

Assessing the Effects of Beaver Dams on Stream Ecology of the Maple River

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Abstract

In this study, we surveyed the physical and biotic characteristics of seven beaver dams on the West branch of the Maple River. The objective was to determine if beaver dams have a negative effect on the trout habitat of the stream. We measured dissolved oxygen and temperature of the water above and below each dam, and we collected macroinvertebrates above and below each dam. There were no significant differences in dissolved oxygen and water temperature above the dams vs. below the dams. There is no significant difference in macroinvertebrate diversity or functional feeding groups on either side of the beaver dams. However, the macroinvertebrate species richness and abundance are both significantly greater downstream of the dams.

Introduction

Beavers are often called ecosystem engineers because they can radically alter stream ecosystems. Beavers are among the few species besides humans that can significantly change the geomorphology, and consequently the hydrological characteristics and biotic properties of an ecosystem (Rosell 2005). Ecosystem engineering has been proposed as an important mechanism for maintaining high species richness at the landscape level by increasing habitat heterogeneity (Wright 2002). One study on beaver dams in the central Adirondacks, New York, shows that ecosystem engineering by beavers leads to the formation of wetland habitat

capable of supporting herbaceous plant species not found elsewhere in the riparian zone (Wright 2002). Thus, by physically modifying habitats and affecting biota, beavers are an integral part of stream ecosystems.

The influence of beaver dams in streams affects the physical and chemical characteristics of the stream ecosystem. Dams tend to slow down the stream current, increasing the upstream depth and width of the stream, and causing fine sediment buildup in the pool (Smith 1991). The stream above a dam changes from lotic to lentic conditions. As a result, beaver pools have been characterized by having increased water temperatures (Collen 2001). Also, dissolved oxygen concentrations tend to be much lower in the beaver pools compared to downstream of the dam because there are no currents or ripples that bring atmospheric oxygen into the water. The reduced dissolved oxygen concentration in the water has been shown to increase immediately during outflow from the dam, and complete reoxygenation is achieved within the next 0.25 km of stream (Collen 2001). The habitat downstream of the dam is much more characteristic of the rest of the stream because there is much less buildup of fine particulate organic matter. Therefore, there tend to be many different habitat types downstream of beaver dams, such as cobble, sand, woody debris, etc. (Smith 1991).

The change in stream dynamics by beaver dams has strong effects on macroinvertebrate communities (Harthun 1999). Macroinvertebrates are mainly affected by the increased retention of fine particulate organic matter in the beaver pool, causing habitat homogeneity and reduced overall species richness in the pool (Anderson 2007). The accumulation of sandy silt in the beaver pool of a dam in Ontario, Canada caused collectors and gatherers (consumers

of fine particulate organic matter) to be the most abundant in the beaver pools. The same study showed that the ecology of the beaver pool reduced the total number of emerging insects, especially of obligate lotic species such as Ephemeroptera, Plecoptera, and Trichoptera, and it increased the proportion of Chironomidae (Collen 2001). Ephemeroptera, Plecoptera, and Trichoptera are three orders that are of particular ecological significance. Diverse communities of these orders indicate a clean stream or river because they are sensitive to pollutants; they thrive in cold, highly oxygenated running waters (Dodds 2002).

Beaver dams also affect fish communities, mainly because of the differences in water flow and temperature upstream vs. downstream of the dams. With the change from lotic to lentic conditions, warm temperature adapted pool dwellers may become more dominant upstream of dams compared to cold water riffle dwellers (Collen 2001). For example, in Wyoming where trout streams are often too cold for optimum trout development, the warming effect of beaver ponds was reported to be advantageous. On the other hand, in West Virginia where warmer streams are considered to be marginal for trout, other species such as Cyprinids and Catostomids could displace trout through competition in areas where beaver activities have majorly impacted the ecosystem (Collen 2001). Thus, various streams and organisms are affected in different ways by beaver activity.

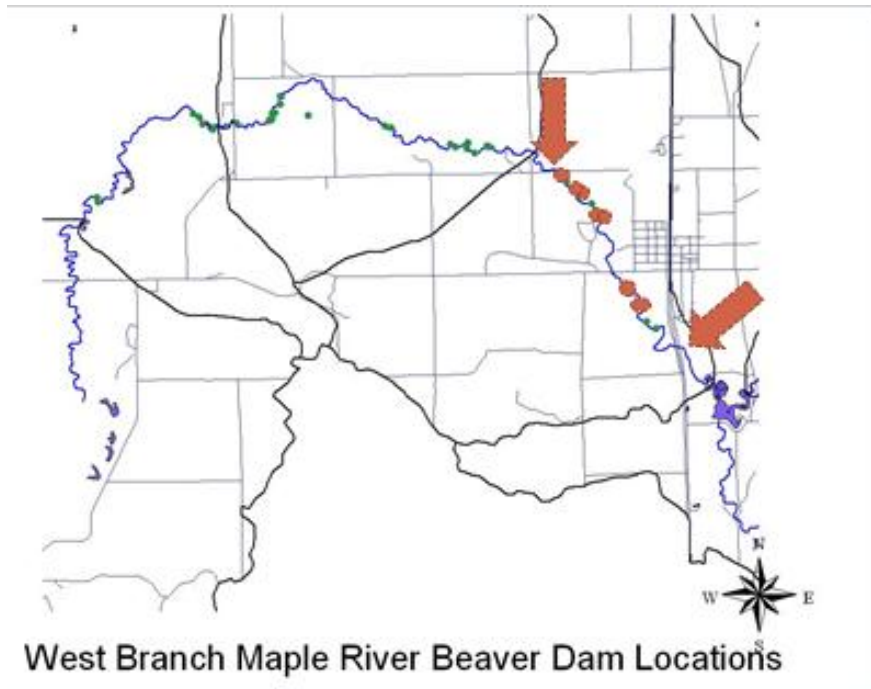
The Maple River in Cheboygan County, Michigan is an example of a cold trout stream that serves as a habitat for many fish species and a recreational ground for many people, especially fishermen. In 1938, 3,300 brook trout were stocked in the West branch of the river, and brown trout and rainbow trout were also stocked sporadically until 1966 (Godby 2010). The most

recent surveys on the West branch show that brook trout are the most dominant fish, both numerically and in biomass. The West branch Maple River is an exceptional brook trout stream; brook trout in the West branch are about one inch larger than the average statewide length at age (Godby 2010). All three species of trout are carnivorous and feed on a wide range of organisms, including aquatic macroinvertebrates (Scott and Crossman 1973).

The West branch of the Maple River is currently monitored by the Michigan Department of Natural Resources. Sites are sampled in three-year rotations, and the goal is to maintain Type 1 trout stream regulations, which includes an 8 inch minimum size limit for brook and brown trout and a 10 inch minimum size limit for rainbow trout (Godby 2010). How to manage the beaver dams on the Maple River has been a long-standing question because it is uncertain whether the dams negatively affect the ecosystem function of the Maple River. Therefore, it is important that the dams be surveyed and studied systematically to determine how they affect the stream ecosystem.

The objective of this study is to determine how beaver dams affect physical characteristics and macroinvertebrate communities in the West branch of the Maple River. We expect that the beaver pools will have higher water temperatures and lower dissolved oxygen levels because of the more lentic conditions. We expect that there will be lower species richness and diversity but a greater proportion of collector/gatherer macroinvertebrates upstream of the beaver dam as a result of the accumulation of fine particulate organic matter in the beaver pool. We hypothesize that there will be more Ephemeroptera, Plecoptera, and Trichoptera downstream because there is more flow and more habitat heterogeneity.

Methods



We sampled the section of the West branch Maple River from Camp Road to E-31 (shown by the two arrows above). We walked downstream, stopping at each beaver dam (the dots on the river between the arrows show the seven beaver dams). If the dam obstructed surface water flow and emerged from the water from one side of the stream to the other, we included it in our study. Dams that were submerged or not affecting water flow were not surveyed. At each dam, we first determined whether it was active or inactive. To do so, we looked for clues of recent activity such as freshly cut wood with teeth marks or green foliage still intact. If we found signs of recent activity, we classified the dam as active. If not, we classified it as inactive.

Overall, we found seven dams that emerged from the water and altered water flow. Out of the seven dams, six were active. We measured the width of each dam from bank to

bank using measuring tape, and we measured the depth of the water downstream of the dam and the distance from the surface of the water to the tallest point on the dam. We used a YSI dissolved oxygen meter to take measurements of dissolved oxygen concentrations and water temperature within one meter above and below each dam. We compared average dissolved oxygen levels and average water temperature upstream vs. downstream of the dam using one-tailed t-tests assuming equal variances.

At each of the active dams, we sampled macroinvertebrates upstream and downstream of the dam. Two people sampled upstream in the beaver pool for ten minutes, and two people sampled downstream of the dam for ten minutes. One person held a dip net and scooped up substrate while the other person kicked up the substrate into the net. Where cobble and woody debris were present, we picked invertebrates off and put them in the net. After ten minutes, we put the contents of the nets into labeled Whirlpaks.

All of the macroinvertebrate samples were brought back to the lab, where they were sieved and put into enamel pans with water. We picked out all of the macroinvertebrates from each sample and put them in labeled jars of 95% ethanol. We identified each macroinvertebrate to family when possible and determined the functional feeding group of each. We compared the average diversity (using the Shannon-Weaver equation) and average species richness of macroinvertebrates upstream vs. downstream of the dams using one-tailed t-tests assuming equal variances. We compared the average abundance of macroinvertebrates upstream vs. downstream using a two-tailed t-test assuming equal variances. We compared the average proportion of collector gatherers upstream vs. downstream using a one-tailed t-

test assuming equal variances. The proportion of each other functional feeding group (scrapers, filtering collectors, predators, and shredders) upstream vs. downstream was compared using two-tailed t-tests assuming equal variances for shredders and assuming unequal variances for filtering collectors, predators, and shredders. We combined the gathering collectors and filtering collectors into one collector group, and compared the average proportion of collectors upstream vs. downstream the dams using a two-tailed t-test assuming equal variances. We compared the average percent of Ephemeroptera, Plecoptera, and Trichoptera upstream vs. downstream the dams using a one-tailed t-test assuming equal variances.

Results

We found six active beaver dams and one inactive dam (Table 1). The width of the dams ranged from 7.1m and 14.4m, and the height of the dams from the surface of the water ranged from 0.19m and 0.98m.

There was no significant difference in average dissolved oxygen levels of the water above the dams compared to below the dams ($t=0.29$, $df=12$, $p=0.28$), and there were no significant differences in water temperature above the dams vs. below the dams ($t=1.78$, $df=12$, $p=0.41$ (Table 2)).

The macroinvertebrate communities above the dams vs. below the dams showed no significant differences in the proportion of gathering collectors ($t=1.81$, $df=10$, $p=0.09$), filtering collectors ($t=2.77$, $df=4$, $p=0.17$), predators ($t=2.36$, $df=7$, $p=0.52$), scrapers ($t=2.57$, $df=5$,

$p=0.18$), or shredders ($t=2.23$, $df=10$, $p=1.00$) above and below the dams. In both macroinvertebrate communities (above and below the dam), gathering collectors were the most abundant functional feeding group (Figure 2, Figure 3). However, when filtering collectors and gathering collectors were combined into one category, we found significantly more collectors below the dams compared to above the dams ($t=1.81$, $df=10$, $p=0.01$ (Figure 4)).

There was no significant difference in the average percent of Ephemeroptera, Plecoptera, and Trichoptera in the macroinvertebrate communities above the dams vs. below the dams ($t=1.81$, $df=10$, $p=0.07$); however, EPT in the beaver pools tended to be lower (32%) than below the dams (52% (Figure 5)).

There was no significant difference in the Shannon Weaver species diversity between the macroinvertebrate communities above the dams vs. below the dams ($t=1.81$, $df=10$, $p=0.07$). The average species diversity of the macroinvertebrate communities in the beaver pools above the dams was 1.81, and the average species diversity of the communities downstream of the dam was 2.10 (Figure 6). Thus, there is a tendency toward greater macroinvertebrate species diversity below the dam.

There was a significantly higher average species richness below the dam compared to above the dam ($t=2.23$, $df=10$, $p=0.02$ (Figure 7)). The average species richness above the dams was 9.2, and the average species richness below the dams was 13.0. There was also a significantly higher average abundance of macroinvertebrates below the dams compared to the beaver pool ($t=2.22$, $df=10$, $p=0.03$ (Figure 8)). The average abundance of macroinvertebrates above the dams was 26.5, and the average abundance of below the dams was 67.3.

Although the diversity was not statistically significant, there are clear differences in the taxa composing the macroinvertebrate communities both above and below the dams. Out of a total of 38 taxa found in all of the samples, six of these taxa were only found above the beaver dams in the pools, and thirteen taxa were found below the dams but not above the dams (Figure 9). For example, no Caenid mayflies were found below the dams, but five were found in the beaver pools of the dams. Also, out of the total number of filtering collectors, 4% were Brachycentridae above the dam, and 34% were Brachycentridae below the dam. Lastly, no Hydropsychidae were found in any of the beaver ponds, but 18% of the total number of filtering collectors downstream of the dams were Hydropsychidae.

Table 1. Physical characteristics of seven dams were measured. The dam height is a measurement of the distance from the surface of the water to the highest point on the dam.

| Dam Number | Location | Active/Inactive | Water Height Below Dam (cm) | Dam Width (m) | Dam Height (cm) |
|------------|--------------------------|-----------------|-----------------------------|---------------|-----------------|
| 1 | N 45.54807 W 84.79326 | Active | 54 | 14.4 | 56 |
| 2 | N 45.54787 W 84.79290 | Inactive | 27 | 13.2 | 98 |
| 3 | N 45.56033 W 84.67720 | Active | 18 | 9.6 | 68 |
| 4 | N 45.56343 W 84.80125 | Active | 45 | 7.1 | 19 |
| 5 | N 45.56058 W 84.80013 | Active | 20 | 10.4 | 63 |
| 6 | N 45.56053 W 84.80022 | Active | 48 | 8.1 | 85 |
| 7 | N 45.55891 W 84.79823 | Active | 24 | 11.4 | 86 |

Table 2. Dissolved oxygen and temperature were measured in the water in the beaver pool and downstream of the dam (within 2 meters of the dam).

| Dam Number | Dissolved Oxygen Above Dam (mg/L) | Dissolved Oxygen Below Dam (mg/L) | Temperature Above Dam (°C) | Temperature Below Dam (°C) |
|--------------------|-----------------------------------|-----------------------------------|----------------------------|----------------------------|
| 1 | 8.71 | 8.77 | 16.7 | 16.4 |
| 2 | 8.71 | 8.72 | 16.7 | 16.4 |
| 3 | 8.57 | 8.69 | 21.9 | 21.5 |
| 4 | 8.71 | 8.66 | 22 | 22.1 |
| 5 | 8.71 | 8.75 | 22.1 | 22 |
| 6 | 8.18 | 8.35 | 18.8 | 18.1 |
| 7 | 8.35 | 8.42 | 18.7 | 18.2 |
| Average | 8.56 | 8.62 | 19.56 | 19.24 |
| Standard Deviation | 0.22 | 0.17 | 2.43 | 2.56 |

Figure 1. This map shows the section of the river we sampled. The arrow on the left marks the intersection of the river and Camp Road, where we started. We ended at the second arrow, which is the intersection of the river and E-31. The dots on the river between the arrows mark the seven dams that we sampled.

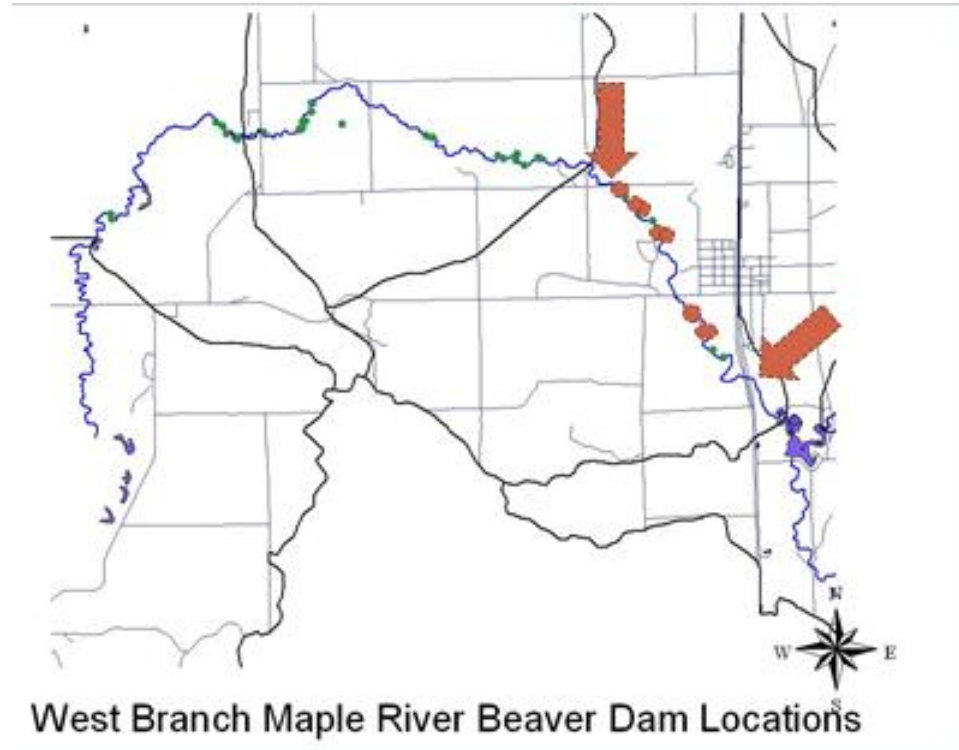


Figure 2. This pie chart shows the average proportion of each functional feeding group in the beaver pools (upstream) of the six active dams.

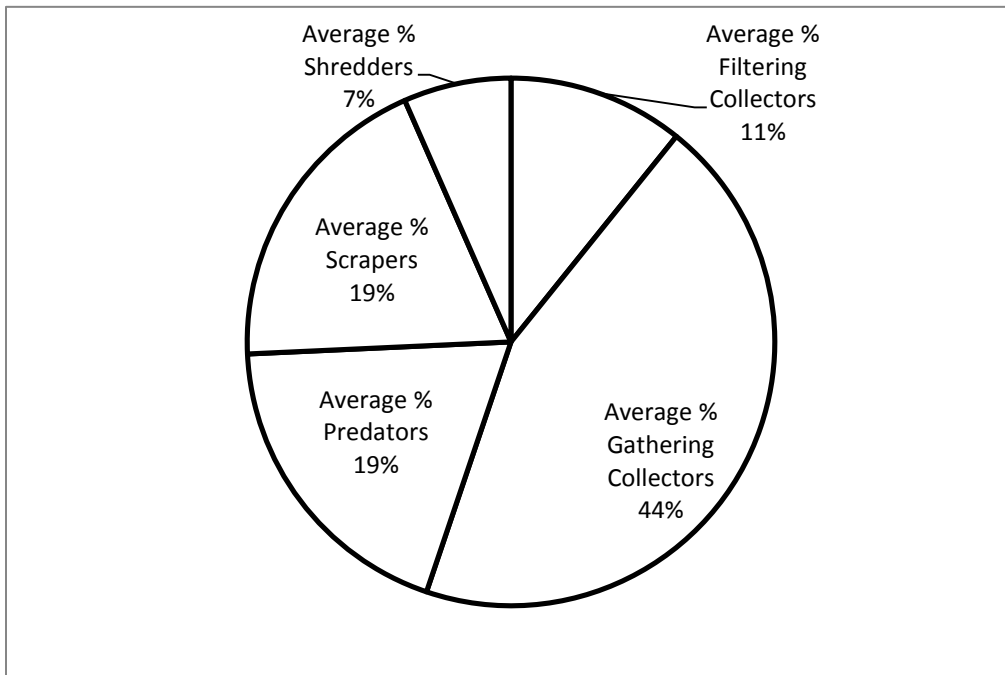


Figure 3. This pie chart shows the average proportion of each functional feeding group downstream of the six active dams.

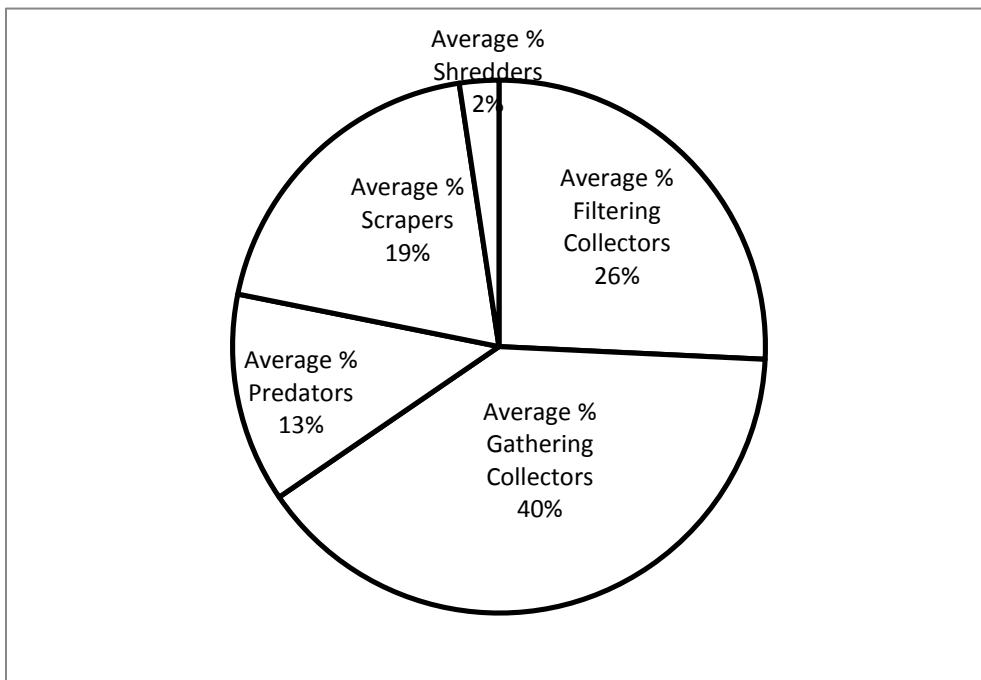


Figure 4. The average total number of collectors (gathering collectors and filtering collectors) is shown. The error bars show two standard errors from the mean.

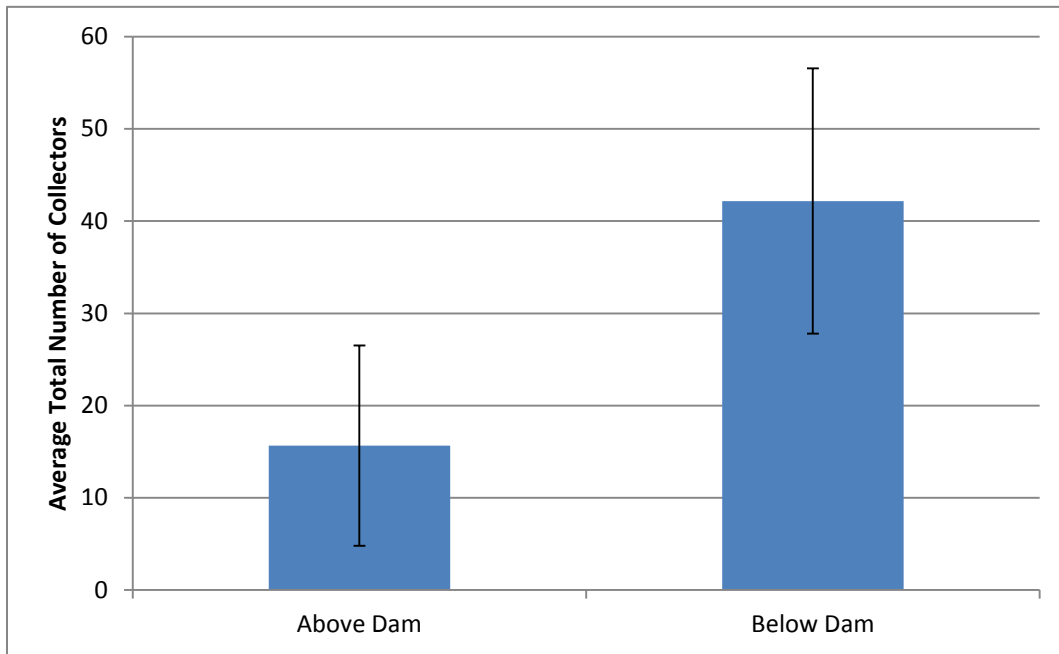


Figure 5. This graph shows the average proportion of Ephemeroptera, Plecoptera, and Trichoptera in the macroinvertebrate communities upstream vs. downstream of the six active beaver dams. The error bars show two standard errors from the mean.

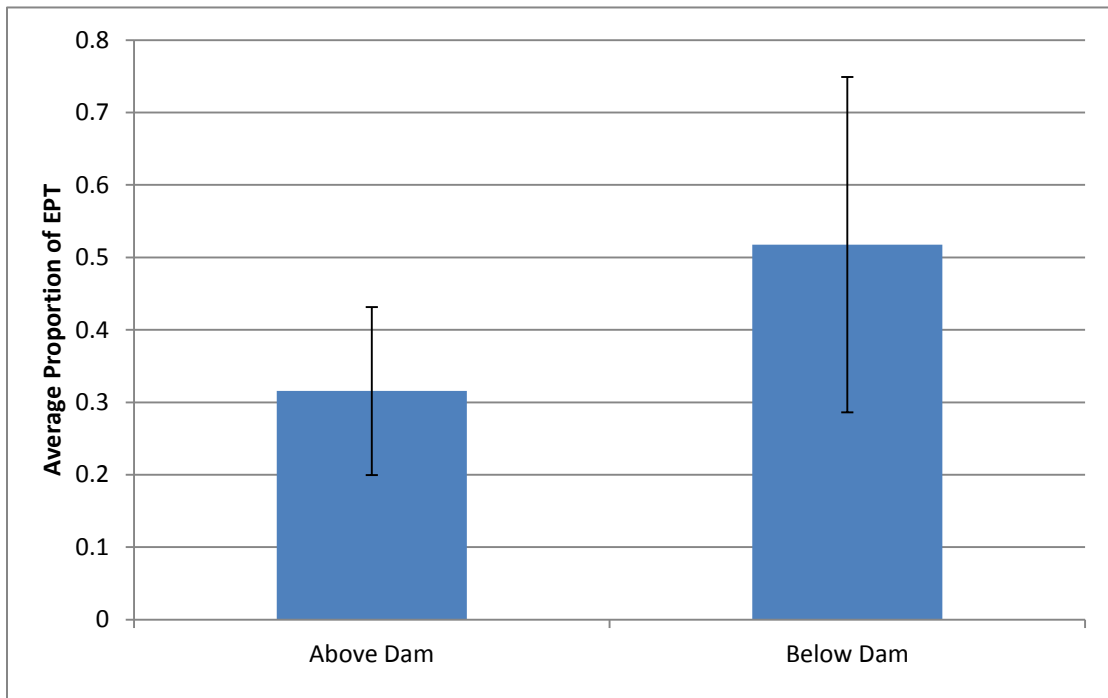


Figure 6. This graph shows the average species diversity of the macroinvertebrate communities upstream vs. downstream of the six active dams. Species diversity was calculated using the Shannon-Weaver index of diversity. The error bars show two standard errors from the mean.

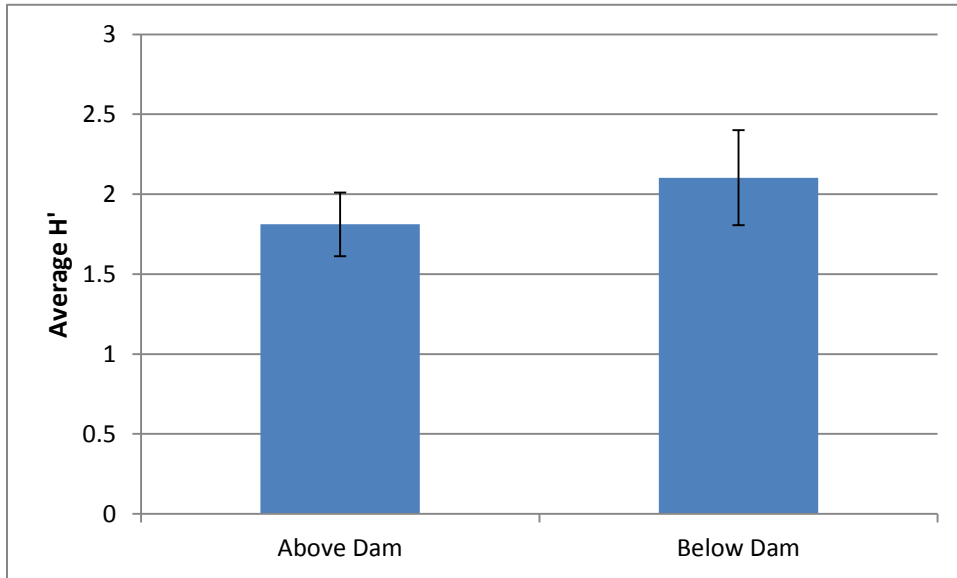


Figure 7. This graph shows the average species richness above the dam compared to below the dam. The error bars show two standard errors from the mean.

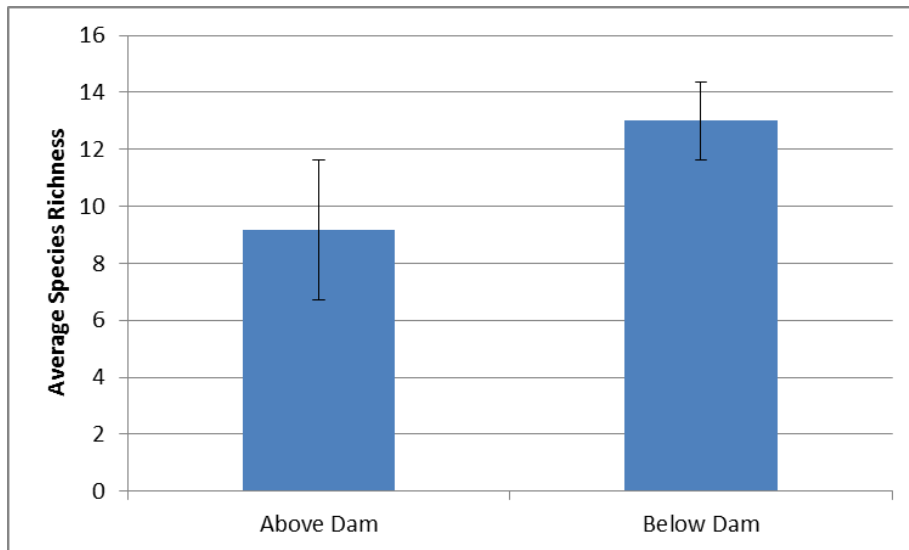


Figure 8. This graph shows the average abundance of macroinvertebrates above the dam compared to below the dam. The error bars show two standard errors from the mean.

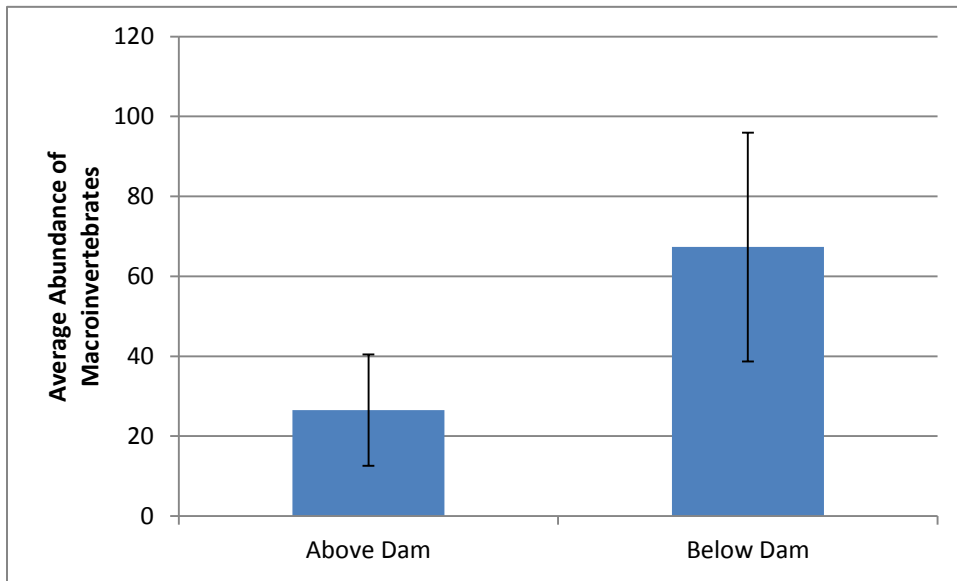
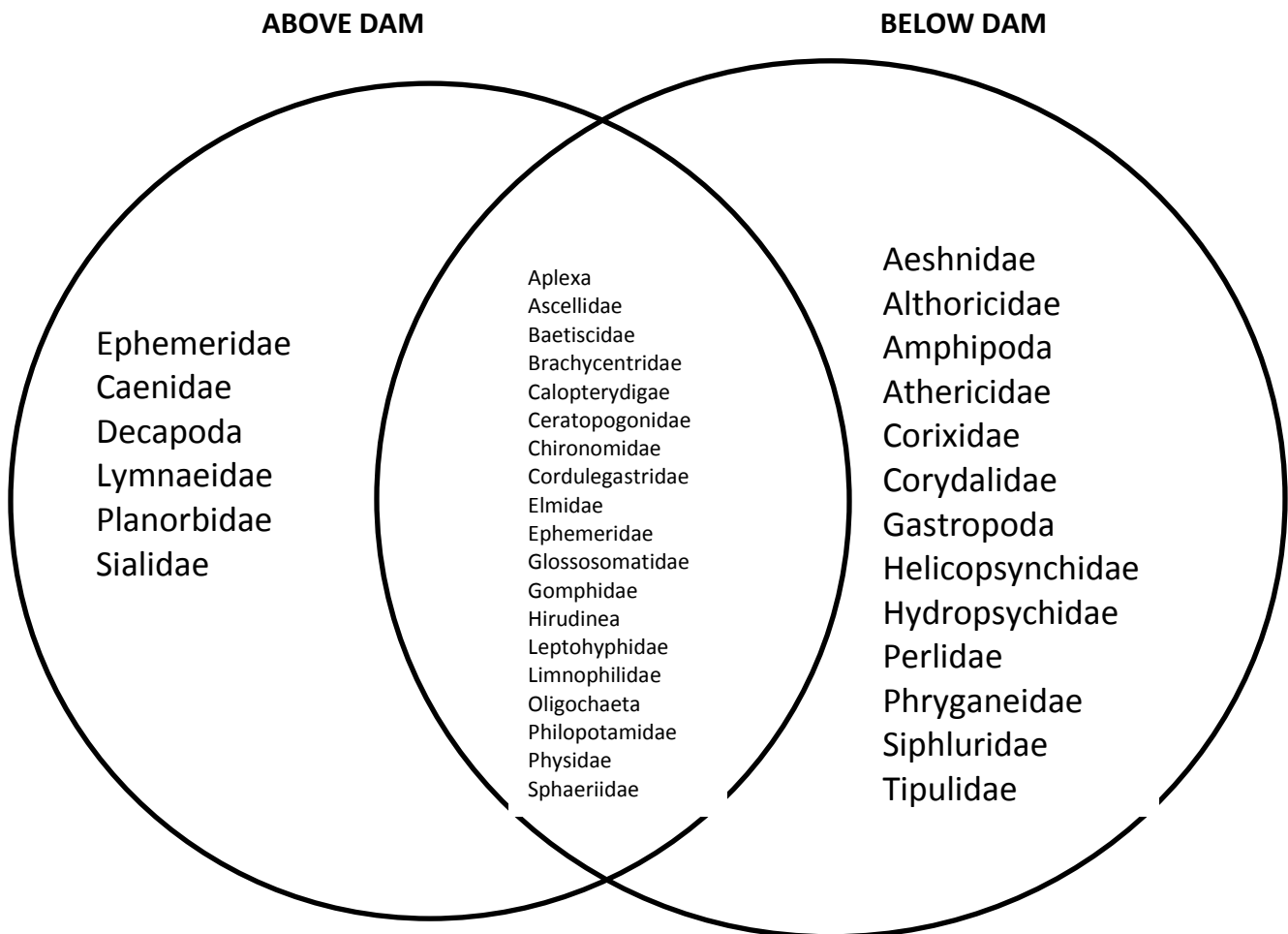


Figure 9. This Venn Diagram shows the taxa (most were identified to family) that were found only above the beaver dams, the taxa that were found only below beaver dams, and the taxa that were found in both sites.



Discussion

Our data suggest that active beaver dams on the West branch of the Maple River do not significantly alter macroinvertebrate diversity, specific functional feeding groups, or EPT proportions. The dams also had no significant effect on water temperature or dissolved oxygen. However, there was a significantly greater abundance, species richness, and proportion of collectors (collector gatherers and filtering collectors) of macroinvertebrates downstream of the dam compared to the beaver pool. In addition, there were apparent differences in the macroinvertebrate community composition upstream vs. downstream of the dam as shown by differences in certain taxa above the dams vs. below the dams (Figure 9).

While our data did not show differences in dissolved oxygen levels above vs. below dams, other studies have shown different results. For example, Schlosser and Kallemeyn (2000) studied beaver dams in Minnesota and found that almost all of the beaver ponds they studied were hypoxic, with dissolved oxygen concentrations throughout the water column less than 0.4 mg/L. In addition, a study of beaver dams in Ontario, Canada showed that hypoxia in beaver ponds resulted in winter fish mortalities that eliminated as much as 96% of the older fish (Fox and Keast 1990). However, the beaver dams in these studies were well established, resulting in beaver ponds that were quite a bit deeper than the dams we sampled. The beaver pools that we sampled were not large or deep enough to prevent mixing, so they remained well oxygenated. In contrast, a study on beaver dams in Alberta, Canada showed that greater light levels in older beaver ponds with reduced canopy may resulted in higher dissolved oxygen concentrations due to photosynthesis by algae and submerged macrophytes (Stevens et al. 2006). However, the beaver dams that we sampled were not big enough to widen the stream

and decrease riparian cover. There was riparian cover shading parts of each beaver pool we sampled, which helped to keep the temperature down. Thus, based on the different physical characteristics of the streams and the dams, the dissolved oxygen levels vary in different beaver pools. We sampled in a cold water trout stream with enough mixing to avoid hypoxia, and the beaver ponds were not large or deep enough to widen the stream.

Our data showed that there is no significant difference in water temperature in the beaver pools compared to downstream of the dams. According to Kemp et al. (2011), beaver dams tend to increase water temperature in the beaver ponds in two ways: by increasing the area of impounded reaches and thus increasing the time available for water to be heated by the sun, and by opening the river to sunlight. Of the seven dams that we sampled, we did not observe any loss of upstream trees due to flooding. Therefore, the water in the beaver ponds may not be exposed to significantly more sunlight than the water downstream, which may explain why the dams did not significantly alter water temperature. However, if the dams become older and more established, there is potential for the beaver ponds to become large enough to widen the stream and reduce riparian cover, thus increasing the water temperature in the pools.

The similar values of dissolved oxygen and temperature above and below the dams have implications for the stream ecosystem as a whole, since many organisms are temperature and oxygen sensitive. An example of a critical trout habitat is a small, cold stream used by trout for reproduction or for refuge from warmer summer temperatures of larger streams. The Michigan Department of Natural Resources has expressed concern that beaver dams in

Michigan streams negatively affects trout populations by increasing water temperature and depleting oxygen. Our data suggest that the dams we sampled do not affect the stream via changes in water temperature and dissolved oxygen levels.

The similar values for dissolved oxygen and temperature above and below dams may help to explain why we found no significant difference in the average percent of Ephemeroptera, Plecoptera, and Trichoptera in the macroinvertebrate communities above the dams vs. below the dams (Figure 5). These three macroinvertebrate orders are significant because they are sensitive to changes in ecosystem characteristics, so diverse populations of these orders indicates good water quality and undisturbed habitat (Dodds 2002). Similar abundances of EPT above and below the dams may suggest that beaver dams do not significantly alter the water quality. In contrast, a study on beaver dams in Lithuanian streams has shown that the number of EPT taxa in beaver ponds is smaller in comparison to downstream sites (Pliūraitė 2011). These dams also showed significantly different water temperature and dissolved oxygen values compared to downstream sites. Thus, the dams in Pliūraitė's study altered the stream ecosystem to a greater degree than the dams we studied, which caused the EPT abundances to be significantly lower in the beaver pools.

Although there was no significant difference in species diversity between the macroinvertebrate communities above the dams vs. below the dams, the trends suggest that diversity was greater below the dam compared to the beaver pool (Figure 6). Other studies have shown that the increased retention of fine particulate organic matter in the beaver pool causes habitat homogeneity and reduced overall species richness in the pool (Anderson 2007).

This study supports our species richness trends because we found a significantly reduced species richness of macroinvertebrates in the beaver pools (Figure 7). These data, along with the trend in diversity, can be explained by the habitat homogeneity in the beaver pools compared to the habitat downstream. At each of the dams, the downstream substrate included cobble, sand, and woody debris. This habitat heterogeneity supported a wider range of macroinvertebrate taxa than the beaver pool.

The greater range of habitat downstream of the beaver dams also supported a significantly greater abundance of macroinvertebrates than the beaver pools (Figure 8). Arndt and Domdei (2011) studied the influence of beaver ponds on macroinvertebrate communities and found that certain taxa decreased in abundance in the beaver pools, while other taxa did not change in abundance but changed in species composition because lentic species replaced the lotic species in the pools. Similarly, we found significant changes in abundance as well as clear shifts in community structure. For example, out of a total of 38 taxa found in all of the samples, six of these taxa were only found above the beaver dams in the pools, and thirteen taxa were found below the dams but not above the dams (Figure 9).

These differences are largely a result of the habitat differences in the beaver pool compared to downstream of the dam. For example, out of the total number of filtering collectors, 4.2% were Brachycentridae above the dam, and 33.8% were Brachycentridae below the dam. Most Brachycentrids use their middle and hindlegs to filter food from the water, so they often live in flowing waters attached to hard substrate such as rocks and logs, which is characteristic of the habitat downstream of the dams (Bouchard 2004). Hydropsychidae is

another family of Trichoptera that is characteristic of the habitat below beaver dams because they are restricted to flowing waters, and they spin silk nets which are used to collect detritus from the water (Bouchard 2004). They are most commonly collected from areas with cobble or areas where solid structures are available on which to attach their nets. Our data showed that no Hydropsychidae were found in any of the beaver ponds above the dams, while 17.6% of the total number of filtering collectors found downstream of beaver dams were Hydropsychidae. On the other hand, the beaver pools supported some organisms that the downstream habitat did not support. For example, five Caenidae were found in the beaver pools above the dams, and no Caenidae were found below any of the dams. Caenid mayfly larvae occur in streams in areas of slow current, and they are adapted to living in habitats with high sediment concentrations, such as beaver ponds. Their operculate gills are designed to cover and protect the other gills to keep the gills free of sediment (Bouchard 2004). Therefore, the differences in habitats above and below the beaver dams resulted in two different macroinvertebrate communities.

These data are important for assessing the consequences of beaver dams on trout streams. Trout eat a variety of aquatic macroinvertebrates including Trichoptera, Diptera, Ephemeroptera, Coleoptera, Odonata, Hemiptera, Annelids, Gastropods, and Amphipods (Becker 1983). Therefore, a change in macroinvertebrate community structure as a result of beaver activity may not affect trout feeding because they eat a wide range of macroinvertebrates. However, the beaver dams in the West branch Maple River decreased the abundance of macroinvertebrates upstream of the dam, causing an overall decrease in macroinvertebrate abundance in the stream. Thus, the food availability for trout in this stream

is reduced as a result of beaver activity. However, while trout feed on many macroinvertebrates, their diet does not solely depend on them. An investigation on the feeding habits of brook trout, brown trout, and rainbow trout in Michigan has shown that these fishes feed on land insects, fish, vegetation, and woody debris in addition to aquatic macroinvertebrates (Metzelaar 2011). Thus, beaver dams can reduce the overall macroinvertebrate abundance in streams, but trout do not exclusively feed on macroinvertebrates. From a management perspective, the seven dams that we studied most likely do not significantly affect trout feeding by reducing macroinvertebrate abundance because the macroinvertebrates are only reduced in the seven beaver ponds. The vast majority of the stream is undisturbed and has abundant macroinvertebrate communities for trout feeding.

Even though the dams may not significantly affect trout feeding on macroinvertebrates, beaver dams have shown to affect trout in other ways. According to Kemp et al. (2011), beaver dams can create semi-permeable barriers to the upstream and downstream movement of fish. This may result in reduced access to essential spawning and rearing habitat, inhibited colonization and increased isolation of populations. The permeability of dams is difficult to define because it depends on many factors, including the size of the dam and the size of the fish. On the other hand, dams have shown to positively affect fish populations. For example, the beaver pools can serve as refuge for fish in winter months during droughts. Also, structures formed as a result of beaver activity can provide fish with cover from adverse flows and predators (Kemp et al. 2011). Because of the protection that the beaver pools provide, they are often good sites for recreational fishing.

All of these factors must be considered when making management decisions. The Michigan Department of Natural Resources has expressed concern about the effects of beaver dams on trout streams, including an increase in water temperature, reduced dissolved oxygen levels, reduced diversity of invertebrate communities, and flooding (Tonello et al.). Our study suggests that beaver dams on the West branch of the Maple River may not be as detrimental to trout streams as anticipated by the MDNR. There is potential for the beaver population on the Maple River to get large enough to have significant consequences on trout habitat, but based on our data, the dams that we studied are not big or numerous enough to have a substantial effect on the ecology of the trout stream. It is important that the dams be monitored to make sure that beaver populations remain stable.

Overall, the seven dams that we studied do not significantly alter water temperature or dissolved oxygen. The dams do not affect macroinvertebrate diversity, functional feeding group proportions, or proportion of EPT in the beaver pool compared to downstream of the dam. However, the dams significantly increase macroinvertebrate abundance and species richness downstream of the dam. Also, there were clear shifts in the community structure of the macroinvertebrates in the beaver pool compared to downstream of the dam. Despite these differences, we concluded that dams are not as detrimental to the trout stream ecology as the MDNR had anticipated. Therefore, dam removal on the West branch of the Maple River is unnecessary.

Literature cited

- Anderson, Christopher, and A. Rosemond. 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Ecosystem Ecology*. 154:141–153.
- Arndt, E, and J. Domdei. 2011. Influence of Beaver Ponds on the Macroinvertebrate Benthic Community on Lowland Brooks. *Polish Journal of Ecology*. 59(4): 799-811.
- Becker, George. 1983. *Fishes of Wisconsin*. Madison: The University of Wisconsin Press.
- Bouchard, R.W., Jr. 2004. *Guide to Aquatic Macroinvertebrates of the Upper Midwest*. Water Resources Center, University of Minnesota, St. Paul, MN. 208 pp.
- Collen, P. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish. *Reviews in Fish Biology and Fisheries* 10: 439–461.
- Dodds, Walter. 2002. *Freshwater Ecology, Concepts and Environmental Applications*. San Diego: Academic Press.
- Fox, Michael, and A. Keast. 1990. Effects of winterkill on population structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. *Canadian Journal of Zoology*. 68(12): 2489-2498.
- Godby, Neal. 2010. *West Branch Mape River*. Michigan Department of Natural Resources; Status of the Fishery Resource Report. P. 1-5.
- Harthun M. 1999. The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) of Brooks in Hesse (Germany). *Limnologica*. 29:449-464.
- Kemp, Paul, T. Worthington, T. Langford, A. Tree, and M. Gaywood. 2011. Qualitative and Quantitative Effects of Reintroduced Beavers on Stream Fish. *Fish and Fisheries*. 13:158-181.
- Metzelaar, Jan. 2011. The Food of the Trout in Michigan. *Transactions of the American Fisheries Society*. 59:1, 146-152.
- Pliūraitė, Virginija. 2011. Ecological Impact of Eurasian Beaver (*Castor fiber*) Activity on Macroinvertebrate Communities in Lithuanian Trout Streams. *Central European Journal of Biology*. 7(1):101-114.

- Rosell, Frank. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Blackwell Science Ltd. 35:3-4.
- Schlosser, Isaac J., and L. Kallemeyn. 2000. Spatial Variation in Fish Assemblages Across a Beaver-Influenced Successional Landscape. *Ecology* 81:1371–1382.
- Scott, W.B., and E.J. Crossman. 1973. *Freshwater Fishes of Canada*. Ottawa: Fisheries Research Board of Canada 184:189,200,212.
- Smith M.E., Driscoll C.T., Wyszowski B.J., Brooks C.M., and Cosentini C.C. 1991. Modification of Stream Ecosystem Structure and Function by Beaver (*Castor canadensis*) in the Adirondack Mountains, New York, Can. J. Zool, 69:55-61.
- Stevens, Cameron, C. Paszkowski and C. Scrimgeour. 2006. Older is Better: Beaver Ponds on Boreal Streams as Breeding Habitat for the Wood Frog. *The Journal of Wildlife Management*. 70: 1360-1371.
- Tonello, Mark, C. Frieburger, A. Nuhfer, and S. Sutton. *Riparian Zone Management and Trout Streams: 21st Century and Beyond*. Michigan Department of Natural Resources: Fisheries Division.
- Wright, Justin. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*. 132:1-3.