mesohabitat heterogeneity existed within the impoundment of the Hersey River, after less than a year post-removal, yet the downstream zone exhibited higher heterogeneity than the reference zone. Other rivers exhibited similarly mixed results with variable indications of recovery. Surprisingly some rivers, such as the Looking Glass River, experiencing removals even up to 40 years ago, showed some indication of limited mesohabitat recovery within the former impoundment, while Turtle Creek (7 years post removal) appears to exhibit higher mesohabitat heterogeneity in both impacted zones when compared to the reference zones.

Mesohabitat diversity appeared to show no clear trend in recovery over time (Figure 1.2). Overall, many of the impacted zones were lower in diversity than the reference zone, even 40 years after dam removal. Some zones within rivers, however, exhibited high diversity compared to the reference zone soon after dam removal. Within 1 year of removal, the Hersey River displayed heterogenous habitat downstream of the former dam, 8% higher diversity than the reference, yet the impoundment showed very limited habitat diversity, 59% lower than the reference. After 7 years following dam removal, both the downstream and impoundment zones of Turtle Creek exhibited 56% higher diversity than the reference zone. The Looking Glass River displayed slightly higher diversity of mesohabitat in the downstream zone (7%) after 40 years, while the impoundment was 20% lower in diversity than the reference.

The difference in percent run between the impoundment and the reference zone also showed no clear pattern over time since removal (Figure 1.3). Half of the impoundments contained proportionately higher amounts of run habitat than the reference zones, even after 40 years. Similarly, downstream of the dams the difference in percent run from the reference showed no patterns. Run type habitat in downstream zones was proportionally higher than the reference zone in 62.5% of cases. Overall, 56% of the impacted zones exhibited proportionately higher amounts of run type habitat when compared to the reference zones.

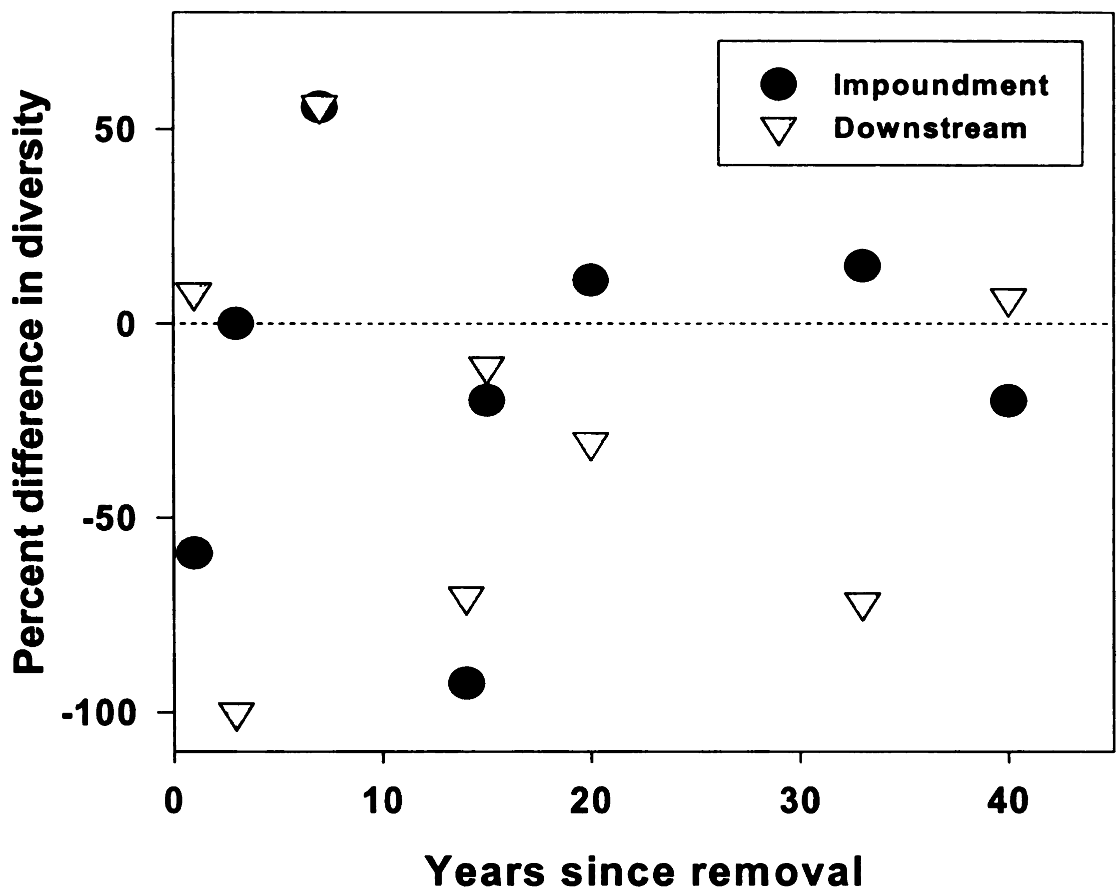


Figure 1.2. Percent difference in mesohabitat diversity for impacted zones compared to the unimpacted reference zones. Shannon-weaver diversity index used.

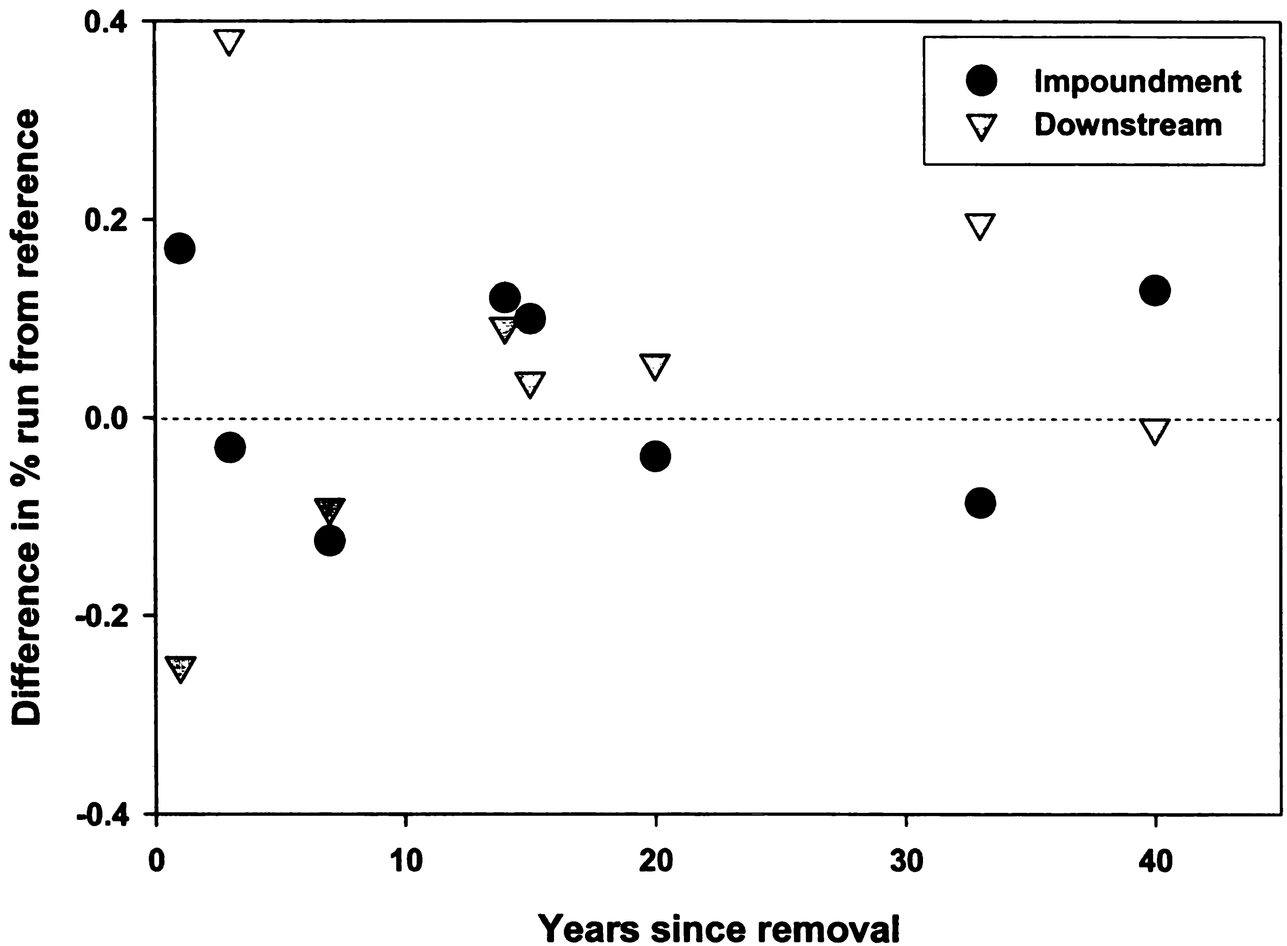


Figure 1.3. Difference in percent run in impacted zones compared to reference zones. Points above dashed zero line indicate zones with higher percent run than the reference.

Qualitative substrate assessments showed an increase in mean percent gravel within the impacted zones over time (Figure 1. 4). By the 15th year following removal, the impoundments of all streams had the same or higher levels of mean percent gravel than the reference zone. Within downstream zones, mean percent gravel levels did not exceed that of the reference until 33 years post-removal. Linear regression indicates a weak positive trend of increasing mean percent gravel over time for both impacted zones ($R^2 = 0.14$, $F_{1,14} = 2.35$, $p = 0.15$). The Au Sable River (14 years post-removal) differed drastically in mean percent gravel between the reference zone and both the impoundment and downstream zones, -50.8% and -58.9%, respectively. When the Au Sable River was removed from the regression, the strength of the trend in gravel recovery over time became significant (Figure 1.4; $R^2 = 0.61$, $F_{1,12} = 18.34$, $p < 0.01$).

Macroinvertebrates

A total of 39,986 macroinvertebrates were collected from the 8 study rivers. The majority of individuals (30,046) were found in riffle habitat (Appendix B) compared to run habitat (9940) (Appendix C). The most dominant taxon in both habitat types was Chironomidae, which accounted for 29% of the individuals from riffle samples and 42% of the individuals from run samples. Within riffles, Hydropsychidae caddisflies were the second most dominant group, accounting for 16% of the individuals, while Elmidae larvae were also common, representing 10% of the individuals. Within run habitat, the two families most prevalent after Chironomidae were Caenidae and Baetidae mayflies which accounted for 10% and 6% of the individuals, respectively.

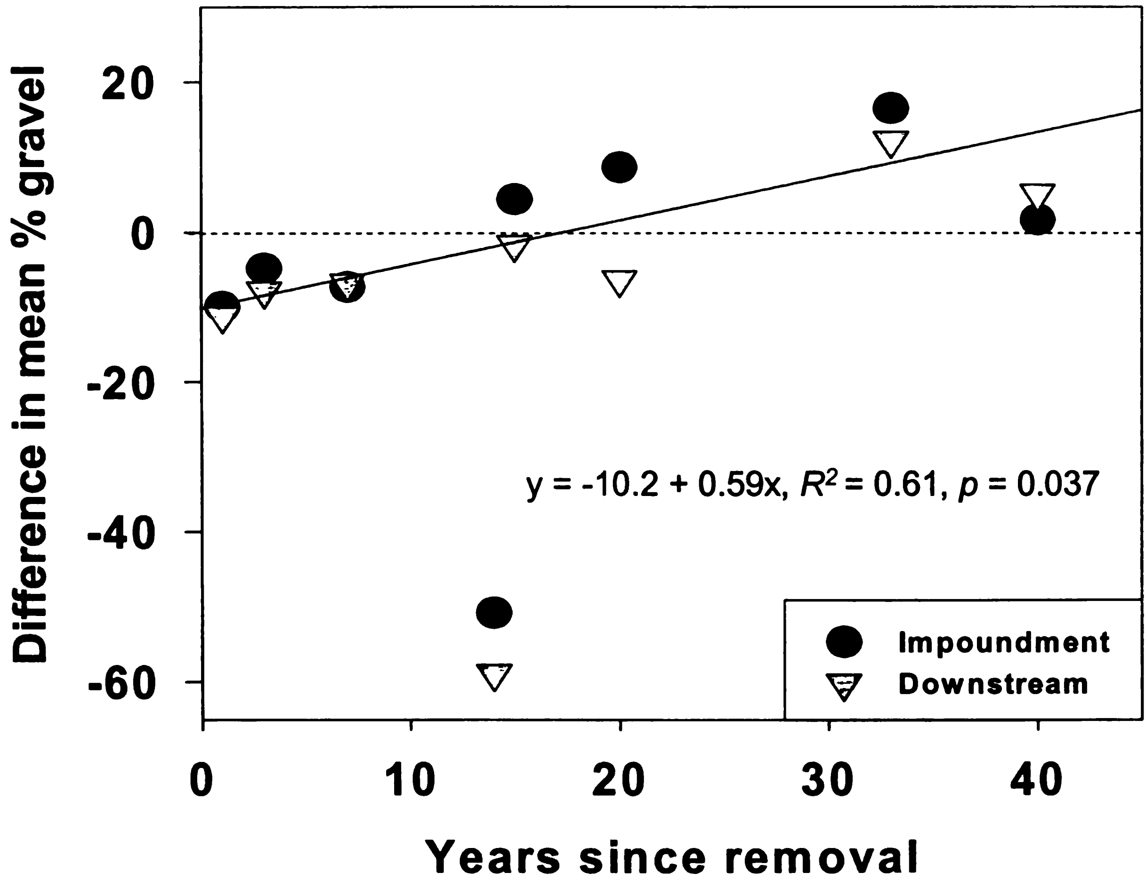


Figure 1.4. Difference in mean percent gravel for impacted zones compared to the reference zones. Solid line indicates regression for downstream zone excluding year 14.

Bray-Curtis classification of the macroinvertebrate communities of all zones and habitat types indicated a strong divergence in similarity of run communities in the impacted zones of the Hersey River (< 1 year post-removal) and run and riffle communities in the Pine River (3 years post-removal) relative to the reference zones (Figure 1.5). In contrast, most of the rivers in later stages of the recovery grouped together, indicating strong similarities between zones of the same river. Non-metric multidimensional scaling displayed the same relationships with an acceptable stress level (Figure 1.6; stress = 0.1).

Macroinvertebrate assemblages were more similar between impacted zones and reference zones after longer amounts of time since removal, as supported by the multivariate classifications and ordinations (Figure 1.7). Within the impoundment, riffle assemblages exhibited lower similarity to the reference zone within the first 3 years than the later years (> 7). The most extreme difference was riffle assemblages in the Pine River's impoundment which were markedly different than those of the reference zone, showing only 30% similarity. Run assemblages within the impoundment showed similar patterns as the riffles over time but were more dissimilar. Initially, run assemblages in impoundments of the Hersey River and the Pine River displayed limited similarity to the reference zone, 32% and 27%, respectively. By the 7th year following dam removal, the riffle and run assemblages appeared to be relatively similar to those of the reference, showing at least 70% and 66% similarity, respectively. With riffle and run samples grouped together, the taxonomic structure of the macroinvertebrate assemblage within the

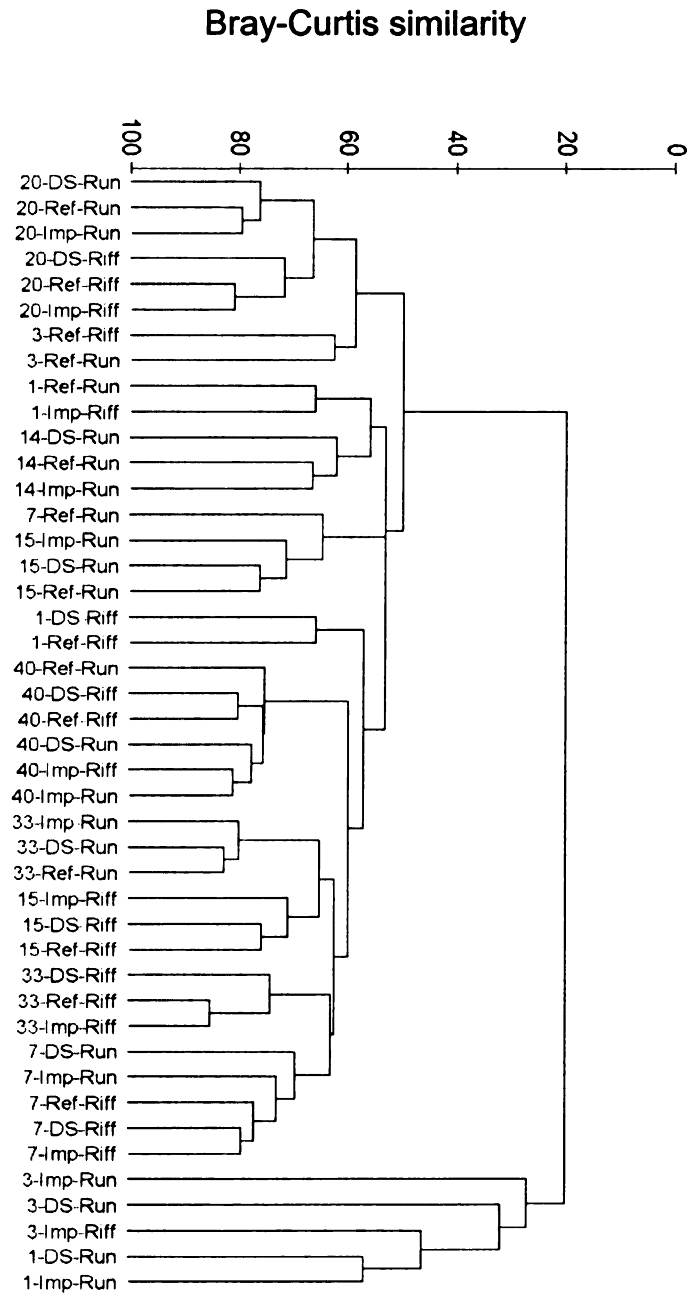


Figure 1.5. Clustering dendrogram of Bray-Curtis similarities. Number in label indicates number of years since removal; Imp = former impoundment zones, DS = downstream zone, Ref = reference zones; followed by habitat type.

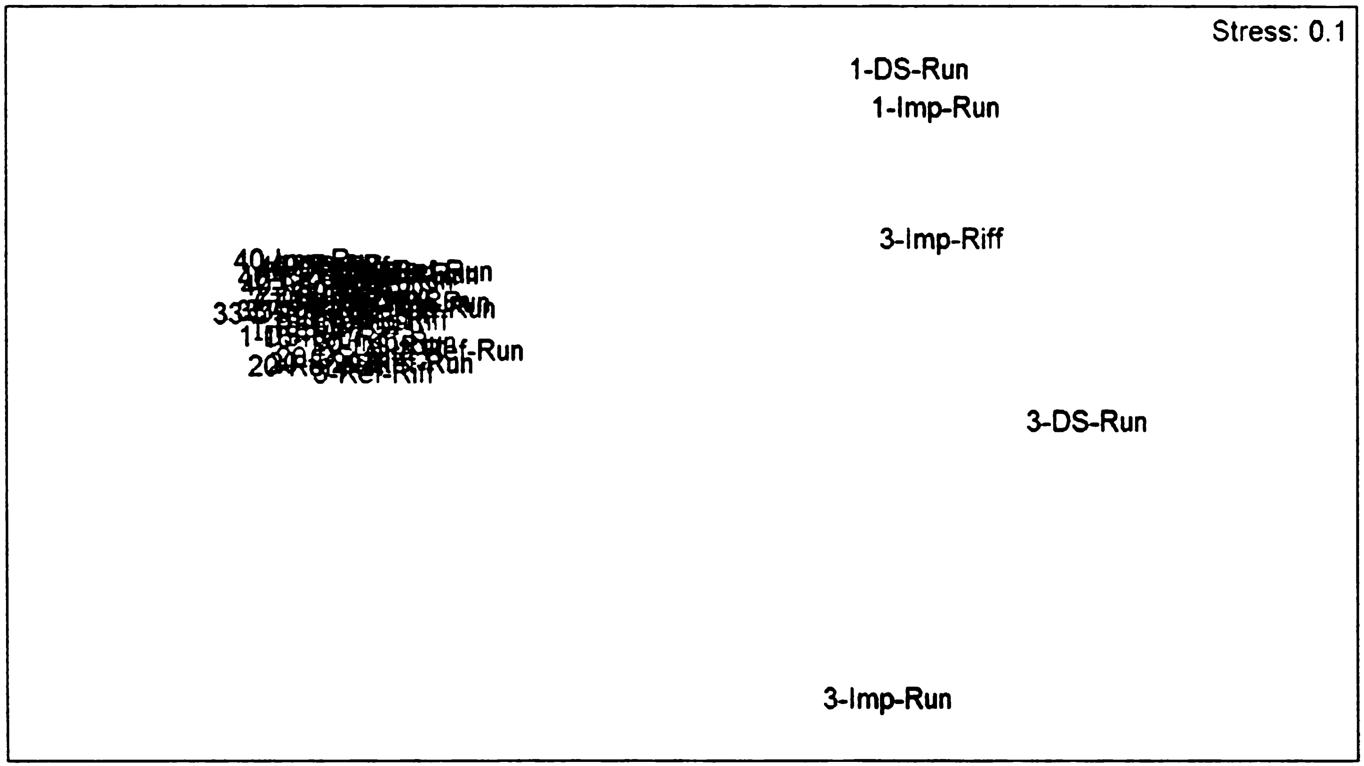


Figure 1.6. Non-metric multidimensional scaling plot of all rivers, zones and habitat types. Number in label indicates number of years since removal; Imp = former impoundment zones, DS = downstream zone; Ref = reference zones; followed by habitat type.

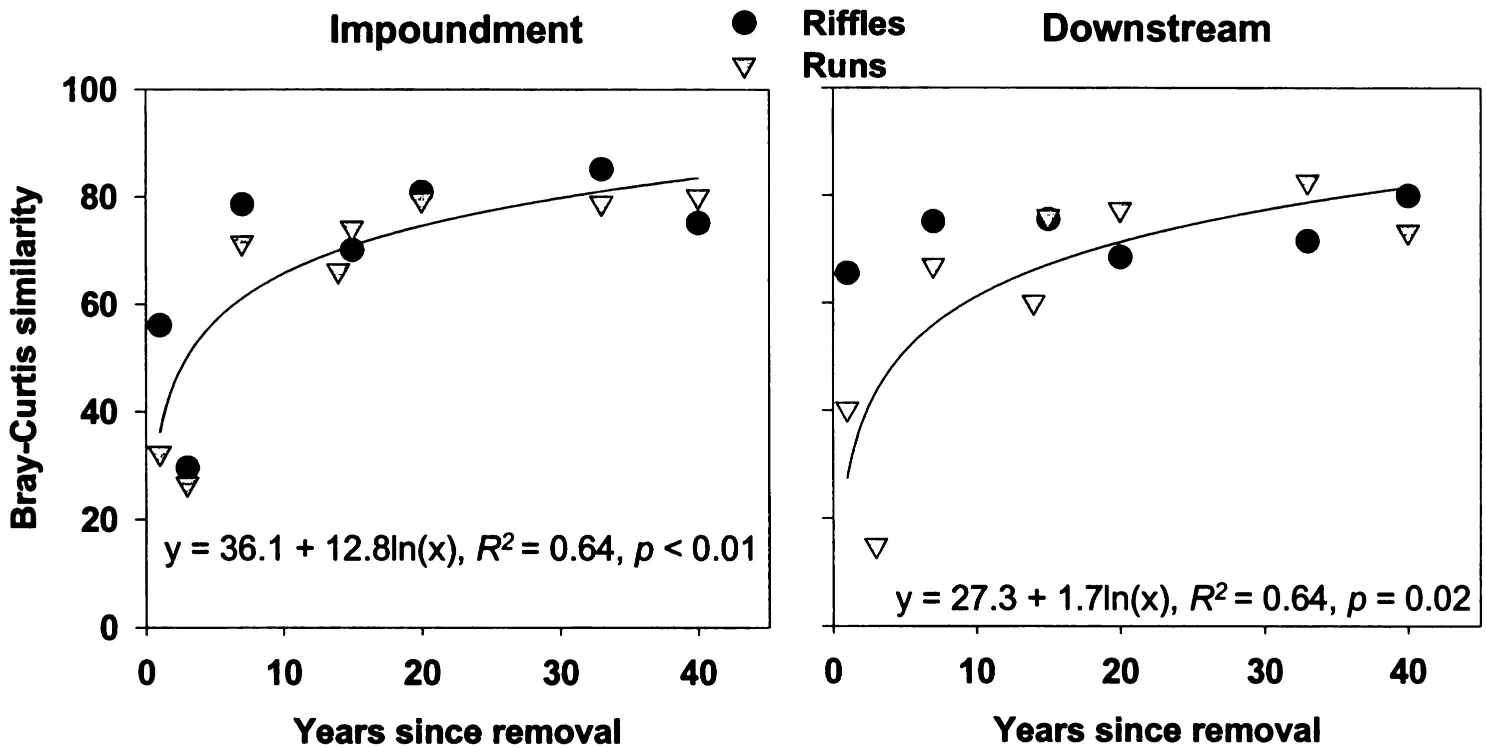


Figure 1.7. Bray-Curtis similarity of taxonomic structure in impacted zones relative to the reference zone over time since removal. Solid lines represent logarithmic relationships between similarity and years since removal for both habitat types in the impoundment zones (left panel) and downstream runs (right panel).

impoundment followed an asymptotic trajectory of recovery (Figure 1.7; $R^2 = 0.64$, $F_{1,13} = 23.37$, $p < 0.01$).

The zones downstream of the former dam exhibited similar patterns of macroinvertebrate assemblage recovery as the former impoundment in runs yet not in riffles. Taxonomic structure of riffle macroinvertebrates within the downstream zone appeared to recovery immediately, returning to > 65% similarity within 1 year of dam removal (Figure 1.7). Run assemblages downstream of the dam appeared to show limited recovery within the first 3 years of dam removal. Downstream run assemblages within the Hersey River were 41% similar to those of the reference zone while downstream runs in the Pine River were only 15% similar. Following the patterns of the impoundment, similarity of the downstream zone to the reference zone asymptotes around 7th year following the dam removal (Figure 1.7; $R^2 = 0.64$, $F_{1,6} = 10.63$, $p = 0.02$).

Functional feeding group composition of the macroinvertebrate communities appeared to be less affected by dam removal than taxonomic structure, exhibiting overall higher similarities across all time steps (Figure 1.8). Specifically, riffle assemblages in both the impoundment and downstream zones returned to at least 83% similarity within 1 year of dam removal, with the exception of riffles in the former impoundment of the Pine River, which showed only 42% similarity after 3 years. Run assemblages within both impacted zones displayed noticeably lower similarities within 3 years of dam removal, while runs within rivers in the 7th year or more following removal exhibited high levels of similarity. Functional recovery within runs in both zones follows the same asymptotic

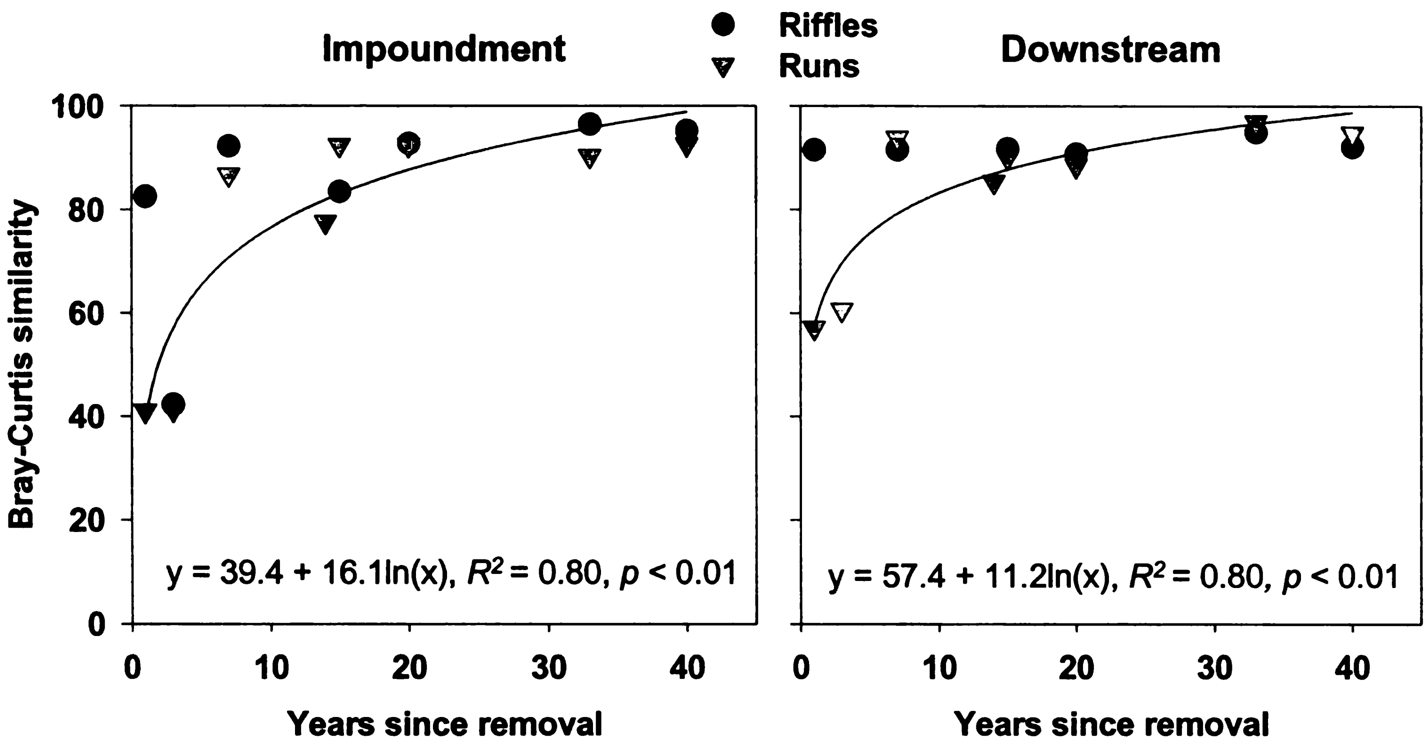


Figure 1.8. Bray-Curtis similarity of Functional Feeding Groups in impacted zones relative to the reference zone over time since removal. Solid lines represent logarithmic relationships between similarity and years since removal for impoundment runs (left panel) and downstream runs (right panel).

trajectory as taxonomic structure (Figure 1.8; $R^2 = 0.80$, Impoundment: $F_{1,6} = 24.20$, Downstream: $F_{1,6} = 25.30$, $p < 0.01$).

The composition of the FFGs within Hersey River and Pine River runs varied by zone (Table 1.3). The FFGs contributing to most of the dissimilarities were predators, scrapers, and collector-gatherers (Table 1.4). The dissimilarities between runs in both the impacted zones of the Hersey River was primarily attributed to predators. Additionally, scrapers contributed to the dissimilarities in both the impoundment and downstream zones, 18% and 22%, respectively. Within the Pine River, collector-gatherers accounted for the majority of the differences between runs in the impacted zones and runs in the reference zones.

Table 1.3. Percent composition of FFGs and total numbers within runs in the Hersey River (<1 year post-removal) and the Pine River (3 years post-removal). CG = Collector-Gatherer; CF = Collector-Filterer; Pr = Predator; Sc = Scraper; Sh = Shredder

	Hersey River			Pine River		
	Ref	Impound	DS	Ref	Impound	DS
% CF	3	7	3	2	0	0
% CG	85	89	94	51	56	10
% Pr	10	4	2	25	22	57
% Sc	1	0	0	3	22	33
% Sh	1	0	0	18	0	0
Total	875	27	123	175	9	30

General linear models failed to reveal any significant patterns in the difference in percent collector-gatherers between the reference and the impoundment or downstream zones (Figure 1.9; Impoundment: $F_{1,13} = 2.38$, p = 0.15; Downstream: $F_{1,12} = 2.62$, $p = 0.13$). Visual examination of the relationships within the impoundment corroborates the

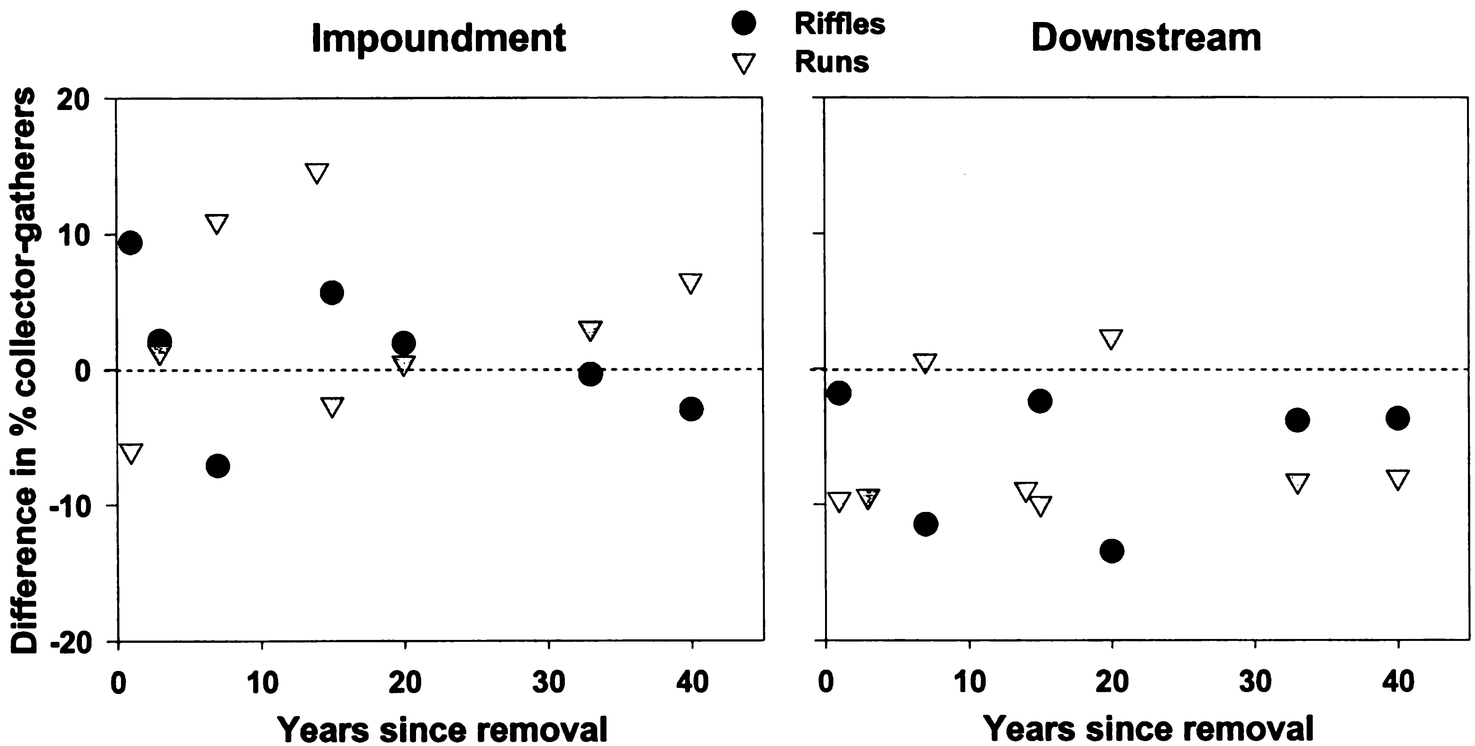


Figure 1.9. Difference in percent collector-gatherers between impacted zones and reference zones over time since removal. Points below dashed zero line indicate areas with lower percentage of scrapers than the reference zone.

lack of any pattern; certain zones and habitat types had higher numbers of collector-gatherers relative to the reference while others have lower numbers. However, the downstream zone appeared to exhibit overall lower numbers of collector-gatherers than the reference. Riffles within the downstream zone of all rivers displayed lower levels of collector-gatherers than the reference zone, with the largest difference being 20% in the Tomorrow River, 20 years post-removal. Similarly, 6 out of the 8 rivers maintained lower levels of collector-gatherers in run habitat, including rivers 33 and 40 years post-removal.

Table 1.4. Percent contributions of FFGs to dissimilarity between runs in reference zones and impacted zones within the Hersey River (<1 year post-removal) and the Pine River (3 years post-removal). CG = Collector-Gatherer; CF = Collector-Filterer; Pr = Predator; Sc = Scraper; Sh = Shredder.

	Hersey River		Pine River	
% FFG	Impoundment	Downstream	Impoundment	Downstream
CF	15	16	14	19
CG	24	14	24	36
Pr	26	26	24	11
Sc	18	22	21	13
Sh	17	21	17	22

Patterns in the difference between percent scrapers in the reference zone and the impacted zones appeared to occur as rivers progressed through the stages of recovery. Habitat factors and the interaction between time since removal and habitat were removed from the model because they were not significant, which resulted in significant negative relationship between the time since removal and the difference in percent scrapers between the reference zone and both the impoundment and downstream zones (Figure 1.10; Impoundment.: $R^2 = 0.30$, $F_{1,13} = 6.68$, $p = 0.03$; Downstream: $R^2 = 0.29$, $F_{1,12} =$

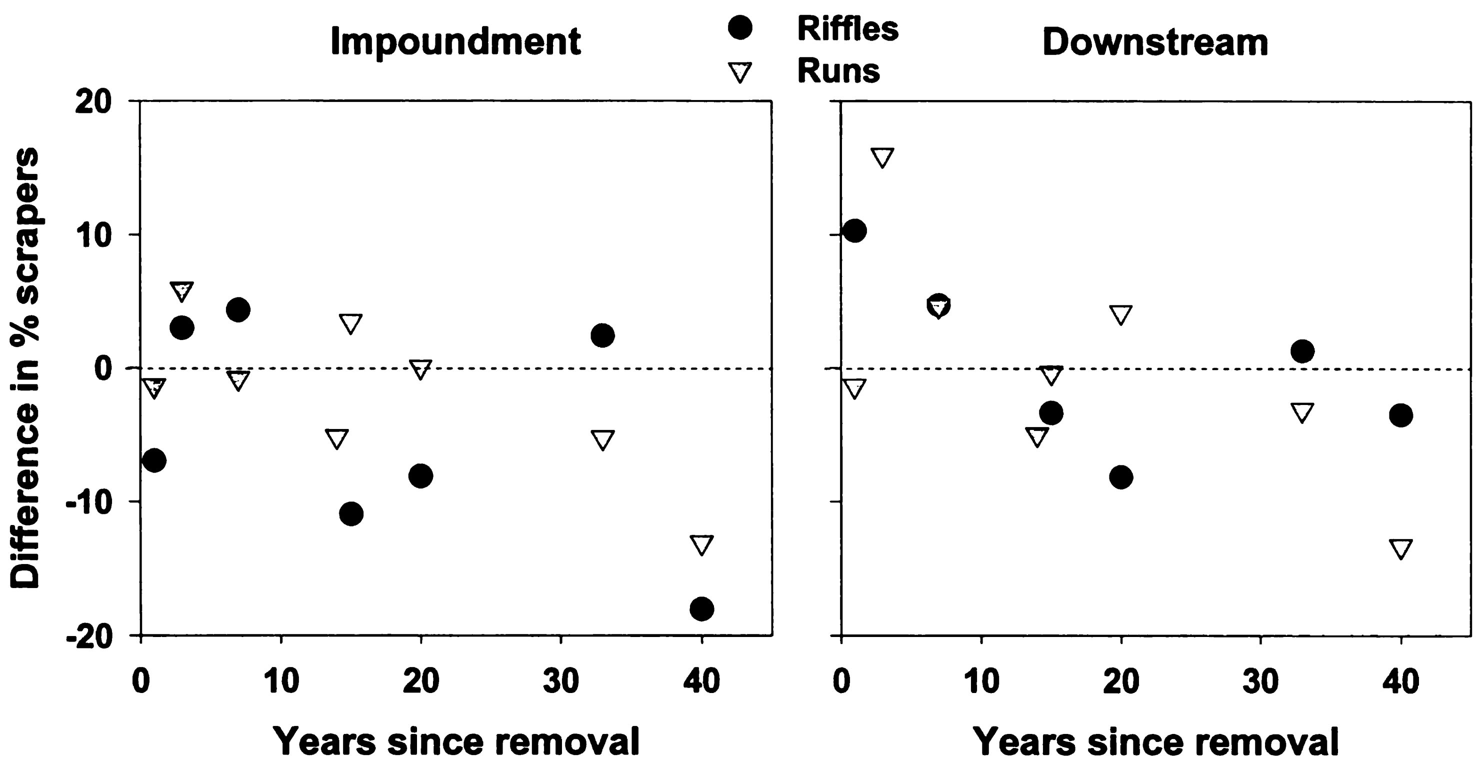


Figure 1.10. Difference in percent scrapers between impacted zones and reference zones over time since removal. Points below dashed zero line indicate areas with lower percentage of scrapers than the reference zone.

4.79, p = 0.05). When both impacted zones and habitat types were combined, a clear negative trend existed (Figure 1.11; $R^2 = 0.34$, $F_{1,27} = 13.77$, $p < 0.01$), indicating a proportionate decrease in the amount of scrapers in the impoundment and downstream zones as these zones recovered.

Percent differences in taxa richness between impacted zones and reference zones generally decreased as time since removal passed (Figure 1.12). Within the former impoundment, richness in both riffle and run assemblages was lower than the reference zone for the rivers 1 and 3 years post-removal. Percent differences in richness followed a logarithmic trajectory for assemblages in both habitat types within the former impoundment ($R^2 = 0.54$, $F_{1,13} = 14.88$, $p < 0.01$), with virtually no difference in richness by the 7th year post-removal. No clear trend in differences in richness existed with riffle assemblages within the downstream zone (Figure 1.12). Run assemblages in the downstream zone within the first 3 years following removal exhibited differences in richness of more than 60% relative to the reference zone, yet taxa richness was virtually the same by the 7th year post-removal. Similar to the former impoundment, recovery of richness within run assemblages in the downstream zone followed a logarithmic pattern (Figure 1.12; $R^2 = 0.65$, $F_{1,6} = 10.99$, $p = 0.02$).

Within the former impoundment of the Hersey River (< 1 year post-removal), run assemblages and riffle assemblages exhibited 7 and 2 fewer taxa, respectively, than the reference zone. Within the downstream zone of the Hersey River, run assemblages exhibited 7 fewer taxa than the reference zone. Selected families found within the reference zone but not within the impacted zones of the Hersey River included Elmidae

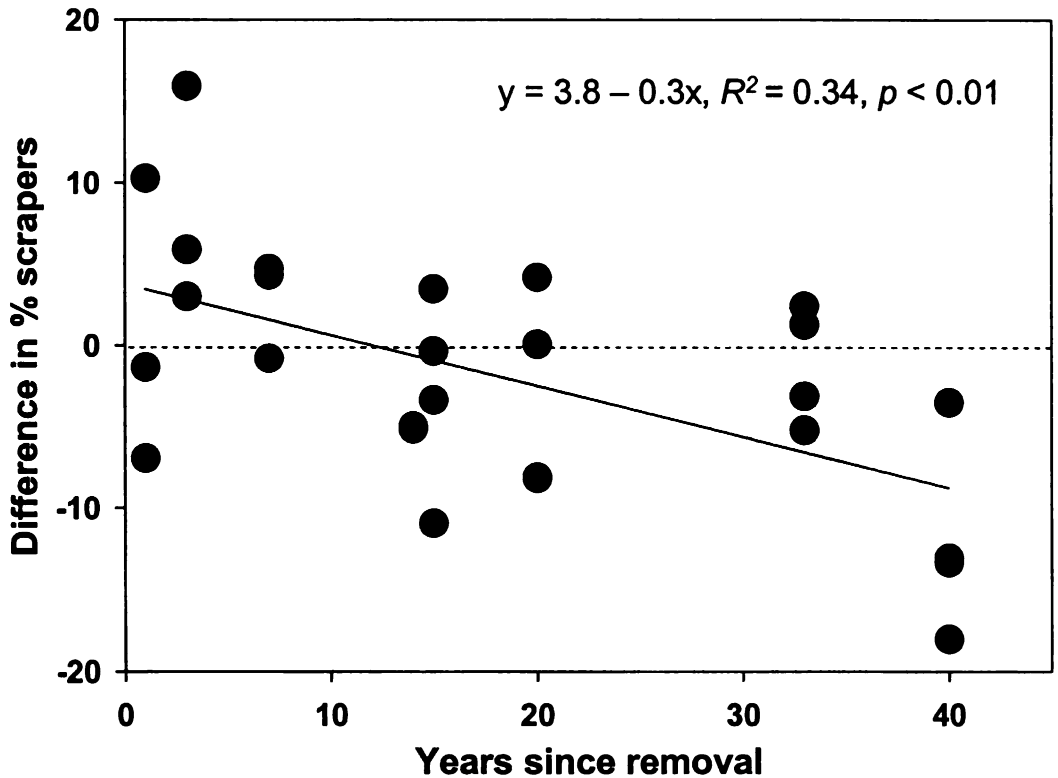


Figure 1.11. Difference in percent scrapers between impacted zones and reference zones over time since removal with both habitat types and zones combined. Points below dashed zero line indicate areas with lower percentage of scrapers than the reference zone.

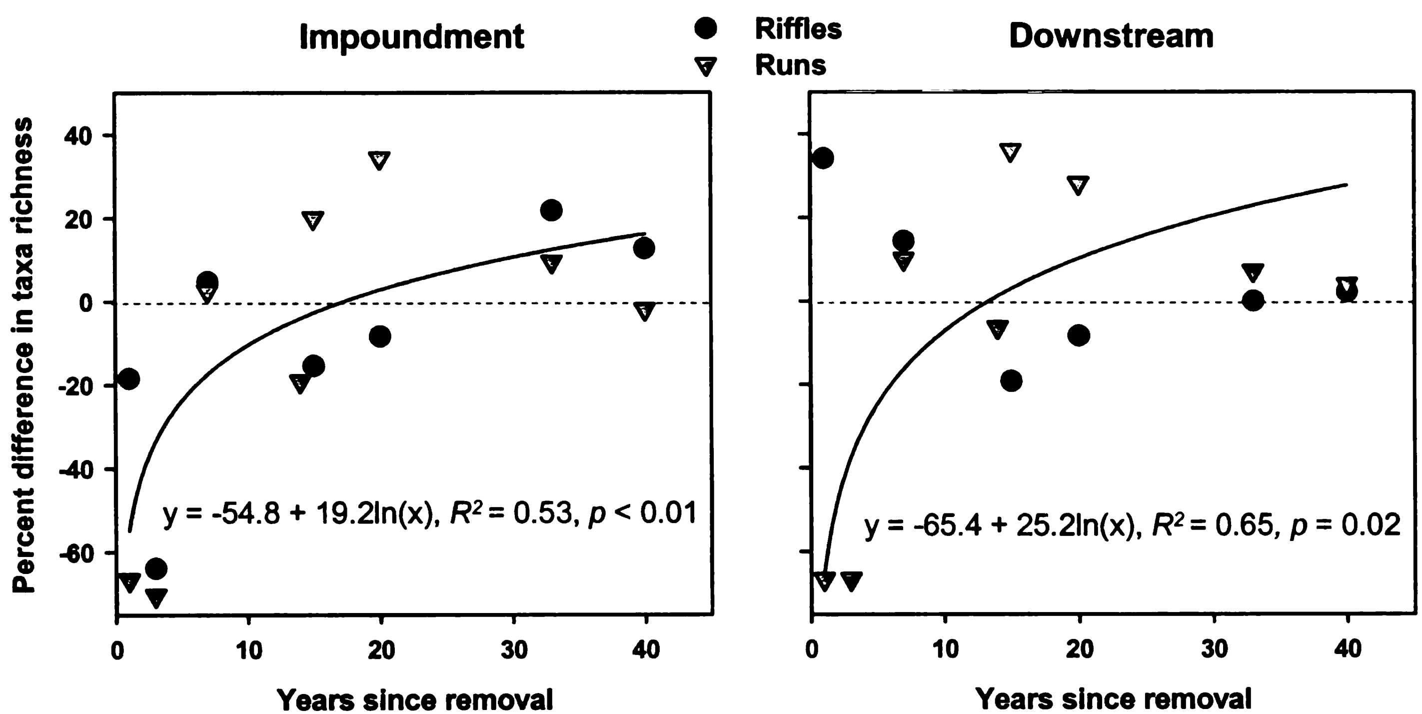


Figure 1.12. Percent difference in taxa richness between impacted zones and reference zones over time since removal. Points below dashed zero line indicate areas with lower percent EPT taxa than the reference zone. Solid lines represent logarithmic relationships between richness and years since removal for impoundment runs and riffles (left panel) and downstream runs (right panel).

larvae, Tricorythidae, Perlidae, Glossosomatidae, Ephemerellidae, and Tipulidae (Table 1.5). Within the former impoundment of the Pine River (3 years post-removal), run assemblages and riffle assemblages exhibited 6 and 8 fewer taxa, respectively than the reference zone. Within the downstream zone of the Pine River, run assemblages exhibited 6 fewer taxa than the reference. Selected families found within reference zone but not within the impacted zones of the Pine River included Brachycentridae, Heptageneidae, Elmidae larvae, Tipulidae, Ephemerellidae, and Athericidae (Table 1.5).

Differences in percent EPT taxa between impacted zones and reference zones do not follow any significant pattern as time since removal increases (Figure 1.13; Impoundment: $F_{1,13} = 0.67, p = 0.43$; Downstream: $F_{1,12} = 0.00, p = 0.95$). Within the impoundment any differences in percent EPT taxa did not exceed 20% and the majority of habitat types exhibit higher levels of percentage of EPT taxa than the reference zone. Within the downstream zone the majority of habitat types of all rivers displayed higher percentages of EPT taxa than the reference as well. The notable exception being runs in the Pine River which had a difference of 40% EPT taxa from runs in the reference zone.

Percent differences in macroinvertebrate densities between impacted zones and the reference zones revealed mixed patterns. Within the impoundment initial linear models were not significant (Figure 1.14; $F_{3,11} = 0.36, p = 0.78$), yet visual analysis indicated Turtle Creek (7 years post-removal) greatly deviated from an apparent trend in the other rivers. When Turtle Creek was removed from the analysis, both macroinvertebrates in both habitat types exhibited a strong positive relationship of increasing densities over time when compared the reference zone (Figure 1.14; $R^2 = 0.70$,

Table 1.5. Taxa found in reference zones which are not found in impacted zones for the two most recent dam removals. Ten most abundant taxa listed. (l) indicates larval stage, (p) indicates pupa stage, and (a) indicates adult stage.

1				3		
Impoundment Runs	Downstream Runs	Impound Riffles	Downstream Riffles	Impound Runs	Downstream Runs	Impound Riffles
Elmidae (l)	Elmidae (l)	Perlidae	Amphipoda	Brachycentridae	Baetidae	Hydropsychidae
Amphipoda	Amphipoda	Hydracarina	Perlidae	Unknown (p)	Elmidae (l)	Elmidae (l)
Tricorythidae	Tricorythidae	Glossosomatidae	Hydracarina	Heptageneidae	Brachycentridae	Brachycentridae
Oligochaeta	Oligochaeta	Ephemerellidae	Phryganeidae	Tipulidae	Oligochaeta	Simuliidae
Tipulidae	Isopoda	Phryganeidae	Cambaridae	Hydracarina	Heptageneidae	Tipulidae
Corixidae	Tipulidae	Cambaridae	Uenoidae	Elmidae (a)	Tipulidae	Tricorythidae
Hydracarina	Hydracarina	Corixidae	Corixidae	Ephemerellidae	Hydracarina	Ephemerellidae
Simuliidae	Ephemerellidae			Empididae	Athericidae	Athericidae
Ephemerellidae	Hydroptilidae			Isonychiidae	Ephemerellidae	Hydroptilidae
Hydroptilidae	Hirudinea			Tabanidae	Empididae	Pteronarcyidae

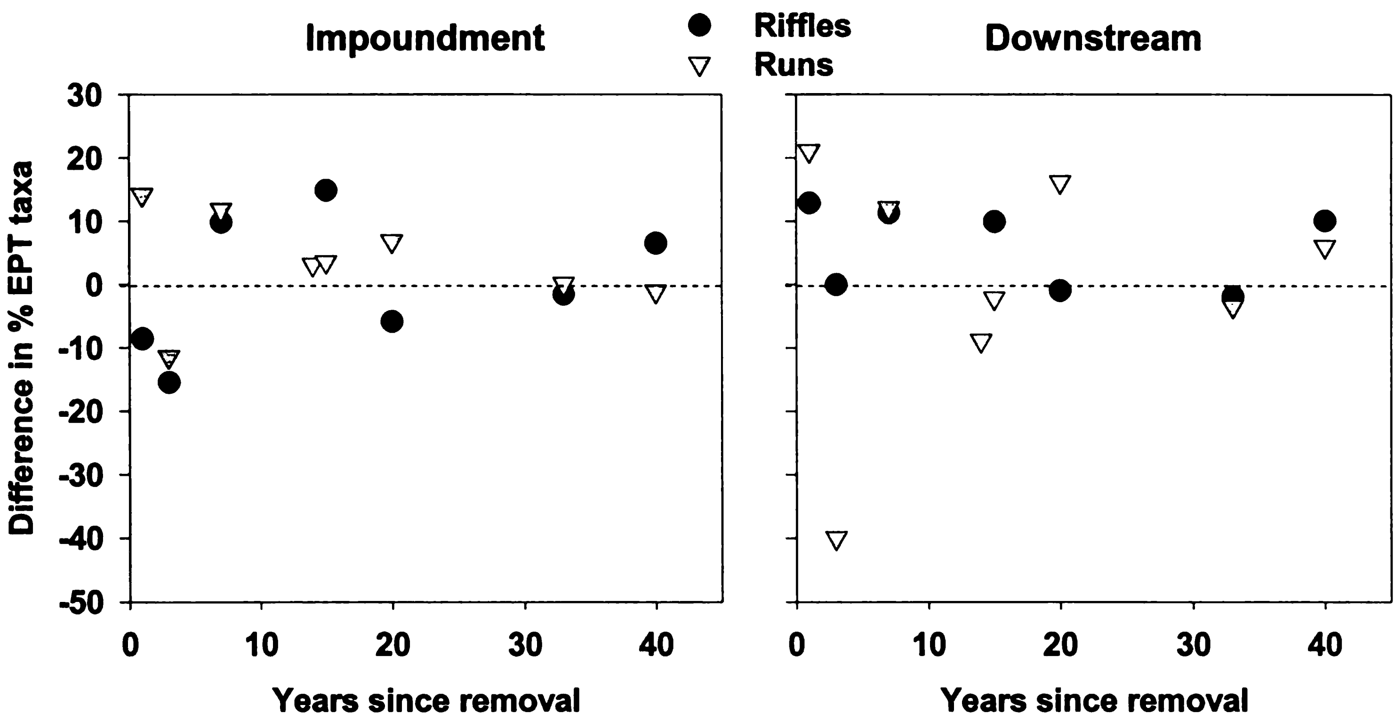


Figure 1.13. Difference in percent Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa between impacted zones and reference zones over time since removal. Points below dashed zero line indicate areas with lower percent EPT taxa than the reference zone.

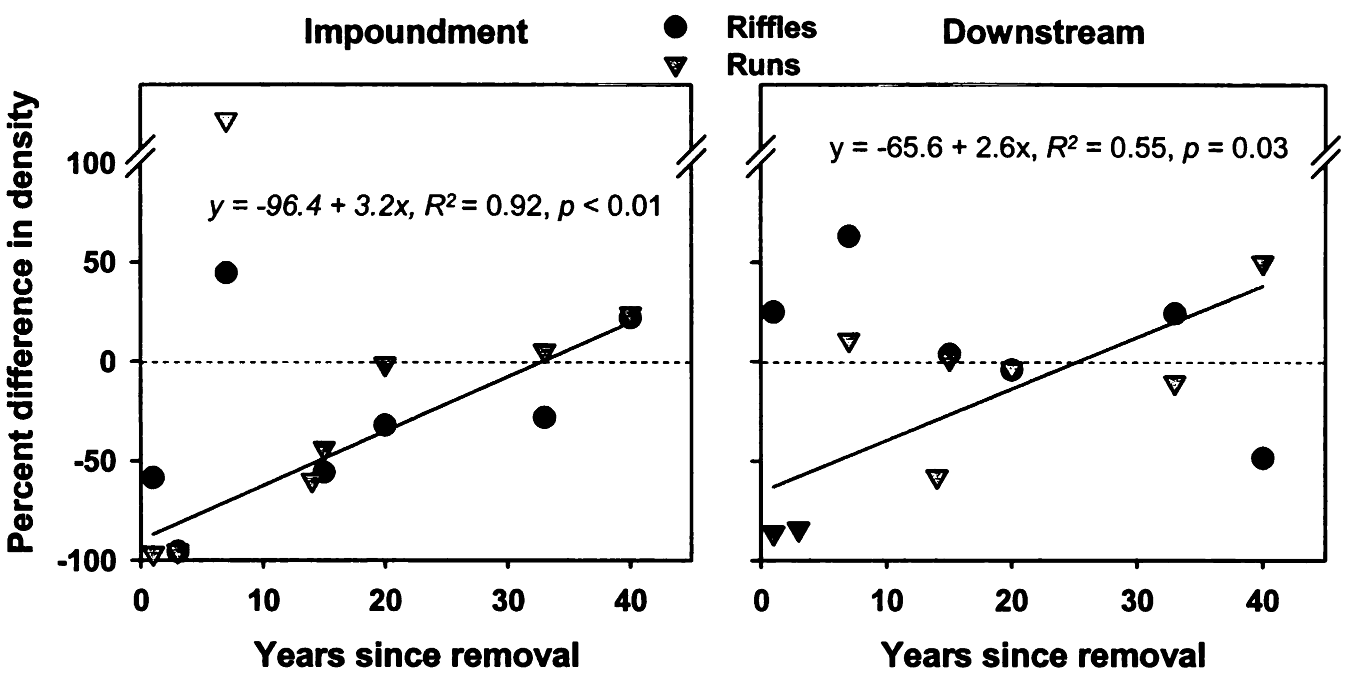


Figure 1.14. Percent difference in densities between impacted zones and reference zones over time since removal. Points below dashed zero line indicate areas with lower densities than the reference zone.

$F_{3,9} = 8.80, p < 0.01$). Within the downstream zone, the full model was significant ($R^2 = 0.56$, $F_{3,10} = 4.33, p = 0.03$) which indicated that habitat and year since removal by habitat interaction were also significant ($F_1 = 10.27, p < 0.01$ and $F_1 = 8.78, p = 0.01$, respectively). The significant habitat and year since removal interaction indicated different relationships of density recovery over time for runs and riffles downstream of the former dam. Linear regression revealed a significant relationship between time since removal and percent difference in density of the downstream runs (Figure 1.14; $R^2 = 0.55$, $F_{1,6} = 7.38, p = 0.03$) yet the relationship in riffles was not significant ($R^2 = 0.48$, $F_{1,4} = 3.68, p = 0.13$).

DISCUSSION

In this study, I examined the ability of mesohabitat and macroinvertebrate communities to recover following dam removal. Patterns in mesohabitat recovery failed to emerge as a function of time since removal and suggest that responses may depend on numerous situation specific attributes. Dissimilarity of the macroinvertebrate community and differences in richness compared to the reference zone were relatively high for 3 years following dam removal, yet were minimal by the 7th year. Some components of the macroinvertebrate community followed linear trends in recovery yet time frames appear to be much longer than other research has suggested, specifically densities and the proportion of scrapers. Macroinvertebrate assemblages appeared to recover at slower rates in run habitat than riffle habitat, which has significant implications for run dominated systems. Generally, important attributes of the macroinvertebrate community appear to recovery 3- 7 years following dam removal while still others remain low after decades have passed.

Pool-riffle-run habitat showed varying levels of recovery without a discernible trend. Mesohabitat diversity appeared to be low in many of the impacted zones even after 40 years with the exception of Turtle Creek that showed high diversity after 7 years. Additionally, along with the downstream zone of Hersey River (< 1 year post-removal), Turtle Creek appeared to be less dominated by run type habitat relative to the impoundment than many of the other study rivers. The low diversity and extended dominance of run type habitat within many of the impacted zones suggest that some components of habitat only partially recover following dam removal. Failure to recover in some downstream zones could be attributed to the presence of impoundments downstream, which was the case for the Pine River (3 years post-removal), the Au Sable River (14 years post-removal), and the Flat River (33 years post-removal). If the downstream zone of the Flat River was excluded from consideration, the difference in diversity appears to be greatly reduced after 20 years.

With the exception of the Au Sable River, substrate coarseness eventually recovered, yet not until 17 years following removal (Figure 1.4). The Au Sable River was much more dominated by sandy substrates throughout the former impoundment and downstream zone than the reference zone. This could be attributed to natural geological differences or possible differences in gradient within the impacted zones compared to the reference zone. If the impacted zones have relatively low gradient the ability of the river to transport sediment may be inhibited. Additionally, the Salling Dam on the Au Sable

River, was 5.2 m (Table 1.1), which was the tallest dam within our study. The impacts due to the original dam construction could have hindered the river's ability to recover more so than the other study rivers.

Generally, the macroinvertebrate taxonomic structure and differences in taxa richness in impacted zones appeared to become similar to unaffected areas 3 - 7 years following dam removal. These findings are contrary to some previous studies which found assemblages within the former impoundment and downstream zones indistinguishable from those in a reference site after only 1 year following a dam removal (Stanley et al. 2002). Similarly, Thomson et al. 2005 found assemblage structure downstream of a dam removal to be similar to an upstream reference site after less than 1 year, yet sampling was conducted only in riffles. Within this study, riffle habitat appeared to recover more rapidly than run habitat, especially downstream of the dam removal where no differences were obvious in less than one year following removal. Run habitat showed lower similarities within both impacted zones and appeared to require more time for macroinvertebrate assemblage structure to recover.

Differences in taxonomic richness were also most prevalent in run type of impacted zones compared to reference zones. The Hersey River (<1 year post-removal) and the Pine River (3 years post-removal) exhibited the largest differences in taxa richness, indicating that dam removal does not immediately restore families lost either by the damming or the removal itself. However, by the 7th year after dam removal, richness differences between the reference zone and the impacted zones in Turtle Creek were negligible. It appears that lower richness in impacted zones soon after dam removal could be attributed to the lack of more sensitive families. Some of the more common families found within the reference zone yet not in the impacted zones associated with recent removals included Brachycentridae, Ephemerellidae, Athericidae, Perlidae, and Glossosomatidae which are all considered relatively sensitive taxa to numerous forms of pollution (Carter et al. 2006). These more sensitive taxa may not appear for up to 7 years following removal especially within runs, which has important implications for monitoring efforts focused on sensitive groups of macroinvertebrates.

The discrepancy between recovery rates for macroinvertebrates between riffles and runs is interesting and noteworthy. Run communities appeared to recover from removal disturbance slower than riffle communities. Most of the limited research regarding macroinvertebrates response to removal has focused on cobble and riffle habitats or used sampling equipment restricted to shallow depths (Pollard and Reed 2004; Thomson et al. 2005). Stanley et al. (2005) sampled impounded reaches, presumably in run type habitat, yet only investigated coarse level assemblage and biotic integrity responses and found that communities become more lentic than lotic following removal.

Run type habitat is often overlooked in sampling because of the inherently higher levels of biomass and richness associated with riffles. Given the predominance of run habitat in rivers within our study region, the composition of macroinvertebrates within runs is important to consider. High water velocities within riffles facilitate rapid removal of deposited sediment while runs are subjected to more deposition due to lower velocities. While macroinvertebrates may be immediately displaced from riffles following the pulse of sediment from a dam removal downstream, they appear to be able to return shortly. This research suggests the runs may recover at slower rates than higher velocity habitats.

The negative trend in percent of scrapers over time was interesting in that it applied to both habitat types and zones. Initially following dam removal, the proportion of scrapers appeared to be higher than that of the reference. These differences declined over time, becoming the same as the reference zone in the 12th year, and continued to lower levels of scrapers than the reference zones in the following years. Scrapers feed on algae which prosper in open canopies, similar to what would be found within a recently drained impoundment. As the extent of riparian shading develops from vegetation growth the dominance of scrapers would decline in the former impoundment. Orr and Stanley (2006) showed that former impoundments become revegetated rapidly after dam removal yet the frequency of trees remains low for decades. Mechanisms explaining this decrease in scrapers over time since removal in downstream zones are not the same as the former impoundment and the cause is unclear. The role of riparian plantings should be considered to facilitate more rapid recovery of the stream-side canopy. Accelerating the riparian development of a formerly impounded zone could additionally buffer against excessive warming and enhance bank stability, thus reducing the influence of slumping banks contributing to downstream sediment transport.

With the exception of Turtle Creek, macroinvertebrate densities within the former impoundment did not recover for nearly 33 years, much longer than anticipated by other studies (Doyle et al. 2005). Downstream of former dams, runs responded similarly to the former impoundment, recovering after 25 years. This extended time may be overestimated due to the strong influence of the two most recent removals, which show greatly reduced densities. Riffles downstream of the dam returned to densities at or above the reference zone within a year of dam removal, similar to the predictions by Thomson et al. (2005).

Answering complex ecological questions on long-term time scale is difficult due to the logistical constraints of funding and foresight and the current need for management recommendations. The space-for-time approach I used was valuable, yet has limitations. Pickett (1989) describes the past successes of space-for-time substitution studies especially when attempting to describe general patterns and generate working hypotheses. I believe this study has done just that, in demonstrating general patterns of recovery of mesohabitat and macroinvertebrates following dam removal. The largest limitation to the approach employed here is the assumption that all of the study rivers have been influenced equally over time by external sources. We have attempted to minimize the role of external influences here by only comparing within rivers to generate the points in time and not treating the rivers as replicates. We also assumed that any external influences on the river acted equally on the reference zone and the impacted zones. The role of external influences cannot be removed, and is an inherent problem in space-for-time substitutions.

A river's ability to recover from massive disturbances like past land use and dam removal depends on numerous factors. Variation within and between rivers is a major concern when making general statements about macroinvertebrate recovery following dam removal. The rivers within this study vary substantially in size, location, gradient, dam size and type, geology, and watershed characteristics. The number of rivers which met the numerous logistical criteria and desired gradient of time since removal was surprisingly small. Ideally, our study would have incorporated numerous replicates with equally, well distributed times between removals, yet this was not possible. Specifically, further investigation between the years 4 and 13 years following removal is worth consideration. I recognize the localized differences between rivers yet our results should hold true as long as within river variation is not greater than between. Multivariate ordination and clustering supported the premise of our approach by revealing the tight grouping of samples by river except those which had been recently affected by dam removal.

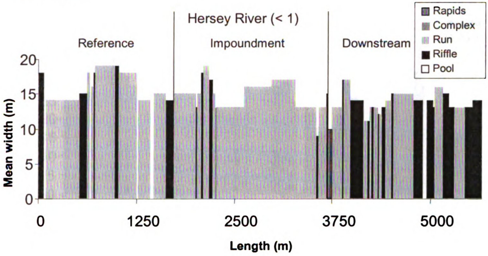
Considering the natural variability of rivers is an integral component of accurately interpreting results. How a river responds to large-scale disturbances such as dam removal will depend on the specific situation. Within this study, we documented some surprising responses which can be partially attributed to river variation. Downstream of the former Hersey Dam on the Hersey River, the mesohabitat was highly heterogenous with more riffle habitat than the reference zone, even after only 8 months following removal. This section of the river happened to have high gradient and comprised the last 2 km of the river before entering the much larger Muskegon River. Alternatively, the Au Sable River maintained relatively homogenous habitat even after 14 years. The former impoundment and downstream zones appeared to be wider and lower gradient than the reference zone. Natural longitudinal changes in ecological parameters of rivers (Vannote et al. 1980) must be acknowledged as potentially muddling the interpretation of our results although, the majority of longitudinal changes occur on a much larger scale than the 5-9 km reaches this study focused on.

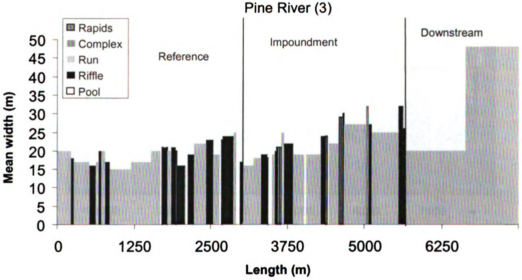
CONCLUSIONS

Despite some of the limitations involved with the approach employed by this study, some informative long-term patterns of recovery were clarified. Before this study, research on macroinvertebrate and physical habitat responses had only been conducted focused on shorter time frames, usually one river, and limited sampling effort restricted to riffle habitats. This work is the first to address long-term questions, including numerous rivers, and incorporating multiple habitat types. Doyle et al. (2005) pose two models of ecological recovery following dam removal (full or partial) and predict the general time frame needed for various parameters to recover. I believe macroinvertebrates may only partially recover and require much longer than anticipated, on the order of decades for certain parameters. Mesohabitat recovery seems to vary greatly by river and may largely depend on site characteristics like dam size, gradient, and the presence of other dams downstream. River variation will play a vital role in forecasting a river's response to dam removal. Certain rivers have much higher restorative capacity than others and a valuable research approach would attempt to identify those differences. Dam removal can not be prescribed for all rivers as an effective and responsible restoration approach, especially considering the plethora of social and economic issues involved (Born et al. 1998).

Considering the long-term ecological implications of dam removal is necessary for responsible and successful management. Managers will continue to face difficult decisions regarding the fate of aging dams and having realistic expectations of recovery levels and rates will ensure the long-term success of removal as a viable restoration technique. As with any restoration, the need for some basic level of evaluation is paramount. Given the dearth of funding for stream restoration, it is understandable that a decision must be made between monitoring and additional restoration. This situation is unfortunate, yet must be addressed. Easy approaches to evaluation exist and should be explored. Simple efforts such as community-based volunteer macroinvertebrate monitoring or site visits with visual documentation are quick and economically accessible approaches to coarse levels of evaluation. If removals continue with little to no evaluation, nearly all of our region's rivers could only partially recover while the possibility of full recovery may exist. Given the variability of rivers, we will never be able to perfectly predict how a river will respond to any restoration technique yet if we learn from removals with monitoring and adjust approaches accordingly, we can continually improve our restoration efforts and strive to reach full recovery.

APPENDIX A. Maps of mesoscale habitat in 8 study rivers. Number of years since removal in parentheses next to river name. Lengths start at upstream extent of reference zone.





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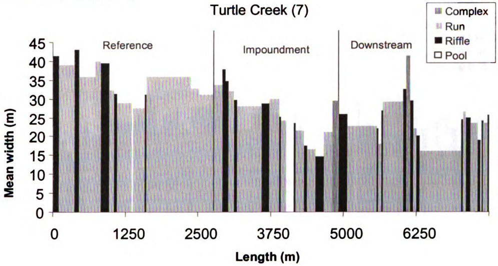

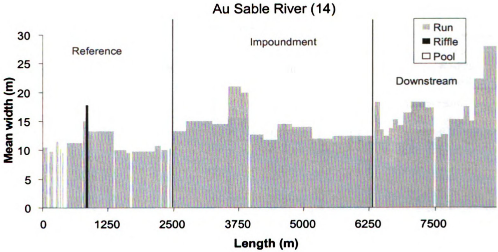

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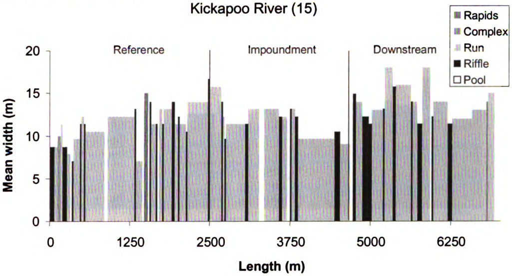

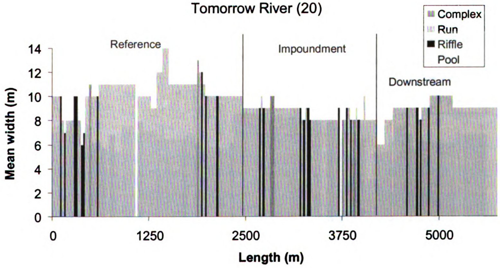

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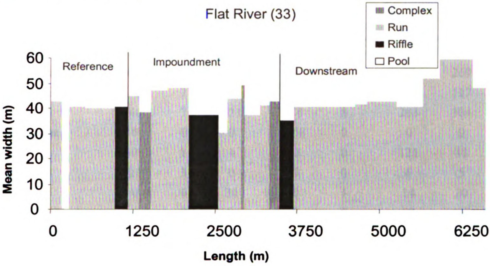

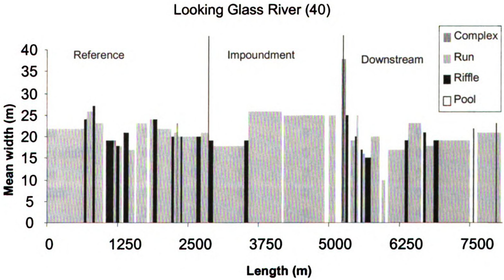

APPENDIX B. Riffle assemblage macroinvertebrate data collected from 8 rivers in various stages of recovery following dam removal. Heading numbers indicate years since removal. Data are sum of three samples within each zone (Ref = Reference; Imp = Former impoundment; DS = Downstream). Taxa sorted by abundance for all rivers.

		1			3		7	
Taxon Name	Ref	Imp	DS	Ref	Imp	Ref	Imp	DS
Chironomidae	468	470	456	206	16	566	817	886
Hydropsychidae	490	32	687	4	0	82	269	195
Elmidae (larvae)	78	7	143	69	0	23	117	75
Baetidae	40	7	121	74	8	203	304	506
Brachycentridae	0	0	0	158	0	0	0	0
Caenidae	0	1	4	0	0	121	48	37
Amphipoda	21	3	0	0	0	6	5	0
Heptageniidae	0	4	34	0	1	14	20	69
Polymitarcyidae	0	0	0	0	0	89	146	161
Unknown pupae	6	20	18	29	1	59	43	77
Simuliidae	292	4	18	4	0	91	4	23
Tipulidae	5	53	109	3	0	3	8	0
Tricorythidae	12	2	13	1	0	0	16	26
Elmidae (adults)	42	5	115	13	4	7	5	29
Oligochaeta	27	8	2	0	0	1	1	2
Isopoda	12	6	6	0	0	0	0	8
Trichoptera pupae	8	1	4	6	0	0	8	12
Perlidae	4	0	0	0	0	32	72	21
Psychomyiidae	0	24	107	0	0	0	0	0
Hydracarina	2	0	0	24	1	0	1	0
Isonychiidae	0	0	12	0	0	0	0	5
Glossosomatidae	16	0	74	0	0	0	0	0
Ephemerellidae	4	0	8	19	0	9	0	5
Athericidae	0	1	1	66	0	0	0	0
Simuliidae (pupae)	24	1	5	0	0	0	0	0
Philopotamidae	0	0	0	0	0	0	0	0
Hydroptilidae	0	0	20	8	0	0	4	0
Psephenidae (adults)	0	0	0	0	0	0	0	0
Phryganeidae	4	0	0	0	0	0	0	4
Unknown adult	0	0	0	0	0	0	0	0
Cambaridae	2	0	0	0	0	4	0	0
Uenoidae	12	0	0	0	0	0	0	0
Corydalidae	0	0	0	0	0	0	0	0
Hirudinea	0	0	0	0	0	0	0	0
Potamanthidae	0	0	0	0	0	4	8	9
Leptophlebiidae	0	0	0	0	0	2	6	0

APPENDIX B (cont'd).

	1			3		7		
Taxon Name	Ref	Imp	DS	Ref	Imp	Ref	Imp	DS
Tabanidae	0	0	4	0	0	0	0	0
Empididae	0	0	0	0	0	0	0	0
Leptoceridae	0	0	0	0	0	0	0	0
Pyralidae	0	0	0	0	0	0	0	0
Pteronarcyidae	0	0	0	1	0	0	4	0
Siphlonuridae	0	0	0	0	0	0	0	0
Ceratopogonidae	0	0	0	0	0	2	0	0
Capniidae	0	0	0	0	0	0	0	0
Chrysomelidae (larvae)	0	0	0	0	0	0	0	0
Culicidae	0	0	0	0	0	0	0	0
Sialidae	0	0	0	0	0	0	0	0
Corixidae	2	0	0	0	0	0	0	0
Lepidostomatidae	0	0	0	0	0	0	0	0
Nemouridae	0	0	0	0	0	0	0	0
Stratiomyidae	0	0	0	0	0	0	0	0
Coenagrionidae	0	0	0	0	0	0	0	1
Haliplidae (larvae)	0	0	0	0	0	0	0	0
Hydrophilidae (larvae)	0	1	0	0	0	0	0	0
Limnephilidae	0	0	0	0	0	0	0	0
Rhyacophilidae	0	0	0	0	0	0	0	0
Sisyridae	0	0	0	0	0	0	0	0
Total of zone	1571	650	1961	685	31	1318	1906	2151

APPENDIX B (cont'd).

Taxon Name	15 Ref	15 Imp	15 DS	20 Ref	20 Imp	20 DS
Chironomidae	581	396	690	800	679	604
Hydropsychidae	138	12	150	60	12	2
Elmidae (larvae)	211	13	142	292	52	93
Baetidae	250	95	166	136	351	111
Brachycentridae	116	10	46	272	181	1150
Caenidae	17	18	100	0	1	16
Amphipoda	60	37	140	600	161	271
Heptageniidae	10	6	18	0	0	8
Polymitarcyidae	0	0	0	0	0	0
Unknown pupae	50	60	38	44	50	80
Simuliidae	38	4	14	20	35	16
Tipulidae	28	3	0	164	52	19
Tricorythidae	0	1	0	0	0	0
Elmidae (adults)	0	2	16	20	16	5
Oligochaeta	33	39	26	12	0	0
Isopoda	3	2	0	8	21	61
Trichoptera pupae	0	2	0	52	99	12
Perlidae	10	4	4	0	0	0
Psychomyiidae	12	1	0	4	0	0
Hydracarina	6	0	12	52	8	32
Isonychiidae	12	1	104	0	0	0
Glossosomatidae	0	0	0	12	8	0
Ephemerellidae	1	1	4	40	2	1
Athericidae	4	0	0	0	0	4
Simuliidae (pupae)	8	0	2	4	44	2
Philopotamidae	0	0	0	0	0	0
Hydroptilidae	2	0	0	0	0	0
Psephenidae (adults)	1	0	0	0	0	0
Phryganeidae	0	1	0	0	0	0
Unknown adult	4	0	0	0	0	1
Cambaridae	0	0	0	0	0	0
Uenoidae	0	0	0	0	0	0
Corydalidae	0	0	0	0	0	0
Hirudinea	0	0	0	0	0	0
Potamanthidae	0	0	0	0	0	0
Leptophlebiidae	7	1	0	0	0	0

APPENDIX B (cont'd).

	15			20		
Taxon Name	Ref	Imp	DS	Ref	Imp	DS
Tabanidae	0	0	0	0	0	8
Empididae	0	0	0	8	4	0
Leptoceridae	0	0	0	0	0	0
Pyralidae	0	0	0	0	0	0
Pteronarcyidae	2	2	0	0	0	0
Siphlonuridae	0	0	0	0	0	6
Ceratopogonidae	2	0	0	0	0	0
Capniidae	0	0	0	4	0	0
Chrysomelidae (larvae)	0	0	0	4	0	0
Culicidae	4	0	0	0	0	0
Sialidae	0	0	0	4	0	0
Corixidae	0	0	0	0	0	0
Lepidostomatidae	0	0	0	0	0	0
Nemouridae	0	0	0	0	0	2
Stratiomyidae	0	0	0	0	0	0
Coenagrionidae	0	0	0	0	0	0
Haliplidae (larvae)	1	0	0	0	0	0
Hydrophilidae (larvae)	0	0	0	0	0	0
Limnephilidae	0	1	0	0	0	0
Rhyacophilidae	0	0	0	0	0	1
Sisyridae	0	0	0	0	0	0
Total of zone	1611	712	1672	2612	1776	2505

APPENDIX B (cont'd).

	33			40			
Taxon Name	Ref	Imp	DS	Ref	Imp	DS	Total
Chironomidae	257	275	406	135	106	33	8814
Hydropsychidae	554	306	954	289	608	93	4844
Elmidae (larvae)	365	200	499	221	291	110	2891
Baetidae	106	77	132	38	108	11	2833
Brachycentridae	19	29	0	0	2	0	1983
Caenidae	200	162	94	95	65	128	979
Amphipoda	12	26	1	1	15	2	1359
Heptageniidae	117	131	114	267	53	101	866
Polymitarcyidae	293	96	73	12	7	10	877
Unknown pupae	20	22	44	5	14	4	680
Simuliidae	26	13	1	0	0	0	603
Tipulidae	9	20	62	2	4	2	544
Tricorythidae	17	19	0	14	34	18	155
Elmidae (adults)	11	38	31	22	6	13	387
Oligochaeta	2	5	0	35	23	34	216
Isopoda	4	2	0	11	74	24	218
Trichoptera pupae	8	12	13	4	0	0	241
Perlidae	5	0	0	4	38	9	194
Psychomyiidae	0	0	22	5	3	0	178
Hydracarina	13	4	13	0	1	0	169
Isonychiidae	2	2	24	0	0	3	162
Glossosomatidae	5	9	0	8	2	3	134
Ephemerellidae	0	0	24	0	0	0	118
Athericidae	0	0	0	0	0	0	76
Simuliidae (pupae)	0	0	0	0	0	0	90
Philopotamidae	0	8	47	0	4	1	59
Hydroptilidae	0	10	3	0	12	0	59
Psephenidae (adults)	0	6	4	20	18	8	49
Phryganeidae	0	0	0	0	0	0	9
Unknown adult	23	4	4	2	0	0	38
Cambaridae	0	7	4	10	3	6	30
Uenoidae	0	0	0	0	4	20	16
Corydalidae	5	5	6	0	0	0	16
Hirudinea	0	0	0	30	0	0	30
Potamanthidae	0	0	0	0	0	0	21
Leptophlebiidae	0	0	0	0	0	0	16
Tabanidae	0	1	0	0	0	0	13
Empididae	0	0	0	0	0	0	12

APPENDIX B (cont'd).

	33			40			
Taxon Name	Ref	Imp	DS	Ref	Imp	DS	Total
Leptoceridae	1	3	0	0	4	0	8
Pyralidae	4	2	4	0	0	0	10
Pteronarcyidae	0	0	0	0	0	0	9
Siphlonuridae	0	0	0	0	0	0	6
Ceratopogonidae	0	0	0	0	0	1	4
Capniidae	0	0	0	0	0	0	4
Chrysomelidae (larvae)	0	0	0	0	0	0	4
Culicidae	0	0	0	0	0	0	4
Sialidae	0	0	0	0	0	0	4
Corixidae	0	0	0	0	0	0	2
Lepidostomatidae	0	0	0	0	2	0	2
Nemouridae	0	0	0	0	0	0	2
Stratiomyidae	0	0	2	0	0	0	2
Coenagrionidae	0	0	0	0	0	0	1
Haliplidae (larvae)	0	0	0	0	0	0	1
Hydrophilidae (larvae)	0	0	0	0	0	0	1
Limnephilidae	0	0	0	0	0	0	1
Rhyacophilidae	0	0	0	0	0	0	1
Sisyridae	0	0	0	0	1	0	1
Total of zone	2078	1494	2581	1230	1502	634	30046

APPENDIX C. Run assemblage macroinvertebrate data collected from 8 rivers in various stages of recovery following dam removal. Heading numbers indicate years since removal. Data are sum of three samples within each zone (Ref = Reference; Imp = Former impoundment; DS = Downstream). Taxa sorted by abundance for all rivers.

		1			3	
Taxon Name	Ref	Imp	DS	Ref	Imp	DS
Chironomidae	763	21	39	58	2	3
Caenidae	0	0	0	0	0	0
Baetidae	1	1	1	28	2	0
Elmidae (larvae)	9	0	0	30	2	0
Amphipoda	5	0	0	0	0	0
Hydropsychidae	23	2	2	0	0	0
Brachycentridae	0	0	1	3	0	0
Tricorythidae	3	0	0	0	0	0
Oligochaeta	6	0	0	3	1	0
Unknown pupae	10	2	1	21	0	1
Polymitarcyidae	0	0	0	0	0	0
Isopoda	22	2	0	0	0	0
Heptageniidae	0	0	0	1	0	0
Tipulidae	11	0	0	6	0	0
Corixidae	15	0	79	0	0	0
Hydracarina	7	0	0	1	0	0
Simuliidae	3	0	1	0	0	0
Elmidae (adults)	0	0	0	1	0	10
Athericidae	0	0	0	30	1	0
Ephemerellidae	1	0	0	6	0	0
Ceratopogonidae	0	0	0	0	1	17
Empididae	0	0	0	4	0	0
Psephenidae (adults)	0	0	0	0	0	0
Phryganeidae	0	0	0	0	0	0
Perlidae	0	0	0	0	0	0
Isonychiidae	0	0	0	1	0	0
Potamanthidae	0	0	0	0	0	0
Cambaridae	0	0	0	0	0	0
Leptoceridae	0	0	0	0	0	0
Psychomyiidae	0	0	0	0	0	0
Tabanidae	0	0	0	3	0	0
Leptophlebiidae	0	1	0	0	0	0
Unknown adult	0	0	0	0	0	0
Baetiscidae	0	0	0	0	0	0
Glossosomatidae	0	0	0	0	0	0
Uenoidae	0	0	0	0	0	0
Aeshnidae	0	0	0	0	0	0
Ephemeridae	0	0	0	0	0	0
Hydroptilidae	3	0	0	0	0	0
Lepidostomatidae	0	0	0	0	0	0
Polycentropodidae	0	0	0	0	0	0
Trichoptera pupae	0	0	0	0	0	0

APPENDIX C (cont'd).

Taxon Name	1 Ref	1 Imp	1 DS	3 Ref	3 Imp	3 DS
Corydalidae	0	0	0	0	0	0
Hydrophilidae (adults)	0	0	0	0	0	0
Perlodidae	0	0	0	0	0	0
Pteronarcyidae	0	0	0	0	0	0
Gomphidae	0	0	0	0	0	0
Hirudinea	2	0	0	0	0	0
Saldidae	1	0	0	0	0	0
Sialidae	0	0	0	0	0	0
Coenagrionidae	0	0	0	0	0	0
Dytiscidae (larvae)	0	0	0	0	0	0
Helicopsychidae	0	0	0	0	0	0
Hydrophilidae (larvae)	0	0	0	0	0	0
Libellulidae	0	0	0	0	0	0
Mesoveliidae	0	0	0	0	0	0
Notonectidae	0	0	0	0	0	0
Philopotamidae	0	0	0	0	0	0
Simuliidae (pupae)	0	0	0	0	0	0
Siphlonuridae	0	0	0	0	0	0
Sisyridae	0	0	0	0	0	0
Total of zone	885	29	124	196	9	31

APPENDIX C (con'd).

Taxon Name	Ref	7 Imp	DS	Ref	14 Imp	DS
Chironomidae	166	584	134	145	168	257
Caenidae	16	47	20	321	48	2
Baetidae	55	39	37	31	70	18
Elmidae (larvae)	18	31	34	63	5	8
Amphipoda	1	0	0	0	0	0
Hydropsychidae	3	10	11	118	9	4
Brachycentridae	0	0	0	26	0	0
Tricorythidae	0	0	21	136	41	13
Oligochaeta	11	9	0	24	7	17
Unknown pupae	15	34	14	4	8	11
Polymitarcyidae	27	88	71	1	3	0
Isopoda	1	2	2	1	7	0
Heptageniidae	4	22	1	0	0	0
Tipulidae	0	5	0	17	1	28
Corixidae	5	0	0	0	0	2
Hydracarina	0	0	1	11	1	2
Simuliidae	4	0	4	6	1	10
Elmidae (adults)	0	0	6	3	2	0
Athericidae	0	0	0	1	0	0
Ephemerellidae	2	3	1	8	0	0
Ceratopogonidae	0	0	0	0	0	1
Empididae	1	0	0	4	0	0
Psephenidae (adults)	0	0	0	0	0	0
Phryganeidae	1	1	4	3	1	7
Perlidae	1	5	3	0	0	0
Isonychiidae	0	1	3	4	1	0
Potamanthidae	0	5	7	0	0	0
Cambaridae	0	0	0	0	0	0
Leptoceridae	0	0	0	1	1	1
Psychomyiidae	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	6
Leptophlebiidae	4	1	0	3	0	0
Unknown adult	2	0	0	0	0	0
Baetiscidae	0	0	0	2	2	3
Glossosomatidae	0	0	1	0	0	0
Uenoidae	0	0	0	0	0	0
Aeshnidae	0	0	0	2	0	1
Ephemeridae	1	0	0	0	0	0
Hydroptilidae	1	0	1	0	0	0
Lepidostomatidae	0	0	0	0	0	0
Polycentropodidae	0	0	0	0	0	0
Trichoptera pupae	0	2	0	0	0	1
Corydalidae	0	0	0	1	0	0
Hydrophilidae (adults)	0	0	0	0	0	0
Perlodidae	0	0	0	0	0	0

APPENDIX C (cont'd).

Taxon Name	7 Ref	7 Imp	7 DS	14 Ref	14 Imp	14 DS
Pteronarcyidae	0	0	0	0	0	0
Gomphidae	0	0	0	0	1	0
Hirudinea	0	0	0	0	0	0
Saldidae	0	0	0	0	0	1
Sialidae	0	0	0	1	0	0
Coenagrionidae	1	0	0	0	0	0
Dytiscidae (larvae)	0	0	0	0	0	0
Helicopsychidae	0	0	0	0	0	0
Hydrophilidae (larvae)	0	0	0	0	0	0
Libellulidae	0	0	0	0	0	0
Mesoveliidae	0	0	0	0	0	0
Notonectidae	0	0	0	0	0	1
Philopotamidae	0	0	1	0	0	0
Simuliidae (pupae)	0	0	0	0	0	1
Siphlonuridae	0	0	0	0	0	0
Sisyridae	0	0	0	0	0	0
Total of zone	340	889	377	937	377	395

APPENDIX C (cont'd).

	15			20		
Taxon Name	Ref	Imp	DS	Ref	Imp	DS
Chironomidae	211	74	135	173	254	216
Caenidae	20	12	88	0	9	4
Baetidae	18	35	14	13	59	28
Elmidae (larvae)	12	9	7	25	21	46
Amphipoda	23	16	27	122	132	162
Hydropsychidae	0	0	4	0	0	1
Brachycentridae	1	1	5	219	68	31
Tricorythidae	0	2	0	0	0	3
Oligochaeta	33	8	36	2	7	0
Unknown pupae	11	19	7	10	22	31
Polymitarcyidae	0	2	0	0	0	0
Isopoda	2	0	1	9	8	45
Heptageniidae	3	6	6	0	0	1
Tipulidae	0	0	0	34	6	8
Corixidae	0	0	0	0	0	0
Hydracarina	0	0	2	3	3	5
Simuliidae	0	0	0	0	6	0
Elmidae (adults)	0	0	0	1	4	2
Athericidae	0	0	0	1	4	0
Ephemerellidae	0	1	1	5	1	4
Ceratopogonidae	0	1	1	0	0	0
Empididae	0	1	0	2	2	6
Psephenidae (adults)	0	0	1	0	0	0
Phryganeidae	0	0	1	0	0	0
Perlidae	0	0	0	0	0	0
Isonychiidae	1	0	1	0	0	0
Potamanthidae	0	0	0	0	0	0
Cambaridae	0	0	0	0	0	0
Leptoceridae	0	0	0	0	0	0
Psychomyiidae	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	2
Leptophlebiidae	0	1	0	0	0	0
Unknown adult	1	0	0	0	0	0
Baetiscidae	0	0	0	0	0	0
Glossosomatidae	0	0	0	0	0	1
Uenoidae	0	0	0	0	0	0
Aeshnidae	0	0	2	0	0	0
Ephemeridae	2	0	0	0	0	0
Hydroptilidae	0	0	0	0	0	0
Lepidostomatidae	0	0	0	0	3	0
Polycentropodidae	0	0	0	0	0	0
Trichoptera pupae	0	0	0	0	1	0
Corydalidae	0	0	0	0	0	0
Hydrophilidae (adults)	0	0	0	0	0	1
Perlodidae	0	0	0	0	0	0

APPENDIX C (cont'd).

Taxon Name	15 Ref	15 Imp	15 DS	20 Ref	20 Imp	20 DS
Pteronarcyidae	0	0	3	0	0	0
Gomphidae	0	0	0	0	0	0
Hirudinea	0	0	0	0	0	0
Saldidae	0	0	0	0	0	0
Sialidae	0	0	0	0	0	0
Coenagrionidae	0	0	0	0	0	0
Dytiscidae (larvae)	0	0	0	0	0	0
Helicopsychidae	0	0	0	0	1	0
Hydrophilidae (larvae)	0	0	0	0	0	0
Libellulidae	0	0	1	0	0	0
Mesoveliidae	0	1	0	0	0	0
Notonectidae	0	0	0	0	0	0
Philopotamidae	0	0	0	0	0	0
Simuliidae (pupae)	0	0	0	0	0	0
Siphlonuridae	0	1	0	0	0	0
Sisyridae	0	0	0	0	0	0
Total of zone	338	190	343	619	611	597

APPENDIX C (cont'd).

Taxon Name	33 Ref	Imp	DS	40 Ref	Imp	DS	Total
Chironomidae	213	144	172	103	118	74	4153
Caenidae	75	97	71	70	71	218	971
Baetidae	22	73	15	6	40	18	606
Elmidae (larvae)	42	10	15	125	66	114	578
Amphipoda	7	28	20	5	5	10	553
Hydropsychidae	40	131	32	29	13	45	432
Brachycentridae	4	7	25	0	0	0	391
Tricorythidae	18	11	18	6	61	107	333
Oligochaeta	7	3	26	46	81	58	327
Unknown pupae	24	4	24	5	1	1	279
Polymitarcyidae	47	7	7	2	11	14	266
Isopoda	1	0	0	31	53	14	187
Heptageniidae	9	12	15	31	43	32	154
Tipulidae	0	2	0	0	0	1	118
Corixidae	0	0	0	0	0	0	101
Hydracarina	8	6	5	3	1	1	59
Simuliidae	0	7	7	0	0	0	49
Elmidae (adults)	0	2	0	5	8	3	44
Athericidae	0	0	0	0	0	0	37
Ephemerellidae	0	0	0	0	0	1	33
Ceratopogonidae	1	1	1	2	0	0	26
Empididae	0	0	0	0	0	0	20
Psephenidae (adults)	0	0	0	8	11	11	20
Phryganeidae	0	0	0	0	0	2	18
Perlidae	1	0	2	1	3	6	16
Isonychiidae	0	0	0	0	0	0	12
Potamanthidae	0	0	0	0	0	0	12
Cambaridae	0	0	2	2	7	1	11
Leptoceridae	0	0	0	0	8	4	11
Psychomyiidae	0	0	1	7	3	0	11
Tabanidae	0	0	0	0	0	1	11
Leptophlebiidae	0	0	0	0	0	0	10
Unknown adult	2	3	2	0	0	0	10
Baetiscidae	0	1	0	0	0	0	8
Glossosomatidae	0	1	1	1	2	0	7
Uenoidae	0	0	0	3	4	0	7
Aeshnidae	0	0	0	0	0	0	5
Ephemeridae	0	0	0	2	0	1	5
Hydroptilidae	0	0	0	0	0	0	5
Lepidostomatidae	0	0	0	0	2	0	5
Polycentropodidae	0	0	0	2	2	0	4
Trichoptera pupae	0	0	0	0	0	2	4
Corydalidae	1	0	1	0	0	0	3
Hydrophilidae (adults)	0	0	0	0	2	0	3
Perlodidae	0	0	3	0	0	0	3
Pteronarcyidae	0	0	0	0	0	0	3
Gomphidae	0	0	1	0	0	0	2

APPENDIX C (cont'd).

Taxon Name	33 Ref	Imp	DS	40 Ref	Imp	DS	Total
Hirudinea	0	0	0	0	0	0	2
Saldidae	0	0	0	0	0	0	2
Sialidae	0	0	1	0	0	0	2
Coenagrionidae	0	0	0	0	0	0	1
Dytiscidae (larvae)	0	0	0	1	0	0	1
Helicopsychidae	0	0	0	0	0	0	1
Hydrophilidae (larvae)	0	0	0	1	0	0	1
Libellulidae	0	0	0	0	0	0	1
Mesoveliidae	0	0	0	0	0	0	1
Notonectidae	0	0	0	0	0	0	1
Philopotamidae	0	0	0	0	0	5	1
Simuliidae (pupae)	0	0	0	0	0	0	1
Siphlonuridae	0	0	0	0	0	0	1
Sisyridae	0	0	0	0	1	1	1
Total of zone	522	550	467	497	617	745	9940

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