The influence of carbon subsidies on stream chemistry and function in northern Michigan streams

by
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Abstract

Headwater streams are largely allochthonous, relying on subsidies to fuel productivity. Carbon inputs are important to streams not only because they fuel productivity but they also strongly affect many instream biological processes and physiochemical characteristics. Terrestrial ecosystems contribute a large component of carbon to streams which varies in quantity and quality, possibly affecting instream carbon concentrations and the biological uptake of that carbon. In addition, tributaries of the Great Lakes provide a unique opportunity to examine carbon sources and sinks more frequently associated with marine environments. For example, potomodromous fish which migrate between the Great Lakes and its tributaries to spawn may deliver a pulse of lake derived nutrients similar to the well-documented pulse of ocean-derived nutrients associated with anadromous fish moving between the ocean and rivers.

The goal of this study was to examine linkages between these allochthonous carbon inputs and steam functioning in a remote largely undeveloped temperate forest. Terrestrial inputs were evaluated by examining dissolved organic carbon (DOC) concentration in 26 streams, and comparing them against riparian and watershed land cover. At the riparian level, forest ($p<0.001$), agriculture ($p<0.001$) and wetlands ($p<0.001$) all significantly influenced instream DOC concentrations. However, at the watershed level, only agriculture explained a significant amount of variation in DOC ($p<0.001$). Watershed land cover was also compared to carbon spiraling turnover length although no significant effects were detected.

Fish derived inputs were evaluated via an evaluation of nutrient influences associated with the spawning migrations of longnose and white sucker in the Salmon Trout River. In total, 1,474 suckers were recorded swimming upstream in 2008. Whole stream metabolism was measured before and after the run, upstream and downstream of a barrier that prevented fish passage to distinguish between the effect of fish-derived carbon and possible temporal effects. Although not found to be significant, there was an obvious spike in metabolism at the downstream site during the run, which may indicate an effect of the sucker runs. The findings suggest that these two sources of allochthonous carbon are important to stream functioning and anthropogenic alterations of these inputs have the potential to affect the aquatic carbon cycle.

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Introduction

Lakes have been identified as net sources of CO_2 to the atmosphere (Anderson et. al 1999, Cole et al. 1994, Kling et al. 1991), yet little information is available regarding sources and sinks within lake carbon budgets. Urban et al. (2005) found that inputs of allochthonous organic carbon via transport from streams into lakes are significant sources of lake carbon budgets (e.g. Lake Superior). This is supported by Klump et al. (2009) who found that Green Bay (Lake Michigan) receives 3.7 mol m^{-2} $year^{-2}$ carbon input from rivers, 80% of which comes in the form of dissolved organic carbon (DOC). Streams and rivers are strongly influenced by the landscapes through which they flow, and stream ecologists are increasingly recognizing the importance of large scale factors such as climate, geology and topography in shaping aquatic communities and regulating biological processes. Headwater streams act as a sink for allochthonous carbon inputs and rely on these carbon sources to fuel production within the stream (Wetzel 1992). Two potential sources of allochthonous carbon in streams are landscape inputs and lake derived carbon inputs from fish migrating into the streams from lakes. These carbon inputs and outputs can be viewed as a bidirectional flow between the streams and the lakes. Headwater streams receive nutrient inputs from their watersheds which get funneled downstream, while potadromous fish which live in the lakes and move upstream to spawn, bring carbon inputs in the opposite direction from downstream entering the mouth of the river and move upstream towards the headwaters.

Primary productivity is typically low in forested headwater streams. Therefore, very few nutrients are derived from autochonous sources and the streams instead rely on nutrient inputs to sustain biological activity. Riparian vegetation in headwater streams commonly shades the stream, reducing the amount of primary production that is possible while contributing detritus to fuel secondary production (Vannote et al. 1980). For example, a small stream with an extensive riparian forest may receive more than 1000 g m^{-2} $year^{-1}$ in inputs (Webster et al. 1995); however, litter inputs are closely tied to latitude and inputs are likely on the order 400 g m^{-2} $year^{-1}$ in the study area (Benfield 2007). Dissolved organic carbon (DOC) is often the largest input of organic carbon to aquatic ecosystems and can strongly affect many physicochemical characteristics and biological processes in freshwaters systems (Kashian et al. 2004, Xenopoulous and Schindler 2001, Williamson et al. 1999). Dissolved organic carbon is defined as the portion of total organic carbon that can pass though a 0.7 μm filter (Kaplan 1994) and is mainly comprised of humic and fulvic acids, which are produced through the degradation of cellulose and lignin from plant material (Engstrom 1987). Dissolved organic carbon plays a large role in many instream processes which can both positively and negatively affect the biotic community. For example, humic and fulvic acids can complex with other elements in the water column and act as a chelating agent which can affect the availability of nutrients and contaminants to organisms. Biologically important elements such as phosphorous can be bound by DOC, altering the amount of those elements which are available (Winch et al. 2002, Maranger and Pullin 2003); however, binding can also occur with harmful metals. Prushia and Clements (2004) found negative correlations between DOC and both zinc and cadmium concentrations indicating that streams with low DOC concentrations are more likely to have high metal concentrations that can be toxic to the biota. Dissolved organic carbon also can either buffer or contribute to the acidity of the stream (Kullberg et al. 1993), potentially influencing metal availability and toxicity. In addition, DOC absorbs solar radiation which reduces the amount of harmful UVB that reaches primary producers (Xenopoulos and Schindler 2001), influences bacterial community structure, and impacts community respiration (Amon and Benner 1994, Vinebrooke and Leavitt 1998, Kelly et al. 2001). In turn, primary production increases with increased DOC (Frost et al. 2007). It is also an important food source for microbes. As microbes fuel production in headwater streams, DOC drives the metabolism of the stream (Tranvik 1998, Hanson et al. 2003).

In general, most DOC in streams is derived from terrestrial vegetation and soil (Palmer et al. 2001). Therefore, differences in terrestrial vegetation and soil composition will likely have a large affect on instream DOC concentrations. Human modifications of terrestrial landscapes are a principal threat to the ecological integrity of river ecosystems through impacts on habitat, water quality, DOC concentrations and the biota via numerous, complex pathways. Thus, qualitative and quantitative changes in DOC resulting from landscape level changes will ultimately impact physical, chemical and biological components of the aquatic environment. Developing a better understanding of how landscape cover and scale influence the quantity of DOC will provide a better understanding of how nutrients and contaminants move from watersheds into the Great Lakes.

Previous research has examined linkages between land cover and DOC concentrations in lakes and streams. Positive correlations have been found between the proportion of the watershed as wetlands and in streams DOC concentrations (Gergel et al. 1999, Frost el al. 2006, Johnston et al. 2008), while a negative correlation has been found between DOC concentration in streams and percent of their watershed with lakes (Frost et al. 2006, Larson et al. 2007). Hanson et al (2003) speculate that this relationship may be due to the ability of lakes to store and transform DOC. DOC has also been shown to be negatively correlated with watershed metrics such as slope, area, and drainage density (Dillon and Molot 1997, Frost et al. 2006). Although, there is a growing body of literature on the relationship of watershed attributes on in stream DOC concentration, little work has been done to evaluate the role of land cover in the riparian zone compared with the overall effects of watershed land cover on in stream DOC concentrations. Osborne and Wiley (1988) found that nutrient concentration is more closely correlated to riparian land cover than watershed land cover which may also hold true for DOC.

In addition to the quantity of carbon exported to streams, the quality of carbon can also be affected by land use. Carbon varies in its quality depending on the molecular weight and chemical structure (Thurman 1985), which is often a function of the parent material. The quality of carbon inputs is often measured by the carbon:nitrogen ratio (Iverson 1974), lignin content, or molecular weight. Litter with low carbon:nitrogen ratio and low lignin content is more readily broken down and biologically incorporated (Nolen and Pearson 1993, Stout 1980, Arsuffi and Suberkropp 1985). Carbon exported into streams from wetlands is often in the form of humic and fulvic acids which are of low quality (Balogh et al. 2006). Monocots such as those that would dominate grasslands and agriculture typically provide lower quality carbon than dicots that dominate hardwood forests in the area (Randolf et al. 1991).

The quality and quantity of carbon inputs can affect many instream processes. Nutrient spiraling is a measure of ecosystem efficiency that takes into account both biological nutrient cycling and longitudinal transport (Elwood et al. 1983). Cycling and transport methodology have been well developed in fluvial ecosystems (Odum 1956, Minshall 1978, Newbold et al. 1981) but have been most often applied to nitrogen and phosphorous. The same methods can be applied to carbon (Newbold et al. 1982). The critical measurement for organic carbon spiraling is turnover length, which is the distance traveled by an atom of organic carbon before it is oxidized by biotic activities. The turnover length is influenced by both the velocity at which the atom of carbon moves downstream and the rate that the biota oxidizes organic carbon (Newbold et al. 1982). The organic carbon turnover length has been found to be closely related to ecosystem efficiency. A smaller value of turnover length indicates a tighter carbon spiral and a more efficient system (Fisher 1977, Newbold et al. 1982, Minshall et al. 1992, Webster and Meyer 1997).

Turnover length correlates with discharge (Webster and Meyer 1997) and hydrologic regime (Acuña et al. 2007). Moreover, turnover length increases as the distance from the headwaters increases (Webster 2007). It has been demonstrated that impounded reaches are less efficient than free-flowing reaches of the same river (Wanner et al. 2002). It is also sensitive to anthropogenic influence so it can be used to monitor stream health (Thomas et al. 2005). Correlations between land cover and carbon turnover length have been inferred but never tested. This response could be due to the difference in quality and quantity of carbon inputs from different terrestrial systems (Young and Huryn 1999). Turnover length can provide a great deal of insight into many aspects of fluvial ecosystems. It is a metric that can be used to compare rivers across biomes and provide useful information on the health of the system. Neumann and Bredweg (2004) have developed a model to allow decision-makers to include possible changes in spiraling in their assessments. The model uses easily measurable parameters such as sunlight and flow rate to predict the productivity and stability of the ecosystem using nutrient spiraling.

Another potential source of nutrient inputs into streams of the Great Lakes Region comes from spawning fish (Polis et al. 2004, Schuldt and Hershey 1995). Nutrient inputs from marine systems into freshwater systems are well documented. For instance, resource subsidies from Pacific salmon (Oncorhynchus spp.) have been studied extensively (e. g. Janetski et al. 2009). Pacific salmon gain about 99% of their mass in marine environments, much of which is deposited in streams during spawning (Gresh et al. 2000). Migrations of Pacific salmon greatly elevate concentrations of DOC and nutrients in streams in Alaska (Hood et al. 2007) and tributaries of Lake Ontario (Sarica et al. 2004). This fish-derived DOC is of high quality relative to humic and fulvic acids derived from the landscape (Hood et al. 2007). These resource subsidies increase the growth rate and abundance of stream macroinvertebrates (Wipfli et al. 2003, Chaloner et al. 2007). The effects of nutrient subsidies on primary production are harder to predict. A number of studies have been completed with conflicting results. Wipfli et al. (1999) and Chaloner et al. (2004) found a positive correlation between the number of spawning salmon and primary production; however, Minakawa and Gara (1999) and Moore et al. (2004) found a negative correlation and Mitchell and Lamberti (2005) found no correlation. Tiegs et al. (2008) found negative or no correlation between the number of spawning salmon and primary production are characteristic of watersheds that have been impacted by anthropogenic actions such as timber harvest.

Despite the overwhelming amount of research on salmon runs and anadromous fishes in marine systems, there is relatively little information on the spawning runs of other fishes, especially potadromous fishes that migrate within freshwater. One such migratory group of fishes is the suckers (Catostomidae). Each spring in North America, multiple species of suckers move into tributaries to breed, then return to the lakes (Page and Johnson 1990). Historically, suckers have run from the Great Lakes into its tributaries in huge numbers; thousands of fish enter small streams while tens or hundreds of thousands arrive in larger tributaries. Though poorly studied, migrations of native suckers may play a seasonally-important role in stream dynamics as suckers constitute the majority of migratory fish biomass in many Great Lakes tributaries (e.g. Klingler et al. 2003). In the Great Lakes, there has been little attention paid to sucker migrations despite the fact that their eggs and fry are forage for many gamefish, and they have long supported economically- and culturally-important fisheries. In addition, sucker runs are threatened by barriers (dams, road culverts) and over-harvesting.

The objectives of this study were to examine the links between two allochthonous sources of carbon and stream functioning in three parts. First, the influence of watershed and riparian land cover on the instream concentration of DOC was determined. The majority of DOC is derived from shallow soil and is delivered through shallow flowpaths (Palmer et al. 2001). Water entering the stream through deeper flowpaths does not come in contact with as much carbon-rich shallow soil and much of the DOC is adsorbed onto deeper soils, both of which result in less DOC delivered to the stream (Hinton et al. 1998). Shallow flowpaths are characteristic of riparian areas, which is why it is hypothesized that riparian-scale land cover will explain more variation in DOC concentration than watershed-scale land cover. Second, the effect of watershed land cover on carbon spiraling was investigated. Turnover length has been shown to respond to land cover. Young and Huryn (1999) observed that streams draining native forests have comparably tighter spirals while streams draining pasture or grassland have a longer spiral; however, this conclusion was reached inferred and not tested. Geographic Information Systems

(GIS) will be used instead to quantify watershed land cover to confirm Young and Huryn's observations. Third, the effects of the spawning runs of two sucker species (longnose suckers: *Catostomus commersonii* and white suckers: *Catostomus catostomus*) on stream metabolism and nutrient inputs in the Salmon Trout River, Michigan was determined. The focal stream is minimally impacted and thus it is expected that metabolism will respond positively to high quality nutrient subsidies from suckers. This study is the first to place sucker runs into an ecosystem context, and evaluate the role of these native fish in lake-stream DOC linkages. They are perhaps the most important natural mechanism for transport of lake-derived carbon into watersheds rather than the reverse direction, and they undertake massive annual migrations into tributaries of all the Great Lakes.

Methods

Study Sites

This study took place on streams located in Marquette County, Michigan, USA from April 24st to August 23rd, 2008. Marquette County is located on the southern shore of Lake Superior in Michigan's Upper Peninsula. The northern part of the county is dominated by the Huron Mountains, remnants of larger peaks that today reach a maximum elevation of 603 meters. Shallow soil depth and frequent outcroppings of bare rock are characteristic of the glaciations that exposed the Canadian Shield. Laurentian granite underlies the Huron Mountains near the Lake Superior shoreline, and Jacobsville sandstone underlies the Lake Superior plain. Soil is classified as Munising loamy sand, produced by the weathering of glacial till. Munising loamy sand has moderate to high permeability (Berndt 1988).

Marquette County is very sparsely populated and minimally disturbed by human activities. County population in 2000 was 64,634, with approximately 30% residing in Marquette, the largest city in the county, approximately 60 km from our sampling site on the Salmon Trout River. The closest settlement to the sampling area is Big Bay (population 265). Despite a history of mining and logging in the county, much of the study area remains relatively untouched, including approximately 40 km^2 of old-growth forest (Flander 1983). Marquette County also includes parts of Hiawatha National Forest and Ottawa National Forest. The area is dominated by boreal vegetation including hemlock and hardwood forests.

Study sites were chosen based on several criteria. Sites were selected that were reasonably accessible from the area's road system, the limited extent of which prohibited sampling in much of the county's interior. Streams with cobble substrates, well developed riffles, and depths of less than 0.5 meters were targeted. Extremely shallow streams ($z < 0.1$ m) were not sampled to avoid potentially intermittent streams. In total, 26 sites on streams ranging in size from first to fourth order were selected for watershed analysis (Figure 1). The fourth order streams were the Salmon Trout River and the Yellow Dog River which drain the majority of the region. Five sites were within the Salmon Trout River Watershed, 8 were within the Yellow Dog River Watershed, and the remaining 13 sites were independent. Of those 26 sites, 5 representative sites were selected for carbon spiraling quantification (Table 1). All samples collected were preserved and transported to the University of Michigan for analysis.

Watershed Analysis

Terrestrial inputs are important for the functioning of headwater streams, and vary among ecosystems with land cover and other factors. To evaluate the influence of land cover on DOC, samples were collected from each of the 26 sampling sites three times during the summer of 2008 to capture natural variability in DOC. These sampling dates were early (April 24th-May 29th), middle (June 14th), and late (August 22nd-23rd) summer. In late summer, only 21 streams were sampled as five streams had dried due to the intermittent nature of first order streams.

A number of additional parameters were measured at all sampling sites. Alkalinity, hardness, conductivity, dissolved oxygen, temperature, and pH were measured on both the early and late sampling trips. Alkalinity and hardness were measured using a Hach digital titrator (Loveland, CO). Conductivity, dissolved oxygen, temperature, and pH were measured with portable meters. All meters were calibrated before use. Environmental Protection Agency's (EPA) rapid habitat assessment was completed in late summer to provide a quantitative measure of instream habitat quality (Barbour et al. 1999).

Water samples were collected to quantify DOC in every stream at each sampling time. Thirty mL of stream water were filtered through a pre-combusted 0.7µm glass fiber filter (Whatman GF/F). Samples were acidified in the field with 2 drops of 1N hydrochloric acid and frozen until returned to the lab. When ready for analysis, samples were thawed to room temperature, further acidified to a pH of 2, and sparged to drive off CO_2 (Sharp et al. 1993). The concentration of DOC was measured with a Shimadzu TOC 5050A (Columbia, MD).

Coordinates for each site were recorded using a handheld Global Positioning System (GPS) unit (Table 1). Watersheds for these coordinates were delineated using ArcGIS Version 9.3 (Environmental Systems Research Institute, Inc. (ESRI)) and Arc Hydro Tools, Version 1.3 (Redlands, CA). The 1992 National Land Cover Dataset (NLCD), the 1994 National Wetlands Inventory (NWI), and Digital Elevation Model (DEM) were downloaded from Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl). There has been little land use change in this region since the development of the landuse coverages as indicated by low economic growth and little development in the area. Dominant land cover at each site was also recorded to verify the GIS classifications. NLCD and NWI land cover were clipped to watershed boundaries and the percent of each land cover class in the watershed was calculated.

Surface water datasets were downloaded from National Hydrography Dataset (http://nhd.usgs.gov/) and merged into a single layer. A buffer of 10 meters was calculated around streams to simulate riparian area. Four sample points were removed from this analysis because the NHD did not plot any streams within their watersheds. This is likely due to the small size of these streams and the intermittent nature of first order streams. NLCD and NWI land cover was clipped to the boundaries of the buffers within watersheds to determine the percent of each land cover class with the riparian area.

Data were checked for normality and converted to percentage data and arcsine square root transformed; however, transformed data were not used for all analyses because the initial data were approximately normal and the transformation resulted in data with a stronger skew. Univariate linear regressions were calculated between average DOC and watershed area, percent

NLCD land cover, and percent NWI wetlands at both the watersheds and riparian scale using untransformed data. To compensate for the large number of regressions, α was set at 0.0025 according to the Bonferroni adjustment.

Carbon Spiraling

Carbon spiraling was quantified in 100 meter reaches of five streams following methods adapted from Thomas et al. (2005). Required measurements of physical parameters (slope, mean depth, mean width, and mean velocity), metabolism, benthic organic carbon (BOC), and transported organic carbon (TOC) were made over a 48 hour period for each stream.

Methods for measuring metabolism were adapted from Marzolf et al. (1994) as modified by Young and Huryn (1998). Metabolism measurements consist of oxygen flux and reaeration rate. Oxygen flux was measured using the two station open system method (Odum 1956), which is considered to yield the most accurate results for turbulent stretches. Two Hydrolab Sondes (Loveland, CO) were calibrated and deployed 100 meters apart to record at least 30 hours of temperature and dissolved oxygen data at five minute intervals.

Reaeration was estimated in two ways. A rhodamine WT slug was released to measure travel time and dilution. Rhodamine samples were collected at 0 and 100 meters below the point of release in opaque bottles and kept at 3°C until processing. Propane was bubbled into the stream using a regulator to measure gas exchange. Water samples were collected when instream propane concentration reached a plateau at 0 and 100 meters below the point of release, placed in airtight glass serum vials and kept in a dark bag at 3°C until processing. Rhodamine WT concentration was measured using Turner Designs Model TD-700 Fluorometer (Sunnyvale, CA). Propane concentration was measured using a Shimadzu Gas Chromatograph 14Awith flame ionization detector (Columbia, MD). Rhodamine dilution was used to correct propane concentrations and determine reaeration:

$$k_{propane} = \frac{1}{T} \ln\left[\frac{G_1/_{CT_1}}{G_2/_{CT_2}}\right] \qquad [1]$$

where: $k_{propane}$ = propane exchange coefficient (min^{-1}), T = travel time (min), G_1 = upstream propane proportion, G_2 = downstream propane proportion, CT_1 = upstream rhodamine WT concentration, and CT_2 = downstream rhodamine WT concentration. The propane exchange coefficient was converted to oxygen exchange coefficient by multiplying by 1.39 (Rathburn et al., 1978). The oxygen exchange coeffiecient was then converted a second time to account for the changing exchange capacity due to diel temperature fluctuations:

$$k_{oxygen\,(t°C)} = k_{oxygen\,(i°C)} \times 1.024^{(t°C - i°C)} \qquad [2]$$

where: k_{oxygen}= oxygen exchange coefficient at temperature i (min^{-1}), t = stream water temperature at time of interest (°C), and i = stream water temperature during propane injection (°C) (Elmore and West 1961).

Reaeration was also calculated using the energy dissipation model (Tsivoglou and Neal 1976). The gas exchange coefficient was calculated:

$$K_{2(20°C)} = K' \times S \times V \qquad [3]$$

where: $K_{2(20°C)}$ = gas exchange coefficient (day^{-1}), K' is a constant determined by stream flow (m^{-1} day^{-1}), S = slope (m/m), and V = velocity (m/s). K' was set at 28.3 x 10^3 m^{-1} day^{-1} according to measured discharge (APHA et al. 1998). $K_{2(20°C)}$ was converted to $K_{(20°C)}$ by division and then adjusted to stream temperature using equation 2. Slope was measured once for each reach using laser level and rod. Mean velocity was measured on each date to account for temporal changes in discharge.

DO concentration at saturation was calculated using temperature. For each time interval the following were calculated:

$$DO_{deficit} = DO_{saturation} - DO_{measured} \quad [4]$$

$$Reaeration = DO\ deficit \times k_{oxygen} \times T \quad [5]$$

$$\Delta DO = DO_{downstream} - DO_{upstream} \quad [6]$$

$$Net\ metabolism = \Delta DO - Reaeration \quad [7]$$

where: T = travel time (minutes), and $DO_{downstream}$ was adjusted by travel time such that ΔDO reflects the change in the parcel of water. Because primary production does not take place at night, net metabolism from dusk to dawn reflects only respiration. Respiration for the hour before dawn and the hour after dusk were averaged and the resulting number was used to project daytime respiration assuming a linear relationship between respiration and time throughout the daylight hours.

Ecosystem respiration is the sum of respiration over the 24 hour period. Production was calculated for daylight hours by subtracting respiration from net metabolism. The resulting terms were summed to calculate gross primary production. Net ecosystem production was the sum of ecosystem respiration and gross primary production.

Transported organic carbon includes both particulate (POC) and DOC. POC and DOC were collected at the top and bottom of the reach three times over 24 hours. POC was collected by filtering a known volume of stream water (1-2 L) through a pre-combusted 0.7 µm glass fiber filter. Filters were frozen and returned to the lab. When ready for analysis, samples were thawed and dried at 80 °C for at least 24 hours. Initial weights were recorded and combusted in a 550°C muffle furnace for three hours. Samples were then re-wetted and dried again at 80 °C for at least 24 hours, and re-weighed. Ash-free dry mass (AFDM) was calculated as the mass lost by combustion. AFDM was corrected to carbon using a 48.4% conversion (Royer et al. 1995). DOC was collected and analyzed as described earlier.

Benthic organic carbon (BOC) consists of coarse and fine benthic organic carbon (CBOC and FBOC). Five samples of each were collected using a random stratified design. A 30 cm diameter stovepipe sampler was created by removing the bottom from a standard plastic 5-gallon bucket. The stovepipe sampler was driven into the substrate so that water was not able to flow in or out, and all CBOM was collected using a 1 cm sieve. Samples were stored in paper bags and air-dried until returned to the laboratory. When ready for analysis, samples were dried at 80 °C for at least 72 hours. Samples were weighed and subsamples were taken when samples were sufficiently large. CBOM was ground using a coffee grinder and combusted at 550°C for three hours. Samples were re-wet and dried in an 80 °C oven for at least 48 hours before their final weight was recorded. Ash-free dry mass (AFDM) was calculated as the mass lost by combustion and converted to carbon. Within the same stovepipe, the remaining benthic material was agitated to form a slurry. A sample of the slurry was collected and frozen for FBOM processing. Before the stovepipe was removed, water depth was measured to determine the volume of water in the slurry. The frozen slurry was thawed in the laboratory and then homogenized using a stir plate. A 20-40 mL subsample of the homogenized slurry was filtered through a pre-combusted 0.7 µm glass fiber filter. Filters were dried in an 80 °C oven for at least 24 hours, then weighed and ashed in a 550°C muffle furnace for three hours. Filters were then re-wetted and dried again in an 80 °C oven for at least 24 hours and then re-weighed. Ash-free dry mass (AFDM) was calculated as described above. Areal benthic carbon was calculated using the known volumes of the subsample and slurry within the stovepipe sampler, assuming the amount of carbon suspended in the water column was negligible.

Carbon spiraling indices were calculated as follows:

$$V_{oc} = \frac{TOC \times Q}{BOC \times w} \qquad [8]$$

$$R_{het} = R_{total} - \rho\, P_G \qquad [9]$$

$$K_{oc} = \frac{R_{het}}{BOC \times (TOC \times z)} \qquad [10]$$

$$S_{oc} = \frac{V_{oc}}{K_{oc}} \qquad [11]$$

$$IR = \frac{V_{wat}}{V_{OC}} \qquad [12]$$

where: Voc = net longitudinal velocity of organic carbon (m day^{-1}), TOC = total transported organic carbon (g C m^{-3}), Q = discharge (m^{3} day^{-1}), BOC = total benthic organic carbon standing stock (g C m^{-3}), w = mean stream width (m), R_{het} = heterotrophic respiration (g C m^{-2} day^{-1}), R_{total} = total respiration (g C m^{-2} day^{-1}), ρ = the fraction of PG oxidized by autotrophic respiration, PG = gross primary production (g C m-^{2} day^{-1}), K_{oc} = biotic turnover rate (day^{-1}), z =

mean water depth (m), S_{oc} = organic carbon turnover length (m), IR = the index of retention, and v_{wat} = mean water velocity (Newbold et al. 1982, Minshall et al. 1992).

The fraction of gross primary production oxidized by autotrophic respiration is represented by ρ. This term has been estimated a number of times in other studies with values ranging from 0.14 (McIntyre et al. 1964) to 0.5 (Webster and Meyer 1997). The value of ρ was assumed to be 0.2 in this study due to the highly heterotrophic nature of the streams sampled.

Sucker Run Characterization

Two trap nets were placed in the Salmon Trout River immediately following spring snow melt to capture migrating fish. Fish swimming upstream were captured in one net, and downstream migrants were captured in the other. The nets were arranged to span the entire stream, such that all migrants were captured. Mesh size was 5 cm stretch, allowing capture of mature suckers and assorted other species. All fish were released daily after recording species and sex. Standard length (from the tip of the snout to the end of the last vertebra) and total length (from the tip of the snout to the tip of the caudal fin) were recorded for the first 100 fish of each day. A small triangle was clipped from the dorsal fin of the first 100 fish daily to determine recapture efficiency. This provides a more accurate estimate of the total sucker run by accounting for any fish not caught. T-tests were used to compare standard lengths between sexes and species. All statistical analyses were completed using SPSS 17 (Chicago, IL).

Additional parameters were recorded to characterize the run and its effects. Water temperature was recorded daily. Water chemistry samples were collected daily at the location where the nets were placed as well as upstream of a dam which served as a barrier to migrating suckers. Water was filtered through pre-combusted 0.7 μm glass fiber filters. Samples for soluble reactive phosphorous, nitrate, and ammonium were frozen and returned to the lab. Soluble reactive phosphorous and nitrate were analyzed on a Technicon auto analyzer II using standard calorimetric techniques as detailed in Davis and Simmons (1979). Nitrate was determined by the cadmium reduction method and soluble reactive phosphorus by the molybdate–ascorbic acid method. Ammonium was analyzed on a Turner Aquafluor fluorometer using the method described by Holmes et al. (1999) as modified by Taylor et al. (2007).

Metabolism was measured in the Salmon Trout River during and after the sucker run to determine whether sucker-derived nutrient subsidies influenced stream metabolism. The Lower Falls (46° 48.91' N, 87° 48.27' W) and a dam (46° 51.58' N, 87° 48.33' W) served as barriers to sucker migration so one site was chosen below the barriers and one above to distinguish the effects of sucker migrations from any temporal effect. Metabolism was quantified using the methods described above.

Results

Watershed Analysis

An analysis of the influence of watershed area and land cover on instream dissolved organic carbon concentration revealed that DOC varied moderately among the streams; however, the only factor that significantly affected DOC in stream concentrations at the watershed level was agriculture (Table 2). Among the 26 streams the mean DOC ranged from 4.22 to

36.76 mg C L^{-1}. Total watershed area ranged from 0.64-145.89 km^2 (Table 2). The relationship between total watershed area and DOC was not significant ($p = 0.54$, $r^2 = 0.02$) (Table 2; Figure 4). Watersheds were largely dominated by forest for the National Land Cover Dataset (Figure 2) and uplands based on the National Wetlands Inventory (Figure 3). The percentage of the watershed wetlands as per the NWI ranged from 0.00 to 92.38%. The correlation between NWI percent wetlands and DOC was not significant (Table 2; $p = 0.14$, $r^2 = 0.10$). For NLCD, percent agricultural was positively correlated with DOC ($p<0.001$, $r^2=0.52$).

An evaluation of riparian land use indicated that in addition to agriculture, the percent of the riparian zone in wetlands and forest also significantly impacted DOC concentrations (Table 3). For the 26 streams the riparian zones were largely forested although wetlands composed a larger portion of the riparian area than the watershed. The percentage of riparian area wetlands as per the NWI ranged from 0.00 to 72.53%. Riparian area ranged from 5,858 to 1,433,095 m^2 (Table 3). The relationship between riparian area and DOC was not significant ($p=0.52$, $r^2=0.02$). There was a significant positive correlation between NWI percent wetlands and DOC ($p<0.001$, $r^2=0.62$) (Table 3; Figure 5). Five NLCD regressions were tested between DOC and percent riparian area open water, transitional, forested, agricultural, and wetlands. The percent riparian area that was forested had a negative influence on in stream DOC concentrations (Table 3; $p<0.001$, $r^2=0.64$). In contrast, the percent of the riparian area identified as being agriculture ($p<0.001$, $r^2=0.54$) and wetlands ($p<0.001$, $r^2=0.70$) had a positive influence on DOC concentrations (Table 3).

Carbon Spiraling

Differences were observed between the two reaeration methods and calculations. Reaeration coefficients ranged from 0.29 to 0.85 min^{-1} when measured by propane evasion, and from 0.004 to 0.13 min^{-1} when using the energy dissipation model. Reaeration coefficients measured by propane evasion were higher than accepted values from similar systems (Hoellein 2008) which can most likely be attributed to poor propane assimilation. Previous studies have favored direct measurement methods such as propane evasion because the energy dissipation model has been shown to underestimate reaeration (Mulholland et al. 2001); however, in this system the energy dissipation model was preferable because it circumvents the difficulty of propane assimilation. The upstream station had a higher reaeration coefficient for both methods and sampling dates but no clear temporal pattern could be attributed to nutrient subsidies.

Benthic organic carbon ranged from 13.94 to 179.80 g m^{-2} with FBOM contributing the majority of carbon in four of the five streams (Table 4). TOC was dominated by POC and ranged from 0.47 to 3.28 g C m^{-3}. Turnover length (S_{OC}) varied from 2.00 to 205.75 m day^{-1}. Regressions between S_{OC} and watershed area, NLCD land cover and NWI land cover were not significant (Table 5, Figure 6).

Characterization of the sucker run

The majority of fish caught were longnose suckers (1293 incoming, and 206 outgoing). This represented 88% of all incoming fish and 91% of all outgoing fish. White suckers made up the next largest component of the run with 154 incoming and 17 outgoing suckers recorded (10% of incoming fish and 7% of outgoing fish). The remainder of the fish captured which represented only 0.1 percent of those captured included Steelhead (*Oncorhynchus mykiss)*, redhorse (*Moxostoma spp.*), a brook trout (*Salvelinus fontinalis)*, and a muskellunge (*Esox masquinongy)* (Figure 7). Fin clips were used to mark 37.8% of suckers swimming upstream. Of the total recapture, only 9.0% were marked individuals, which represented 3.9% of the total marked fish. The low recapture percentage made it difficult to accurately quantify the size of the sucker run using mark/recapture calculations.

Further characterization of the sucker community identified a total of 227 incoming female longnose suckers that were measured with an average total length of 44.01 ± 3.31 cm (mean ± 1 standard deviation) and an average standard length of 36.49 ± 2.99 cm. Likewise, 175 male longnose suckers were captured and measured with an average total length of 39.96 ± 3.46 cm and an average standard length of 32.85 ± 2.93 cm. There were a total of 30 female white suckers measured which averaged a total length of 45.23 ± 5.62 cm and a standard length of 37.40 ± 4.99 cm. There were a total of 45 male white suckers measured which averaged a total length of 40.51 ± 3.98 cm and a standard length of 33.18 ± 3.24 cm. The total length of females was significantly longer than the total length of males for both longnose suckers ($\alpha = 0.05$, $p < 0.001$) and white suckers ($p<0.001$). The total length of males did not significantly differ between longnose and white suckers ($p = 0.36$). Similarly, the total length of females did not significantly differ between longnose and white suckers ($p=0.079$).

Timing of catostomid migration was likely temperature dependant. There was a large pulse of incoming fish when water temperature reached approximately 10 °C (Figure 8). This is consistent with other studies which have found that catostomids run when water temperature reaches 9-12 °C (Corbett and Powles 1983, Weiss et al. 1998). Water collected upstream and downstream of the barrier showed no differences in soluble reactive phosphorous, nitrate, or ammonium that could be attributed to suckers (Figure 9).

Metabolism at the downstream reach during the sucker run was more than double (-89.53 g C m^{-2} day $^{-1}$) all other measurements of metabolism (-14.34 to -36.67 g C m^{-2} day $^{-1}$, Table 4). This was largely driven by the ecosystem respiration portion of metabolism. Ecosystem respiration was -92.88 g C m^{-2} day $^{-1}$ for the downstream site during the sucker run while the other measurements ranged from -26.05 to -42.60 g C m^{-2} day $^{-1}$.

Discussion

This study investigated the dynamics of DOC in a relatively pristine setting of minimal human disturbance. It addressed both the influence of land use on the quantity of dissolved organic carbon in streams along with addressing how land cover may influence stream functioning via a measure of carbon cycling. Based on the analysis of watershed coverage in 26 streams, land cover does affect instream DOC concentrations; particularly land use in the riparian zones of the streams. However, ecosystem function as evaluated by measures of carbon spiraling was not significantly influenced by land cover. In addition, these streams receive migrating fish, which may elevate DOC levels and increase ecosystem metabolism as a result of their reproductive products and carcasses. Research on nutrient inputs into streams systems via fish migrations has historically focused on marine based systems, specifically focusing on the anadromous salmon. Much less is known about nutrient inputs from fish migrating between two freshwater systems, including suckers which are widespread and potentially run in large numbers in the Great Lakes.

My data suggests that there is a substantial sucker run in the Salmon Trout River which originates in Lake Superior and may stimulate whole stream metabolism. This effect may be similar to the way that salmon runs influence instream production in analogous marine tributaries; however, suckers have a very different life history from salmon so the mechanisms of that effect may vary.

Watershed land cover has been found to influence many stream processes including biotic integrity (e.g. Wang et al. 1997), denitrification (e.g. Inwood et al. 2005), and water chemistry (e.g. Herlihy et al. 1998). It has also been shown to influence DOC concentration. The strongest relationships have been found between DOC and the proportion of the watershed with wetlands (Gergel et al. 1999, Frost el al. 2006, Johnston et al. 2008) and lakes (Frost et al. 2006, Larson et al. 2007). While neither the percent lakes nor wetlands influenced DOC stream concentrations in this study, the percent of the watershed in agriculture did show a significant positive correlation with DOC. Surprisingly, agriculture only made up a maximum of 3.14% of the watersheds, which indicates that even small-scale agriculture can affect DOC concentrations. However, this relationship may not hold true in high intensity agricultural operations where fields are drained by tile drainage systems. Tile drainage systems shunt runoff directly into streams, bypassing soil interactions where DOC would be assimilated; however, they can deliver up to 18 kg ha^{-1} year^{-1} DOC directly into streams (Royer and David 2005). Wilson and Xenopoulous (2008) found that soil drainage more strongly influenced DOC than agricultural intensity; however, they also found that increasing agricultural land cover could significantly change the delivery of DOC to streams.

Land cover has the potential to affect stream ecosystems at multiple scales (Allan 2004) and different variables respond to different scales. Biotic integrity (Wang et al. 1997, Roth et al. 1996) and nitrogen concentration (Dodds and Oakes 2006) are more accurately predicted by watershed-level land use than riparian land use; however, phosphorous and total suspended solids are more accurately predicted by riparian land cover (Johnson et al. 1997). This study found that DOC is more strongly correlated with riparian land cover than watershed land cover. Four land cover classes had a significant effect on DOC at the riparian level whereas only one class had a significant effect on DOC at the watershed level. The percent of the riparian zone classified as agriculture explained slightly more variation in DOC than percent of the overall watershed as agriculture indicating that riparian land use better explains in stream DOC concentrations. This study supports these previous studies that showed wetlands to have a strong positive correlation with DOC (Gergel et al. 1999, Frost et al. 2006, Johnston et al. 2008). Contrary to expectation, the percent of the riparian zone as forest had a negative correlation with DOC. Though forests have a negative correlation with DOC, the streams in this study may be a special case. Forest and wetlands comprise more than 90 percent of the riparian areas for 18 of the 21 sites sampled. In this case, where forest and wetland are clearly the dominant landcover classes, the effect of forest on DOC may be overshadowed by the effect of wetlands to the point where the influence of forest on DOC is not discernable.

The importance of riparian areas to streams is well documented (e. g. Gregory et al. 1991, Naiman and De´camps 1997, Roth et al. 1999). Carlisle et al. (2009) found that riparian land cover was the most accurate predictor of biological condition so it is unsurprising that riparian land cover is correlated DOC, which is highly importance to biological condition. Stream restoration efforts often largely focus on managing the riparian zone, due to its ability to regulate the addition of sediment, nutrients, metals, and other toxins (e. g. Osborne and Kovacic 1993). The influence on DOC is another reason that intact riparian areas are important to maintaining stream functioning.

Ecosystem processes such as carbon spiraling were not as heavily influenced by land cover as instream DOC concentration. A significant influence of watershed land cover on carbon spiraling was not observed based on a comparison of five streams with varied watershed coverage. Though Young and Huryn (1999) visually observed that watershed land cover seemed to influence carbon spiraling turnover length, this was not quantitatively confirmed in this study. The sites selected in Young and Huryn's study were harvested exotic forest and grazed and fertilized farmland among others. Their systems were much more likely to be disturbed than the systems in this study which have relatively pristine watersheds and high rapid habitat assessment scores (Appendix A). The pristine nature of the streams in this study may impact instream functioning which is reflected in carbon spiraling. Carbon spiraling combines many structural (carbon standing stocks, discharge, etc.) and functional (carbon uptake, whole stream metabolism, etc.) variables. These variables are vulnerable to various anthropogenic influences; however, more research is needed to determine the ways in which carbon spiraling as a whole is influenced by land cover.

In addition to examining the inputs of carbon from terrestrial sources that are ultimately exported downstream and into the Great Lakes, carbon inputs into these Great Lake tributaries are influenced by migrating fish. Much is known about the spawning runs of anadromous fishes like salmon but there has been little work on potadromous fishes such as suckers. Salmon serve as a vector for moving marine-derived nutrients into freshwater systems; it is possible that suckers perform a similar service.

Very little is known about the sucker migrations in the tributaries of Lake Superior both in terms of their impacts on nutrient dynamics but also in regards to basic population dynamics. A large number of both longnose suckers and white suckers were captured during their spring spawning migration in the Salmon Trout River. These suckers made up the vast majority of fish caught, which may indicate their importance for stream functioning. Sexual dimorphism was found in both the longnose and white suckers in the Salmon Trout River with females of both species longer than males. Though these species have not been extensively studied, more data is available on other catostomids. No sexual dimorphism was observed in the Alabama hog sucker (*Hypentelium etowanum)* (O'Kelley and Powers 2007); however, differences were found in the spotted sucker *(Minytrema melanops)* and the robust redhorse (*Moxostoma robustum*) (Grabowski et al. 2008). The catostomid family is very diverse and varied life histories are to be expected (Cooke et al. 2005).

Potadromous migrations within the Great Lakes have received some attention due to the introduction and stocking of salmon. Although the salmon population and the corresponding spawning run is much smaller than that of the suckers in Lake Superior, Great Lakes salmon have received more attention. Since salmon were introduced into the great Lakes and because they are regularly stocked, they have established a naturally breeding population. These introduced salmon have adapted well and now use many Great Lakes tributaries as spawning habitat. Naturally reproduced salmon make up between 40 to 94 percent of salmon in Lake Superior (Peck 1992, Peck et al. 1999), indicating that salmon spawning runs are successful and may influence Great Lake tributaries in similar ways as their anadromous counterparts. Schuldt and Hershey (1995) found that total phosphorous, soluble reactive phosphorous, and periphyton biomass are elevated in Lake Superior tributaries that receive salmon runs. Likewise, if sucker runs deliver similar subsidies, then the higher nutrient levels could fuel an increase in whole stream metabolism. This corresponds with the spike in metabolism observed during the sucker run in this study at the downstream site which may be a result of nutrient subsidies. Though dissolved nutrient concentrations do not show a similar spike, it may be that the nutrients delivered by the spawning run are of high quality and are biologically assimilated faster than they are delivered which would cause a change in metabolism but not water chemistry as observed.

Though it appears that suckers can influence instream processes as salmon do in marine and freshwater systems, there are important differences in the life histories of the fish which may result in different influences on the ecosystem. Salmon elevate nutrient concentrations by three identified pathways: direct input of nutrients through reproductive products and waste, decomposition of carcasses, and bioturbation. Salmon gain approximately 99% of their mass in the ocean before moving into rivers to spawn. Much of that is delivered to streams as gametes and waste. Salmon are semelparous, meaning they reproduce once and die, and the remainder of their mass is released into the stream through decomposition. Johnson et al. (2004) found that salmon carcasses lose about half their carbon, nitrogen, and phosphorous in their first 20 days of decomposition. Salmon also affect nutrients indirectly. In order to spawn, salmon excavate redds. These redds can range in depth from 15 to 30 centimeters below the surface of the streambed (Peterson and Quinn 1996, Scrivener and Macdonald 1998) and 1 to 17 m^2 in area (Groot and Margolis 1991). A dense population of salmon can modify the entire surface of their spawning reach (Gottesfeld et al. 2004). By doing so, they resuspend material that previously was biologically unavailable, a process known as bioturbation.

Though suckers contribute nutrients through their gametes and waste as salmon do, they may have different impacts on stream ecosystem processes than salmon. Unlike salmon, suckers are iteroparous and likely have a low mortality rate associated with spawning. No literature is available to offer support; however, visual surveys of the Salmon Trout River found no carcasses in 2008. Three carcasses were found when visual surveys were repeated in 2009. This indicates that while there are cases of mortality, carcasses are unlikely to be significant contributors to nutrient inputs. Additionally, suckers do not dig redds as salmon do. The majority of catostomids deposit gametes over substrate (Corbett and Powles 1983, Weiss et al. 1998) or in very shallow spawning depressions (Maddux and Kepner 1988). Suckers differ from salmon in that any subsidy effect is likely due to deposited reproductive products and waste rather than carcass decomposition or bioturbation.

Conclusion

This ecosystem-based project provides a foundation to understand how stream ecosystem processes such as the biogeochemical cycle are influenced by carbon inputs from terrestrial and aquatic sources. Land use affects instream DOC concentrations, particularly riparian land use, which was observed to be more highly correlated with DOC than watershed land use. Carbon spiraling was not correlated with watershed land use although land use has been shown to affect many of its components, such as organic material standing stock and processing. In the early spring, the Salmon Trout River in northern Marquette County, Michigan receives a large number of migrating suckers coming into the river from Lake Superior to spawn. During this process they deliver high quality carbon and affect stream metabolism. Understanding the linkages between allochthonous carbon sources, such as fish migrations and land cover, and in stream DOC concentrations will aid in predicting the consequences of anthropogenically-driven changes in this and similar remote regions. Since streams contribute a substantial portion of Great Lakes DOC, understanding the carbon budgets of the lakes will benefit from understanding watershed linkages via DOC.

Table 1: Coordinates of northern Marquette County, Michigan.USA streams sampled for watershed assessment in 2008

Site	Stream Name	Stream Order	Coordinates	
YD 550	Yellow Dog River	4th	46° 45.435' N	87° 39.663' W
YD 510	Yellow Dog River	4th	46° 43.588' N	87° 42.884' W
YDP 1	Yellow Dog River	3rd	46° 43.598 N	87° 52.312' W
YDP 2	Yellow Dog River	3rd	46° 42.799' N	87° 50.406' W
AAA[1]	East Branch Salmon Trout River	1st	46° 50.628' N	87° 47.469' W
STMB	Middle Branch Salmon Trout River	3rd	46° 47.317' N	87° 52.904' W
STMF	Salmon Trout River	4th	46° 48.689' N	87° 49.604' W
550 A	Alder Creek	1st	46° 47.507' N	87° 42.089' W
550 B	Wilson Creek	3rd	46° 43.727' N	87° 37.293' W
550 C	Unnamed	1st	46° 42.849' N	87° 36.195' W
510 A	Lost Creek	3rd	46° 44.495' N	87° 43.783' W
510 B	Unnamed	1st	46° 43.868' N	87° 43.783' W
510 C[2]	Big Pup Creek	3rd	46° 22.758' N	87° 41.978' W
510 D	Little Pup Creek	1st	46° 41.069' N	87° 41.978' W
510 E[2]	Unnamed	1st	46° 39.356' N	87° 40.264' W
510 F[2]	Unnamed	1st	46° 37.245' N	87° 37.548' W
510 G	Unnamed	1st	46° 36.219' N	87° 36.613' W
WL A	Second River	2nd	46° 31.525' N	87° 52.113' W
HMC A	Rush Creek	1st	46° 53.024' N	87° 53.401' W
HMC B[12]	Conway Creek	1st	46° 51.635' N	87° 47.997' W
HMC C	Unnamed	1st	46° 50.624' N	87° 47.471' W
HMC D[12]	Unnamed	1st	46° 51.243' N	87° 48.667' W
BB A[1]	Unnamed	1st	46° 51.241' N	87° 48.668' W
BB B	Unnamed	1st	46° 49.330' N	87° 44.049' W
NW 1	East Branch Salmon Trout River	2nd	46° 46.512' N	87° 52.042' W
NW 2[1]	East Branch Salmon Trout River	1st	46° 46.105' N	87° 50.612' W

[1] Sites at which carbon spiraling was quantified

[2] Sites not sampled in August, 2008

Site names are used in place of stream names throughout this study.

Table 2: Dissolved organic carbon (DOC), watershed area and land cover for streams in Northern Marquette County, Michigan USA in

	DOC	Area	NLCD %							NWI%
	(mg L^{-1})	(km^2)	Open Water	Commercial/ Industrial/ Residential	Transitional	Forest	Grassland	Agricultural	Wetlands	Wetlands
HMC A	5.00	11.44	18.23	0.00	0.00	61.58	0.06	0.20	19.93	19.61
HMC B	29.59	0.95	2.07	0.00	0.00	93.38	0.09	2.37	2.08	3.78
HMC C	22.09	3.04	0.15	0.00	0.00	76.98	0.00	0.71	22.17	23.58
HMC D	11.90	1.35	0.59	0.00	0.00	96.74	0.53	1.47	0.67	14.81
BB A	23.69	4.51	0.16	0.00	0.00	93.49	0.48	3.14	2.73	21.54
BB B	36.76	0.94	0.00	0.00	0.00	96.41	0.19	2.54	0.86	0.00
STMF	9.10	60.36	0.65	0.00	3.53	88.85	0.27	0.58	6.12	17.50
STMB	5.68	23.47	0.08	0.00	7.71	85.61	0.33	0.79	5.49	33.89
NW 1	7.18	2.02	0.00	0.00	0.09	99.14	0.40	0.09	0.28	15.51
NW 2	3.54	3.11	9.41	0.00	1.00	87.59	0.15	0.08	1.77	6.28
AAA	12.57	5.22	0.09	0.00	0.14	99.69	0.02	0.02	0.05	2.37
550 A	5.40	11.33	0.05	0.03	0.00	95.01	0.51	2.13	2.28	92.38
YD 550	7.83	145.89	1.04	0.06	6.60	81.41	0.24	0.64	10.02	12.38
550 B	7.87	16.08	0.30	0.17	0.00	95.94	0.99	0.21	2.39	2.90
550 C	9.48	1.59	0.00	0.17	0.00	97.34	0.96	0.34	1.19	10.70
YDP 1	12.73	51.43	0.86	0.01	7.87	66.80	0.12	0.39	23.95	26.66
YDP 2	13.17	62.72	0.78	0.01	10.65	67.07	0.10	0.39	21.00	24.33
510 A	6.14	9.84	0.02	0.00	0.00	99.09	0.38	0.29	0.21	0.58
YD 510	10.15	98.20	1.27	0.01	9.73	73.68	0.16	0.68	14.46	17.34
510 B	4.22	0.34	0.00	0.00	0.00	100.00	0.00	0.00	0.00	0.00
510 C	5.16	13.44	1.02	0.00	0.50	96.26	0.01	0.05	2.16	1.19
510 D	5.95	0.68	0.00	0.00	0.00	99.87	0.00	0.00	0.13	0.00
510 E	4.82	0.75	3.20	0.00	0.12	96.07	0.00	0.00	0.61	0.52
510 F	8.25	1.48	0.00	0.00	0.61	99.38	0.00	0.00	0.01	7.85
510 G	11.71	0.67	0.40	0.00	1.50	96.52	0.00	0.00	1.58	29.10
WL A	18.15	16.37	2.13	0.00	0.10	62.29	1.08	0.89	33.51	30.67
p		0.545	0.297	n/a	0.608	0.687	n/a	**<0.001**	0.414	0.143
r^2		0.015	0.045	n/a	0.011	0.007	n/a	**0.519**	0.028	0.095

P-values and r^2 for regressions of watershed area and land cover against DOC are included. NLCD is land cover from the National Land Cover Dataset. NWI is land cover from the National Wetland Inventory. Significant regressions are denoted in bold print.

Table 3: Dissolved organic carbon (DOC), riparian area and land cover for streams in Northern Marquette County, Michigan USA in

	DOC	Area	NLCD %							NWI%
	(mg L^{-1})	(m^2)	Open Water	Commercial/ Industrial/ Residential	Transitional	Forest	Grassland	Agricultural	Wetlands	Wetlands
HMC A	5.00	11264.00	0.00	0.00	0.00	88.18	0.00	0.00	11.82	25.59
HMC C	22.09	10601.00	0.00	0.00	0.00	57.56	0.00	0.00	42.44	72.53
BB A	23.69	15801.00	0.00	0.00	0.00	52.38	0.00	0.00	47.62	0.00
BB B	36.76	9113.00	0.00	0.00	0.00	93.42	0.00	6.58	0.00	0.00
STMF	9.10	457137.00	0.68	0.00	0.18	78.21	0.05	0.28	20.60	8.79
STMB	5.68	248858.00	1.04	0.00	0.05	77.86	0.00	0.03	21.02	19.13
NW 1	7.18	33991.00	0.00	0.00	0.00	98.17	0.03	0.00	1.79	0.00
NW 2	3.54	5858.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00	0.00
AAA	12.57	11930.00	0.00	0.00	0.00	99.76	0.00	0.00	0.24	14.29
550 A	5.40	68728.00	0.67	0.00	0.00	92.21	0.36	0.64	6.13	30.80
YD 550	7.83	1433095.00	5.29	0.02	1.13	83.07	0.38	1.06	9.06	7.37
550 B	7.87	223438.00	2.87	0.64	0.00	88.00	0.00	0.23	8.26	19.16
YDP 1	12.73	353406.00	9.84	0.00	2.87	65.69	0.15	0.49	20.95	33.62
YDP 2	13.17	86379.00	5.62	0.00	1.82	69.22	0.00	0.67	22.68	28.29
510 A	6.14	89897.00	0.00	0.00	0.00	98.52	0.03	0.00	1.45	3.42
YD 510	10.15	834157.00	7.40	0.00	1.75	75.75	0.60	0.82	13.68	11.96
510 B	4.22	16607.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00	0.00
510 C	5.16	234763.00	5.43	0.00	0.68	88.95	0.00	0.00	4.94	5.97
510 D	5.95	15867.00	0.00	0.00	0.00	99.26	0.00	0.00	0.74	0.00
510 G	11.71	12143.00	0.00	0.00	0.23	99.77	0.00	0.00	0.00	18.04
WL A	18.15	190668.00	14.86	0.00	0.00	48.93	0.71	2.16	33.33	52.34
p		0.518	0.690	n/a	0.903	**<0.001**	n/a	**<0.001**	**<0.001**	**<0.001**
r^2		0.021	0.008	n/a	0.001	**0.636**	n/a	**0.532**	**0.685**	**0.608**

P-values and r^2 for regressions of watershed area and land cover against DOC are included. NLCD is land cover from the National Land Cover Dataset. NWI is land cover from the National Wetland Inventory. Significant regressions are denoted in bold print.

Table 4: Organic carbon spiraling parameters for five streams in northern Marquette County, Michigan, USA in May 2008

Site	Q (m^3 day$^{-1)}$	V_{wat} (m day^{-1})	BOC (g m^{-2})	TOC (g m^{-3})	R_{het} (g C m^{-1} day^{-1})	V_{oc} (m day^{-1})	K_{oc} (m day^{-1})	S_{oc} (m)	IR
BB A	5200.82	11381.39	13.94	0.55	56.81	78.18	4.05	19.30	145.57
NW 2	3376.34	7987.02	120.52	0.98	37.49	11.90	0.31	38.29	671.39
AAA	66.24	676.36	179.80	0.52	11.04	0.12	0.06	2.00	5515.82
HMC B	3483.37	7210.81	116.07	3.28	22.09	39.00	0.19	205.75	184.90
HMC D	1682.46	9431.20	41.22	0.47	44.60	10.79	1.08	9.98	874.36

Q = discharge (m^3 day^{-1}), Voc = net longitudinal velocity of organic carbon (m day^{-1}), BOC = total benthic organic carbon standing stock (g C m^{-3}), TOC = total transported organic carbon (g C m^{-3}), R_{het} = heterotrophic respiration (g C m^{-2} day^{-1}), Voc = net longitudinal velocity of organic carbon (m day^{-1}), K_{oc} = biotic turnover rate (day^{-1}), S_{oc} = organic carbon turnover length (m), IR = the index of retention

Table 5: Organic carbon turnover length, watershed area and land cover for streams in northern Marquette County, Michigan, USA in May 2008

Site	S_{OC}	Area	NLCD %					NWI %
	(m)	(km^2)	Open Water	Forest	Grassland	Agricultural	Wetlands	Wetlands
BB A	19.30	4.51	0.16	93.49	0.48	3.14	2.73	21.54
NW 2	38.29	3.11	9.41	87.59	0.15	0.08	1.77	6.28
AAA	2.00	5.22	0.09	99.69	0.02	0.02	0.05	2.37
HMC B	205.75	0.95	2.07	93.38	0.09	2.37	2.08	3.78
HMC D	9.98	1.35	0.59	96.74	0.53	1.47	0.67	14.81
p		0.248	0.890	0.679	n/a	0.533	0.488	0.511
r^2		0.405	0.007	0.065	n/a	0.141	0.172	0.156

S_{OC} is organic carbon turnover length (m). NLCD is land cover from the National Land Cover Dataset. NWI is land cover from the National Wetland Inventory. P-values and r^2 for regressions of watershed area and land cover against S_{OC} are included.

Table 6: Whole stream metabolism in upstream and downstream sites on the Salmon Trout River, Michigan, USA during and after the 2008 spawning migration of two catostomid species

Site	Date	Reaeration Coefficient (min^{-1})	Ecosystem Respiration (g C m^{-1} day^{-1})	Gross Primary Production (g C m^{-1} day^{-1})	Net Ecosystem Production (g C m^{-1} day^{-1})
Upstream During	5/17/2008	0.10	-26.05	11.71	-14.34
Upstream After	5/27/2008	0.13	-33.81	8.05	-25.76
Downstream During	5/18/2008	0.0040	-92.88	3.35	-89.53
Downstream After	5/26/2008	0.0048	-42.60	5.93	-36.67

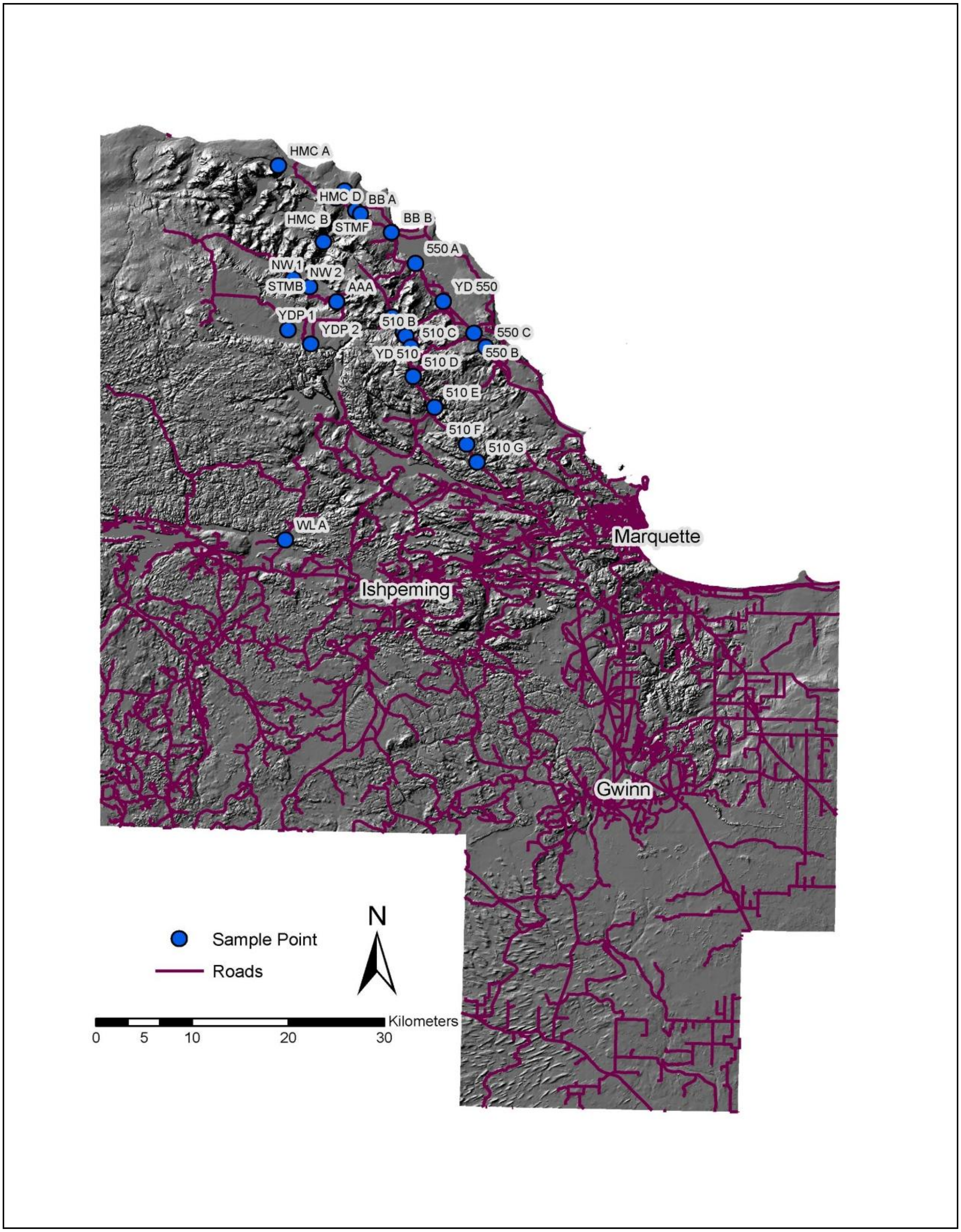

Figure 1: Sampling locations (n=26) for watershed analyses in northern Marquette County, Michigan, USA.

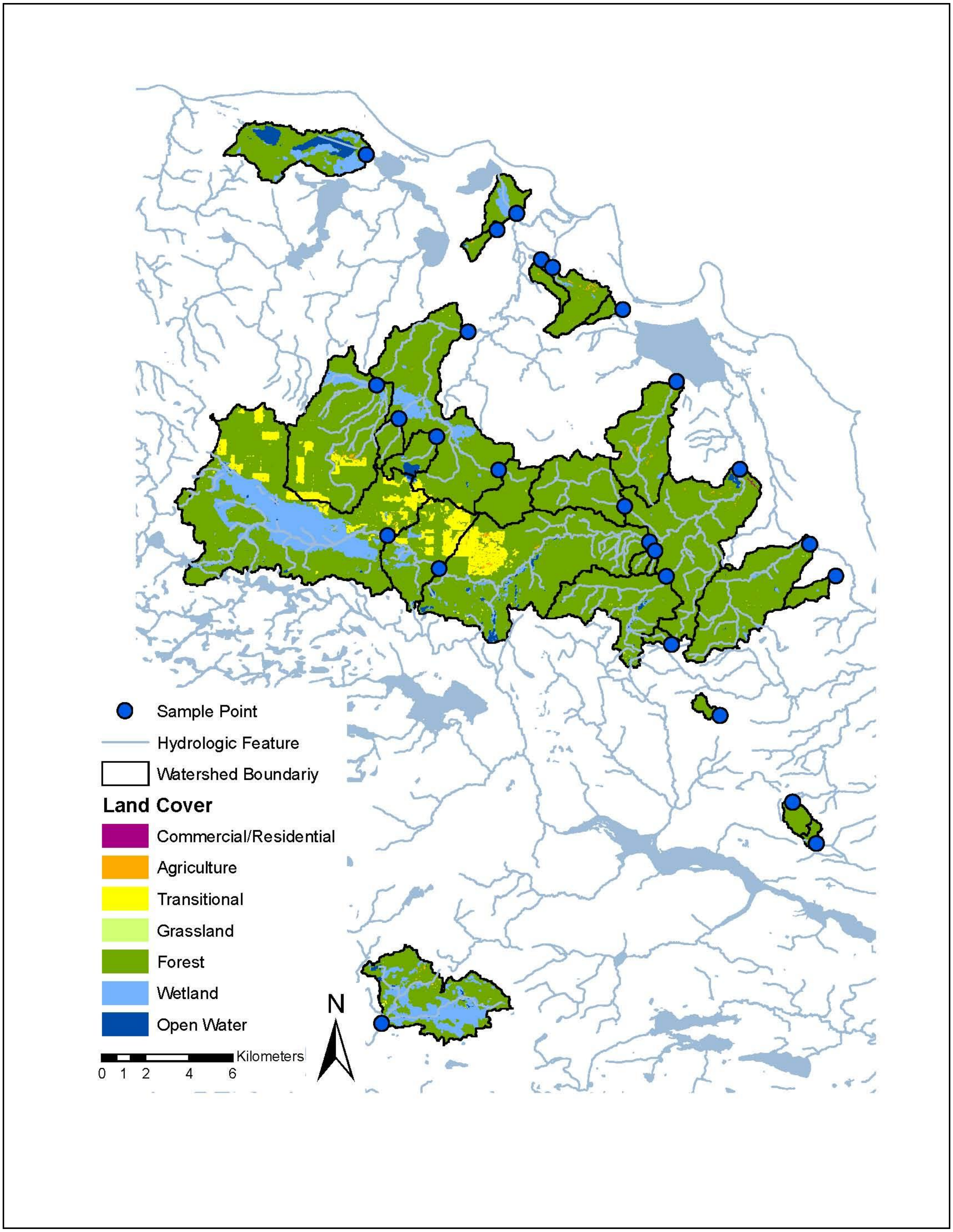

Figure 2: Land cover from the National Land Cover Dataset for 26 sampling sites in northern Marquette County, Michigan, USA in 2008.

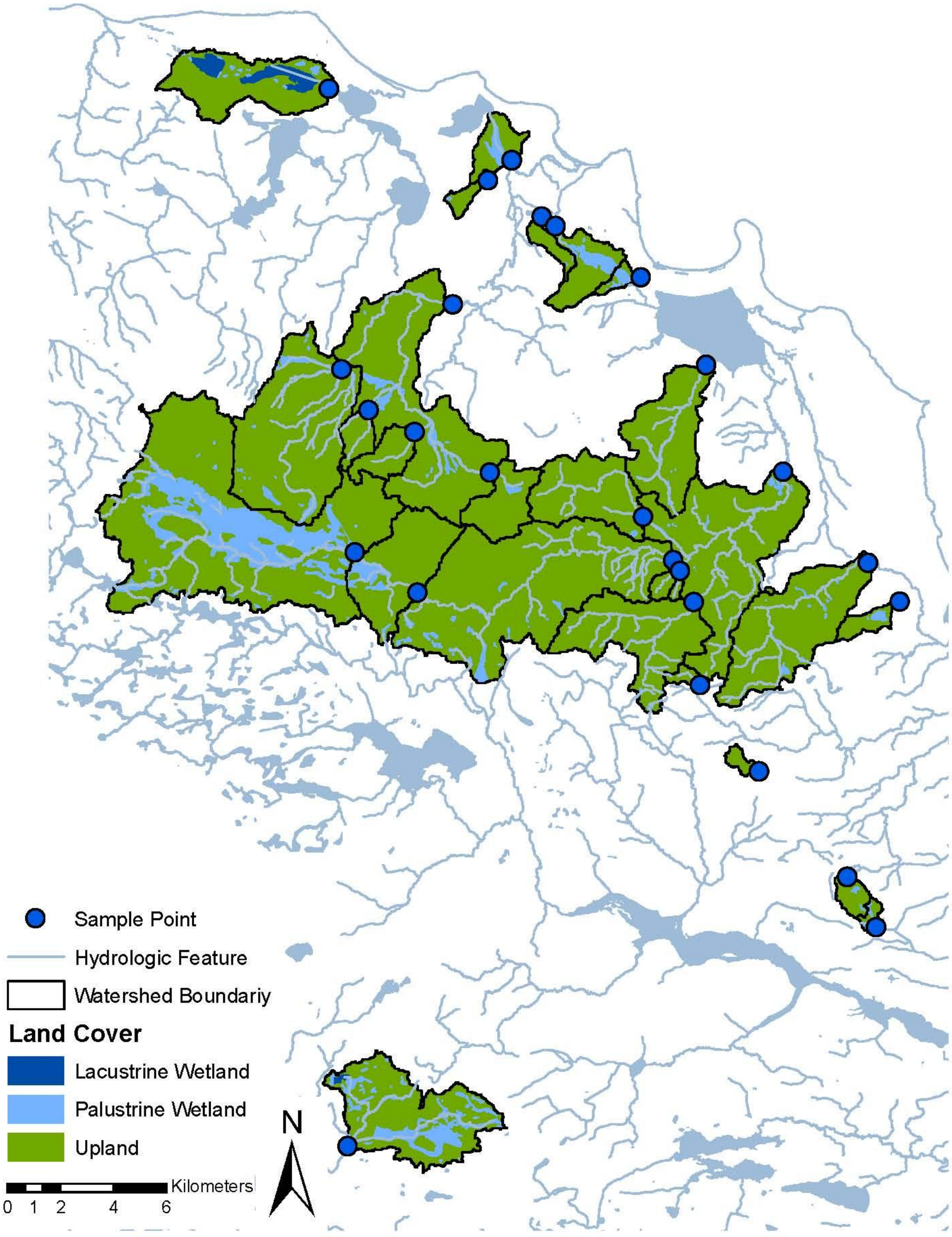

Figure 3: Land cover from the National Wetlands Inventory for 26 sampling sites in northern Marquette County, Michigan, USA in 2008.

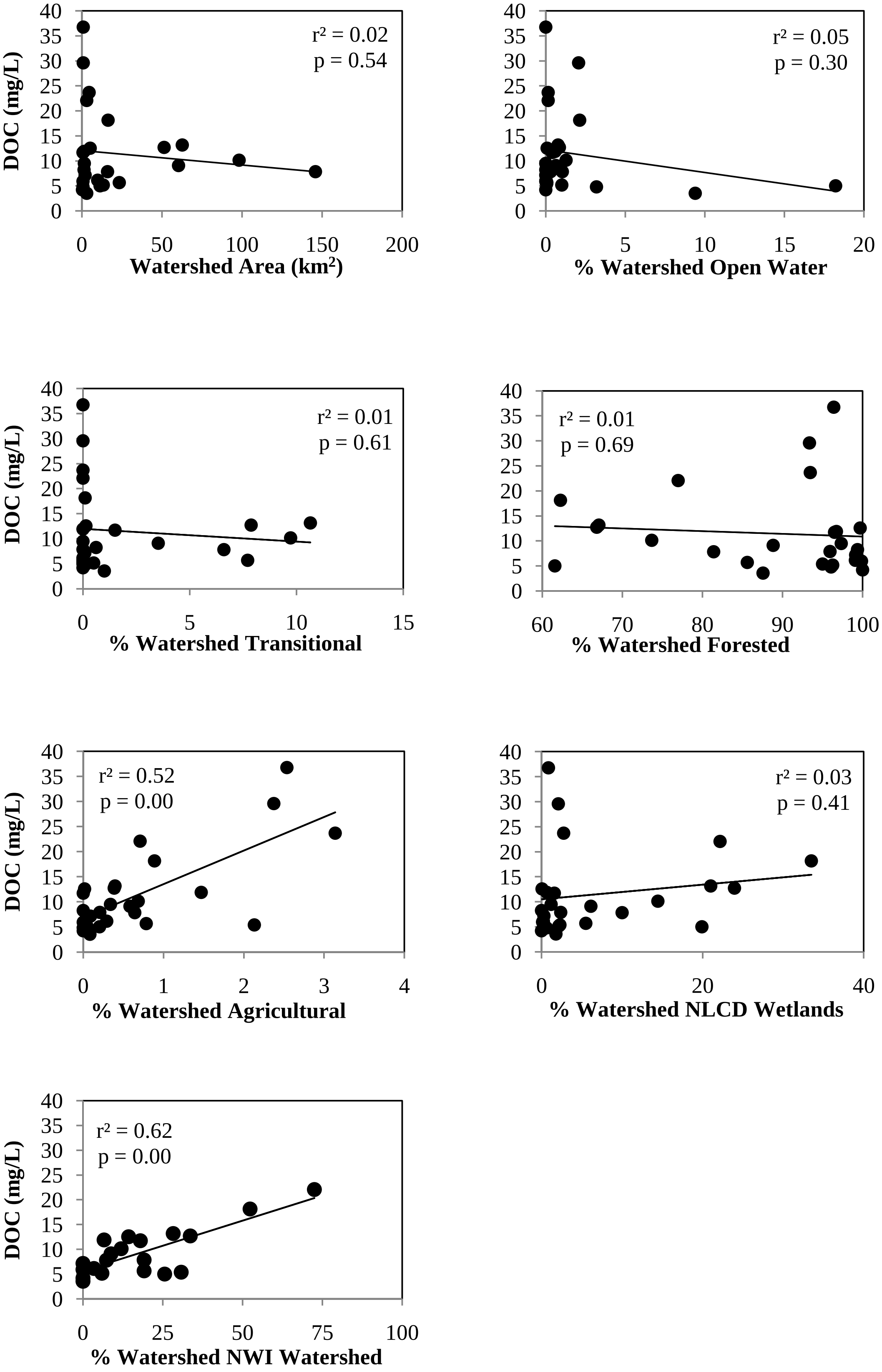

Figure 4: The influence of watershed area and land cover on dissolved organic carbon in 26 streams in northern Marquette County, Michigan in 2008. . NLCD is land cover from the National Land Cover Dataset. NWI is land cover from the National Wetland Inventory.

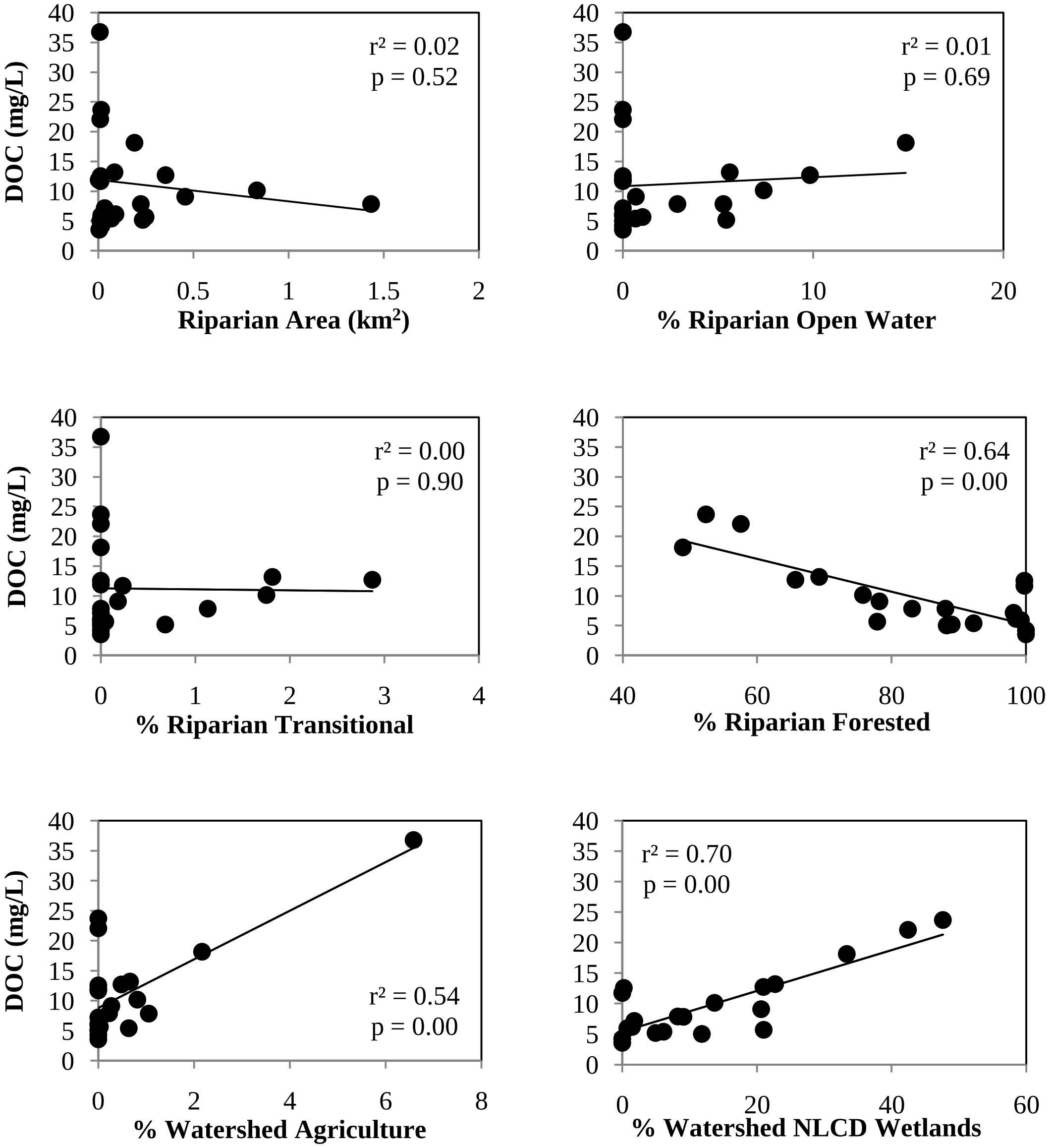

Figure 5: The influence of riparian area and land cover on dissolved organic carbon (DOC) in 26 streams in northern Marquette County, Michigan USA in 2008. NLCD is land cover from the National Land Cover Dataset. NWI is land cover from the National Wetland Inventory.

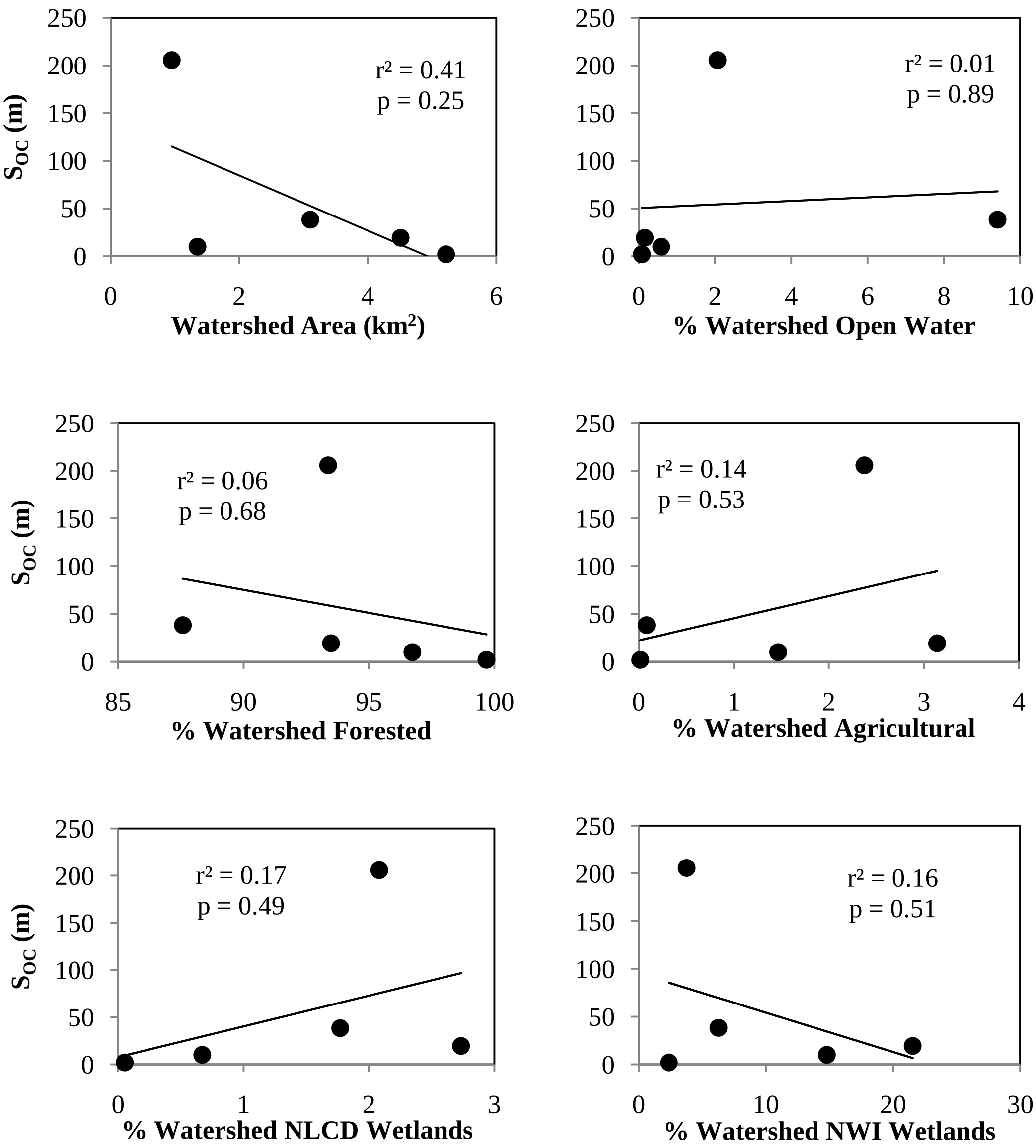

Figure 6: The influence of watershed area and land cover on organic carbon turnover length in five streams in northern Marquette County, Michigan USA in 2008. NLCD is land cover from the National Land Cover Dataset. NWI is land cover from the National Wetland Inventory.

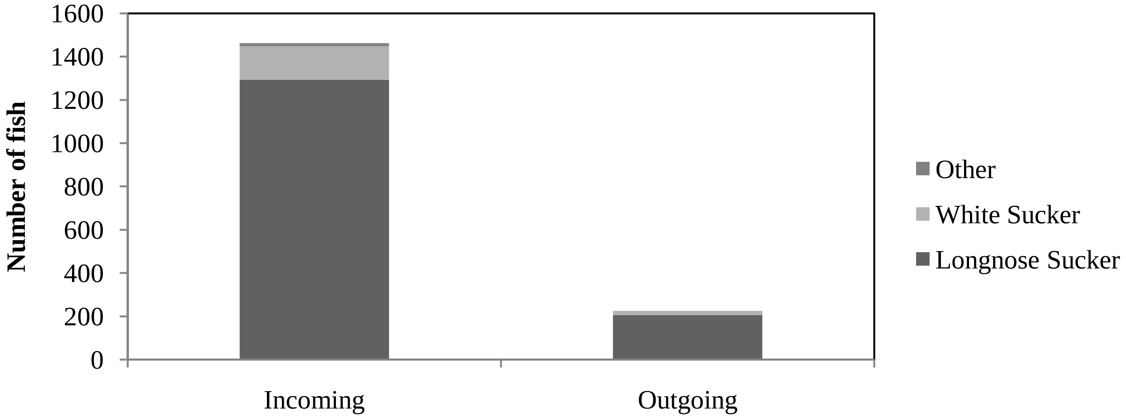

Figure 7: Number and type of incoming and outgoing fish collected in the Salmon Trout River, Michigan during the Spring 2008 catostomid spawning migration. Other fish collected were steelhead (*Oncorhynchus mykiss)*, redhorse (*Moxostoma spp.*), brook trout (*Salvelinus fontinalis)*, and muskellunge (*Esox masquinongy)*.

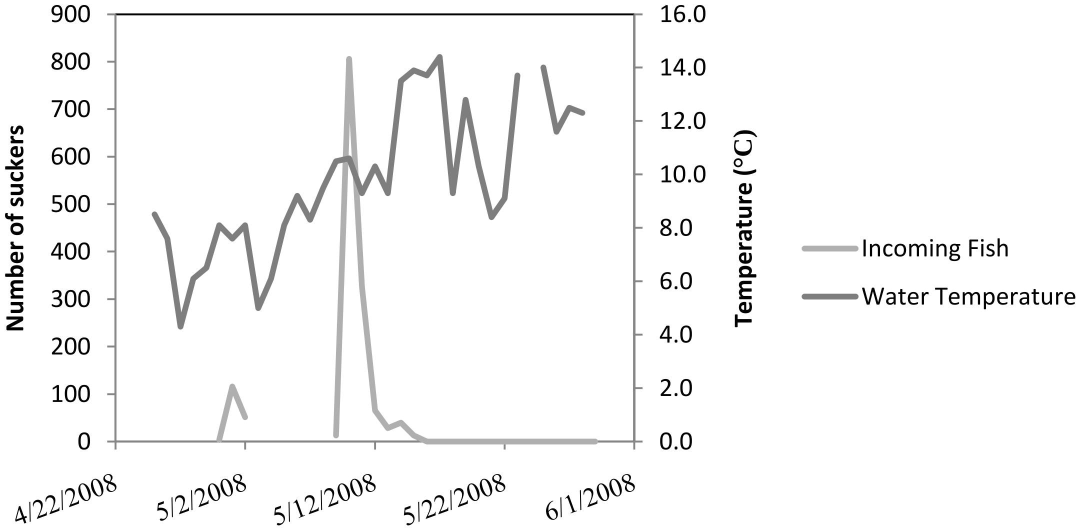

Figure 8: Timing and water temperature of the sucker run in the Salmon Trout River, Marquette County, Michigan. Catostomid runs are thought to be triggered by temperature (Corbett and Powles 1983, Weiss et al. 1998).

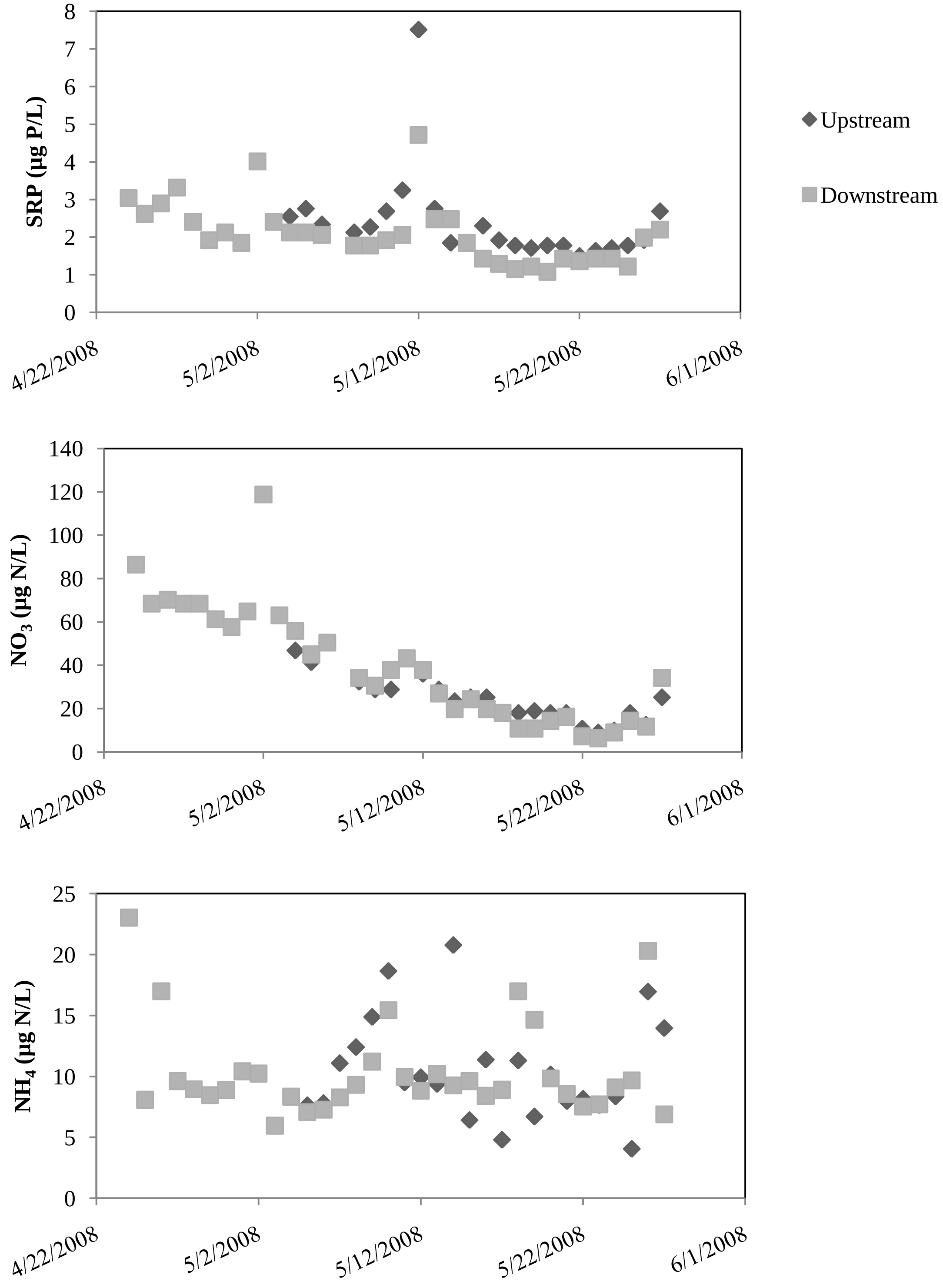

Figure 9: Water chemistry during the 2008 sucker run in the Salmon Trout River, Marquette County, Michigan. Soluble reactive phosphorous (SRP), nitrate (NO_3), and ammonium (NH_4) are plotted upstream and downstream of a dam that serves as a barrier for sucker migration.

Literature Cited

Acuña, V., A. Giorgi, I. Muñoz, F. Sabater, and S. Sabter. 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. Journal of the North American Benthological Society 26(1):54-69.

Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology and Systematics 35:257–284.

Amon, R. M. and R. Benner. 1994. Rapid cycling of high-molecular-weight dissolved organic matter in the ocean. Nature **369**:549–551.

Anderson, D. E., R. G. Striegl, D. I. Stannard, C. M. Michmerhuizen, T. A. McConnaughey, and J. W. LaBaugh. 1999. Estimating lake-atmosphere CO_2 exchange. Limnology and Oceanography 44:988-1001.

APHA (American Public Health Association). 1992. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, DC.

Arsuffi, T. L. and K. Suberkropp. 1985. Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. Oikos 45:50-58.

Balogh, K, V., M. Pressing, L. Voros, and N. Toth. 2006. A study of the decomposition of reed (*Phragmites australis*) as a possible source of aquatic humic substances by measuring the natural abundance of stable carbon isotopes. International Review of Hydrobiology 91(1):15-28.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency; Office of Water; Washington, D.C.

Benfield, E. F. 1997. Comparison of litterfall input to streams. Journal of the North American Benthological Society 16:104-108.

Berndt, L. W. 1988. Soil survey of Baraga County area, Michigan. U.S . Dept . of Agriculture, Soil Conservation Service, Washington, D .C.

Carlisle, D. M., J. Falcon, and M. R. Meador. 2009. Predicting the biological condition of streams: use of geospatial indicators of natural and anthropogenic characteristics of watersheds. Environmental Monitoring and Assessment 151:1-4.

Chaloner, D. T., G. A. Lamberti, A. D. Cak, N. L. Blair, and R. T. Edwards. 2007. Inter-annual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. Freshwater Biology 52:478–490.

Chaloner, D. T., G. A. Lamberti, R. W. Merritt, N. L. Mitchell, P. H. Ostrom, and M. S. Wipfli. 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. Freshwater Biology 49:587–599.

Cole, J. J., N. E. Caraco, G. W. Kling, and T. K. Kratz. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265:1568-1570.

Cooke, S. J., C. M. Bunt, S. J. Hamilton, C. A. Jennings, M. P. Pearson, M. S. Cooperman, and D. F. Markle. 2005. Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fish. Biological Conservation 121:317–331.

Corbett, B. and P. M. Powles. 1983. Spawning and early-life ecological phases of the white sucker in Jack Lake, Ontario. Transactions of the American Fisheries Society 112:308-313.

Davis, C.O. and M. S. Simmons. 1979. Water Chemistry and Phytoplankton Field and Laboratory Procedures, Great Lakes Research Division Special Report No. 70. University of Michigan, Ann Arbor, Michigan.

Dodds, W. K. and R. M. Oakes. 2006. Controls on nutrients across a prairie stream watershed: land use and riparian cover effects. Environmental Management 37:634–646.

Dillon P. J. and L. A. Molot. 1997. Dissolved organic and inorganic carbon mass balances in central Ontario lakes. Biogeochemistry 36:29–42.

Elmore, H. L. and W. F. West. 1961. Effect of water temperature on stream reaeration: Journal of the Sanitary Engineering Division, American Society of Civil Engineers 87:59–71.

Elwood, J. W., J. D. Newbold, R. W. O’Neil, and W. Van Winkle. 1983. Resource spiraling: an optimal paradigm for analyzing lotic ecosystems. in T. D. Fontaine ed. Dynamics of Lotic Ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Engstrom, D. R. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Canadian Journal of Fisheries and Aquatic Sciences 44:1306-1314.

Fisher, S. G., 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Internationale Revue der gesamten Hydrobiologie und Hydrographie 62:701–727.

Flader, S. L. 1983. The Great Lakes forest: An environmental and social history. The University of Minnesota Press, Minneapolis.

Frost, P. C., C. T. Cherrier, J. H. Larson, S. Bridgham, and G. A. Lamberti. 2007. Effects of dissolved organic matter and ultraviolet radiation on the accrual, stoichiometry and algal taxonomy of stream periphyton. Freshwater Biology 52:319–330.

Frost, P. C., J. H. Larson, C. A. Johnston, K. C. Young, P. A. Maurice, G. A. Lamberti, and S. D. Bridgham. 2006. Landscape predictors of stream dissolved organic matter concentration and physiochemistry in a Lake Superior river watershed. Aquatic Science 68:40–51.

Grabowski, T. B., N. L. Ratterman, and J. J. Isely. 2008. Demographics of the spawning aggregations of four catostomid species in the Savannah River, South Carolina and Georgia, USA. Ecology of Freshwater Fish 17(2): 318-327.

Gergel, S. E., M. G. Turner, and T. K. Kratz. 1999. Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers**.** Ecological Applications 9(4):1377-1390.

Gottesfeld, A. S., M. A. Hassan, J. F. Tunnicliffe, and R. W. Poirier. 2004. Sediment dispersion in salmon spawning streams: the influence of floods and salmon redd construction. Journal of the American Water Resources Association 40:1071–1086.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–51.

Gresh T., J. Lichatowich, P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25:15–21.

Groot, C. and L. Margolis. 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, Canada.

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. Limnology and Oceanography 48:1112–1119.

Herlihy A, J. L. Stoddard, and C. B. Johnson. 1998. The relationship between stream chemistry and watershed land cover data in the Mid- Atlantic region, USA. Water Air and Soil Pollution 105:377–86.

Hinton, M. J., S. L. Schiff, and M. C. English. 1998. Sources and flowpaths of dissolved organic carbon during storms in two forested watersheds of the Precambrian Shield. Biogeochemistry 41:175–197.

Hoellein, T. J. 2008. The effects of seasonality and restoration on stream nutrient cycling at multiple spatial scales. Ph.D. Dissertation, University of Notre Dame, South Bend, Indiana.

Holmes, R. M., A. Aminot, R. Kérouel, B. A. Hooker, and B. J. Peterson. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 56:1801-1808.

Hood, E., J. Fellman, and R.T. Edwards. 2007. Salmon influences on dissolved organic matter in a coastal temperate brown-water stream: an application of fluorescence microscopy. Limnology and Oceanography 52:1580-1587.

Inwood, S. E., J. L. Tank, and M. J. Bernot. 2005. Patterns of denitrification associated with land use in 9 midwestern headwater streams. Journal of the North American Benthological Society 24: 227–245.

Iversen, T. M. 1974 Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of digested leaves. Oikos 25:278-282.

Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecolgia 159:583-595.

Johnston, N. T., E. A. MacIsaac, P. J. Tschaplinski, and K. J. Hall. 2004. Effects of the abundance of spawning sockeye salmon (Oncorhynchus nerka) on nutrients and algal biomass in forested streams. Canadian Journal of Fisheries and Aquatic Sciences 61:384–403.

Johnson, L. B., C. Richards, G. E. Host, and J.W. Arthur. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. Freshwater Biology 37:193–208.

Johnston, C. A., B. A. Shmagin, P. C. Frost, C. Cherrier, J. H. Larson, G. A. Lamberti, and S. D. Bridgham. 2008. Wetland types and wetland maps differ in ability to predict dissolved organic carbon concentrations in streams. Science of the Total Environment 404: 326-334.

Kaplan, L. A. 1994. A field and laboratory procedure to collect, process, and preserve freshwater samples for dissolved organic carbon analysis. Limnology and Oceanography 39:1470-1476.

Kashian, D. R., B. A. Prusha, and W. H. Clements. 2004. Influence of total organic carbon and UV-B radiation on zinc toxicity and bioaccumulation in aquatic communities. Environmental Science and Technology 38:6371–6376.

Kelly, D. J., J. J. Clare, and M. L. Bothwell. 2001. Attenuation of solar ultraviolet radiation by dissolved organic matter alters benthic colonization patterns in streams. Journal of the North American Benthological Society 20:96–108.

Kling, G. W., G. W. Kipphut, and M. C. Miller. 1991. Arctic lakes and streams as gas conduits to the atmosphere: implications for tundra carbon budgets. Science 251:298-301.

Klingler, G. L., J. V. Adams, and J. W. Heinrich. 2003. Passage of four teleost species prior to sea lamprey (*Petromyzon marinus*) migration in eight tributaries of Lake Superior, 1954 to 1979. Transactions of the American Fisheries Society 29: 403-409.

Klump, J. V., S. A. Fitzgerald, and J. T. Waples. 2009. Benthic biogeochemical cycling, nutrient stoichiometry, and carbon and nitrogen mass balances in a eutrophic freshwater bay. Limnology and Oceanography 54(3): 692–712.

Kocik, J. F. and M. L. Jones. 1999. Pacific salmonines in the Great Lakes basin. in W. W. Taylor and C. P. Ferreri (editors). Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing, Michigan.

Kullberg, A., K. H. Bishop, A. Hargeby, M. Jansson, and R. C. Petersen Jr. 1993. The ecological significance of dissolved organic carbon in acidified waters. Ambio 22:331–337.

Larson, J. H., P. C. Frost, Z. Zheng, C. A. Johnston, S. D. Bridgham, D. M. Lodge, and G. A. Lamberti. 2007. Effects of upstream lakes on dissolved organic matter in streams. Limnology and Oceanography 52:60–69.

Maddux, H. R. and W. G. Kepner. 1998. Spawning of bluehead sucker in Kanab Creek, Arizona (Pisces: Catostomidae). Southwestern Naturalist 33:364-365.

Maranger, R. and M. J. Pullin. 2003. Elemental complexation by dissolved organic matter in lakes: Implications for Fe speciation and the bioavailability of Fe and P. Pages 186-207 in S. E. G. Findlay and R. L. Sinsabaugh (editors), Aquatic ecosystems: Interactivity of dissolved organic matter. Academic Press, San Diego, California.

Marzolf, E. R., P. J. Mulholland, and A. D. Steinman. 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Science 51:1591-1599.

McIntyre, C. D., and H. K. Phinney. 1964. Laboratory studies of periphyton production and community metabolism in lotic ecosystems. Technical Paper No. 1798, Oregon Agricultural Experimental Station.

Minakawa, N. and R. I. Gara. 1999. Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning salmon run in a small stream of the Pacific Northwest. Journal of Freshwater Ecology 14:327–335.

Minshall, G. W. 1978. Autotrophy in stream ecosystems. Bio-Science 28:767–771.

Minshall, G. W., R. C. Petersen, T. L. Bott, C. E. Cushing, K. W. Cummins, R. L. Vannote, and J. R. Sedell. 1992. Stream ecosystem dynamics of the Salmon River, Idaho: an 8th-order system. Journal of the North American Benthological Society 11:111–137.

Mitchell, N. L., and G. A. Lamberti. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. Limnology and Oceanography 50:217–227.

Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia 139:298–308.

Mulholland, P. J., C. S. Fellows, J. L. Tank, D. M. Sanzone, J. R. Webster, W. M. Wollheim, B. J. Peterson, and J. L. Meyer. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology 46:1503–17.

Naiman R. J. and H. De´camps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621–658.

Neumann, M. and B. Bredeweg. 2004. A qualitative model of the nutrient spiraling in lotic ecosystems to support decision makers for river management. Pages 159-164 in J. de Kleer and K. D. Forbus (sditors), Proceedings of the 18th International Workshop on Qualitative Reasoning. Evanston, Illinois.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and W. Van Winkle. 1981. Nutrient spiraling in streams: the concept and its field measurement. Canadian Journal of Fisheries and Aquatic Sciences 38:860–863.

Newbold, J. D., P. J. Mulholland, J. W. Elwood, and R. V. O'Neill. 1982. Organic carbon spiraling in stream ecosystems. Oikos 38: 266–272.

Nolen, J. A. and R. G. Pearson. 1993. Factors affecting litter processing by *Anisocentropus kirramus* (Trichoptera: Calamoceratidae) from an Australian tropical rainforest stream. Freshwater Biology 29:469-479.

Odum, H. T. 1956. Primary production in flowing waters. Limnology and Oceanography 1:102–117.

O'Kelley, C. T. and S. L. Powers. 2007. Life -history Aspects of *Hypentelium etowanum* (Alabama Hog Sucker) (Actinopterygii: Catostomidae) in Northern Georgia. Southeastern Naturalist 6(3):479-490.

Osborne, L. L. and D. A. Kovacic. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. Freshwater Biology 29:243-258.

Osborne, L. L. and M. J. Wiley. 1988. Empirical relationships between land use/cover and stream water quality in an agricultural watershed. Journal of Environmental Management 26:9-27.

Page, L.M. and C. E. Johnston. 1990. Spawning in the Creek Chubsucker, *Erimyzon oblongus*, with a review of spawning behaviors in suckers (Catostomidae). Environmental Biology of Fishes 27:265– 272.

Palmer, S. M., D. Hope, M. F. Billett, J. J. C. Dawson, and C. L. Bryant. 2001. Sources of organic and inorganic carbon in a headwater stream: evidence from carbon isotope studies. Biogeochemistry 52:321–338.

Peck, J. W. 1992. The sport fishery and contribution of hatchery trout and salmon in Lake Superior and tributaries at Marquette, Michigan, 1984-1987. Michigan Department of Natural Resources, Fisheries Research Repor, Ann Arbor, Michigan.

Peck, J. W., T. S. Jones, W. R. MacCallum, and S. T. Schram. 1999. Contribution of hatchery-reared fish to chinook salmon populations and sport fisheries in Lake Superior. North American Journal of Fisheries Management 19:155–164.

Peterson, N. P. and T. P. Quinn. 1996. Persistence of egg pocket architecture in redds of chum salmon, *Oncorhynchus keta*. Environmental Biology of Fishes 46:243–253.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois.

Prusha, B. A and W. H. Clements. 2004. Landscape attributes, dissolved organic C, and metal bioaccumulation in aquatic macroinvertebrates (Arkansas River Basin, Colorado). Journal of the North American Benthological Society 23:327-339.

Randolf, J. C., G. N. Cameron, and J. A. Wrazen. 1991. Dietary choice of a generalist grassland herbivore, *Sigmodon hispidus*. Journal of Mammology 72:300–313.

Rathbun, R. E., D. W. Stephens, D. J. Schultz, and D. Y. Tai. 1978. Laboratory studies of gas tracers for reaeration. Proceedings of the American Society of Civil Engineering 104:215-229.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141–56.

Royer, T. V. 1995. The decomposition of plant material in the middle reach of the Snake River, Idaho. M.S. Thesis, Idaho State University, Pocatello, Idaho.

Royer, T. V. and M. B. David. 2005. Export of dissolved organic carbon from agricultural streams in Illinois, USA. Aquatic Sciences 67:465–471.

Sarica, J., M. Amyot, L. Hare, M. Doyon, and L.W. Stanfield. 2004. Salmon-derived mercury and nutrients in a Lake Ontario spawning stream. Limnology and Oceanography 49:891-899.

Schuldt, J.A. and A. E. Hershey. 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. Journal of the North American Benthological Society 14:259–68.

Scrivener, J. C., and J. S. Macdonald. 1998. Interrelationships of streambed gravel, bedload transport, beaver activity and spawning sockeye salmon in Stuart-Takla tributaries, British Columbia, and possible impacts from forest harvesting. Pages 267–282 in M. K. Brewin and D. M. A. Monita (editors) Forest Fish Conference: Land management practices affecting aquatic ecosystems. Ministry of Natural Resources, Canadian Forest Service, Northern Forestry Centre, Informational Report NOR-X-356, Edmonton, Alberta, Canada.

Sharp, J. H., R. Bennett, C. A. Carlson, R. Dow, and S. E. Fitzwater. 1993. Reevaluation of high-temperature combustion and chemical oxidation measurements of dissolved organic-carbon in seawater. Limnology and Oceanography 38:1774-1782.

Stout, J. 1980. Leaf decomposition rates in a Costa Rican lowland tropical rainforest stream. Biotropica 12:264- 272.

Taylor, B. W., C. F. Keep, R. O. Hall, B. J. Koch, and L. M. Tronstad. 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence, and standard additions. Journal of the North American Benthological Society 26(2):167-177.

Thomas, S. A., T. V. Royer, E. B. Snyder, and J. C. Davis. 2005. Organic carbon spiraling in an Idaho river. Aquatic Sciences 67: 424-43.

Thurman, E. M. 1985. Organic geochemistry of natural waters. Springer Science and Business, New York, New York.

Tiegs, S. D., D. T. Chaloner, P. Levi, J. Rueegg, J. L. Tank, and G. A. Lamberti. 2008. Timber harvest transforms ecological roles of salmon in Southeast Alaska rain forest streams. Ecological Applications 18:4–11.

Tranvik, L. J. 1998. Degradation of dissolved organic matter in humic waters by bacteria. Pages 259-283 in D. O. Hessen and L. J. Tranvik (editors), Aquatic humic substances. Springer-Verlag, Berlin.

Tsivoglou, B. C. and L. A. Neal. 1976. Tracer measurement of reaeration: predicting the capacity of inland streams. Journal of the Water Pollution Control Federation 48:2669-2689.

Urban, N. R., M. T. Auer, S. A. Green, X. Lu, D. S. Apul, K. D. Powell, and L. Bub. 2005. Carbon cycling in Lake Superior. Journal of Geophysical Research–Oceans 110:C06S90.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Vinebrooke, R. D. and P. R. Leavitt. 1998. Direct and interactive effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food web. Limnology and Oceanography 43:1065–1081.

Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22:6–12.

Wanner, S.C., K. Ockenfeld, M. Brunke, H. Fischer, and M. Pusch. 2002. The distribution and turnover of benthic organic matter in a lowland river: influence of hydrology, seston load, and impoundment. River Research Application 18:107-122.

Webster, J. R. 2007. Spiraling down the river continuum: stream ecology and the U-shaped curve. Journal of the North American Benthological Society 26(3):375-389.

Webster, J. R., J. B. Wallace, and E. F. Benfield. 1995. Organic processes in streams of the eastern United States. Pages 117-187 in C. E. Gushing, G. W. Minshall, and K. W. Cummins (editors) Ecosystems of the World 22: River and Stream Ecosystems. Elsevier, Amsterdam.

Webster, J. R. and J. L. Meyer. 1997. Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

Weiss, S. J., E. O. Otis, and O. E. Maughan. 1998. Spawning ecology of flannelmouth sucker, *Catostomus lattipinnis* (Catostomidae), in two small tributaries of the lower Colorado River. Environmental Biology of Fishes 52:419-433.

Wetzel, R. G. 1992. Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems. Hydrobiology 229:181-198.

Williamson, C. E., D. P. Morris, M. L. Pace, and O. G. Olson. 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. Limnology and Oceanography 44:795–803.

Wilson, H. F. and M. A. Xenopoulos. 2008. Ecosystem and seasonal control of stream dissolved organic carbon along a gradient of land use. Ecosystems 11:555-568.

Winch, S., J. Ridal, and D. Lean. 2002. Increased metal bioavailability following alteration of freshwater dissolved organic carbon by ultraviolet-B radiation exposure. Environmental Toxicology 17:267-274.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Couette. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Xenopoulos, M. A. and D. W. Schindler. 2001. Physical factors determining ultraviolet flux into ecosystems. Pages 36-62 in C.S. Cockell and A.R. Blaustein (editors) Ecosystems, evolution and UV radiation. Springer, New York.

Young, R. G. and A. D. Huryn. 1998. Comment: further improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Sciences 55:1784-1785.

Young, R. G. and A. D. Huryn. 1999. Effects of land use on stream metabolism and organic matter turnover. Ecological Applications 9:1359–1376.

Appendix

Appendix A: Water quality parameters for streams in northern Michigan in 2008. RHA represents the Rapid Habitat Assessment which is a visual assessment of stream habitat ranging from 1 to 200 with higher values indicating higher quality.

Site	Date	RHA	pH	Conductivity (µS)	Alkalinity (µg CaC0$_3$ L^{-1})	Hardness (µg CaCO$_3$ L^{-1})	DO (mg O L^{-1})	Temperature (°C)	DOC (mg C L^{-1})
510 A	4/27/2008		6.82	36.8	15.4	24.9	13.63	2.6	4.612
	8/23/2008	122	7.71	99.4	99.4	54.4	7.61	18.0	3.339
510 B	4/27/2008		6.81	58.0	22.9	26.0	12.7	4.0	6.268
	8/23/2008	145	8.31	178.0	10.3	93.2	8.96	14.4	1.979
510 C	4/27/2008		6.41	44.6	19.8	23.0	12.01	2.4	3.838
	8/23/2008	189	8.02	106.4	7.4	49.2	8.82	16.5	4.057
510 D	4/27/2008		6.79	24.6	15.9	11.3	12.99	2.4	3.999
	8/23/2008	172	7.80	68.6	4.6	35.1	7.48	16.3	3.255
510 E	4/27/2008		7.04	51.4	14.3	20.3	11.85	4.5	3.317
510 F	5/4/2008		6.45	48.0	18.6	23.2	13.44	3.2	8.892
	8/23/2008	165	7.85	877.3	9.3	99.2	6.74	18	5.07-
510 G	5/4/2008		6.36	61.0	20.6	26.9	12.50	3.2	12.72
	8/23/2008	148	8.02	196.5	9.7	95.6	7.42	16.5	2.453
550 A	4/26/2008		6.70	62.7	28.7	33.1	12.23	6.5	5.799
	8/22/2008	137	8.27	158.0	11.3	86.4	10.04	15.9	3.14
550 B	4/26/2008		6.84	39.9	14.7	21.8	N/A	6.8	6.641
	8/22/2008	183	7.82	138.9	6.5	66.4	7.78	19.1	3.346
550 C	4/26/2008		7.27	95.0	36.4	52.9	12.41	5.6	6.657
	8/22/2008	183	8.15	185.0	14.8	100.8	7.87	19.5	2.784
AAA	5/13/2008		6.63	60.3	23.2	34.3	11.47	6.4	17.27
	8/22/2008	172	7.84	188.6	8.6	105.6	9.21	12.9	2.247
BB A	5/13/2008		7.07	39.9	6.0	24.0	10.64	8.8	24.56
	8/23/2008	182	8.13	35.6	2.2	24.8	6.31	19.4	11.94
BB B	5/8/2008		4.82	30.5	12	50.8	11.22	5.2	25.40
HMC A	5/5/2008		6.41	66.8	2.3	27.5	12.35	5.7	6.135
	8/22/2008	177	7.34	63.0	3.7	32.7	15.30	20.2	3.661
HMC B	5/5/2008		6.27	41.8	12.6	28.4	9.30	10.4	28.63
HMC C	5/6/2008		6.08	27.4	9.0	14.4	6.44	12.4	16.41
HMC D	5/19/2009		6.29	49.3	16.7	26.3	11.59	7.1	13.81
NW 1	5/19/2008		7.20	109.5	8.0	50.8	8.82	13.3	9.309
	8/22/2008	171	7.70	151.4	8.7	76.4	7.85	18.2	4.059
NW 2	5/19/2008		7.96	119.6	59	42.0	10.14	10.7	3.342
	8/22/2008	192	8.21	130	8.8	70.4	10.70	12.0	3.269
STMB	5/24/2008		7.91	83.8	39.5	39.4	10.24	12.6	10.86
	8/22/2008	189	8.04	96.6	4.9	49.2	9.29	15.4	2.029

Site	Date	RHA	pH	Conductivity (µS)	Alkalinity (µg CaC0$_3$ L^{-1})	Hardness (µg CaCO$_3$ L^{-1})	DO (mg O L^{-1})	Temperature (°C)	DOC (mg C L^{-1})
STMF	5/6/2008		6.38	77.6	34.8	39.0	12.75	6.1	13.45
	8/23/2008	190	8.70	123.3	12.7	66.0	9.02	17.9	3.100
WL A	5/4/2008		6.37	33.9	1.2	30.8	10.89	5.5	17.24
	8/23/2008	149	7.70	112.3	6.4	79.6	6.73	18.6	3.876
YD 510	5/13/2008		7.25	58.8	24.4	33.9	11.17	7.6	10.75
	8/23/2008	145	8.56	128.8	6.4	65.6	8.38	19.1	4.556
YD 550	5/13/2008		7.60	71.9	32.4	53.2	11.44	7.2	7.882
	8/22/2008	143	8.35	138.2	8.1	73.6	9.41	18.1	2.592
YDP 1	5/19/2008		6.39	42.0	16.2	25.6	9.05	10.8	12.38
	8/22/2008	157	7.46	91.4	4.7	52.4	7.31	18.1	5.099
YDP 2	5/19/2008		6.37	41.3	18.3	12.2	9.74	12.1	12.82
	8/22/2008	169	7.61	88.9	4.3	52.0	8.58	18.6	5.454