Journal of Great Lakes Research 37 (2011) 521–527

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

The influence of land use and potamodromous fish on ecosystem function in Lake Superior tributaries

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ARTICLE INFO

Article history:
Received 12 October 2010
Accepted 22 April 2011
Available online 17 June 2011

Communicated by Michael Sierszen

Index words:
Nutrients
Ecosystem function
Streams
Fish migrations
Land use

ABSTRACT

Allochthonous nutrients and carbon are recognized as dominant controls on biogeochemistry of low-order streams. In some systems, potamodromous fish may provide a complementary source of material as they deliver lake-derived materials to spawning streams. This study examines nutrient and carbon inputs from terrestrial ecosystems and migratory fishes to streams in undeveloped watersheds in northern Michigan, USA. We compared watershed and riparian area, slope, and landcover to nutrient concentrations at 26 sites, as well as whole-stream metabolism at 5 sites. Despite low levels of agricultural land use (0–3%), agriculture had the largest influence on stream chemistry as indicated by higher dissolved organic carbon (DOC), ammonium, silica, and chloride concentrations at the watershed level, and increased DOC and chloride at the riparian level. Ecosystem respiration and net primary production increased with watershed and riparian area, and the proportion of managed forest. To quantify inputs from fish, we monitored the spawning migrations of white (*Catostomus commersonii*) and longnose (*C. catostomus)* suckers at one site, and measured nutrients and stream metabolism above and below an impassable dam. Nutrient concentrations were uniformly low and did not increase during the fish migration; however, temporal shifts in stream metabolism during sucker migration suggest that fish influenced respiration, presumably by providing high-quality carbon and bioavailable nutrients. We conclude that both watershed land use and fish migrations provide important sources of allochthonous material to these oligotrophic streams. Recognizing the bi-directional nature of allochthonous inputs is important for understanding controls on ecosystem functioning in low-order streams.

Introduction

Allochthonous sources of carbon and nutrients are essential for the functioning of low-order streams (Allan and Castillo, 2007). Riparian vegetation of small streams often shades the channel, reducing primary productivity while contributing detritus to fuel secondary production (Vannote et al., 1980). Spawning migratory fish also deposit allochthonous carbon and nutrients in streams. Although the importance of allochthonous energy sources relative to local instream production likely varies with riverine setting, external subsidies often exceed local in-stream production.

Subsidies from the surrounding landscape are generally considered to be the dominant source of allochthonous materials in streams. Concentrations of dissolved organic carbon (DOC) in streams have been reported to be positively correlated with the proportion of the watershed as wetlands (Frost et al., 2006; Gergel et al., 1999; Johnston et al., 2008) and negatively correlated with extent of lakes (Frost et al., 2006; Larson et al., 2007). These nutrient inputs vary in both quality and quantity, which can affect many instream processes (e.g. Elwood et al., 1983; Young and Huryn, 1999). Disturbance to the landscape has been shown to affect stream processes and nutrients. For instance, nitrogen (Dodds and Oakes, 2006; Johnson et al., 1997; Sliva and Williams, 2001) and phosphorous (Hunsaker and Levine, 1995; Jones et al., 2001; Osborne and Wiley, 1988) concentrations in streams correlate closely with watershed-level land use. Houser et al. (2005) found declines in ecosystem respiration associated with catchment disturbance, and agriculture has been associated with elevated nutrients that correlate with elevated gross primary production and ecosystem respiration (Wilcock et al., 1998; Wiley et al., 1990; Young and Huryn, 1999). The influence of watershed subsidies can extend well downstream; Morrice et al. (2008, 2009) found that nutrient concentrations in Great Lakes coastal wetlands are influenced by upstream land use.

In addition to the well-established effects of land use on nutrient inputs, another source of subsidies to streams is spawning fish. The importance of marine-derived nutrients and carbon is particularly well-studied in oligotrophic streams of the Pacific Northwest which receive large runs of salmon that die following their spawning

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doi:10.1016/j.jglr.2011.05.014

migrations (e. g. Janetski et al., 2009). Marine-derived nutrient and carbon inputs delivered by these anadromous fish elevate concentrations of DOC and nutrients in Alaskan streams (Hood et al., 2007); these materials are generally more labile than those derived from the landscape (Hood et al., 2007). As a result, fish-derived subsidies may influence whole stream metabolism (Chaloner et al., 2004; Wipfli et al., 1999), yielding increased growth and abundance of stream macroinvertebrates (Chaloner et al., 2007; Wipfli et al., 2003). In the Great Lakes region, salmon spawning in tributaries of Lake Ontario have also been found to elevate DOC and nutrient concentration (Sarica et al., 2004).

The effects of nutrient subsidies on primary production are harder to predict and a number of studies show 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 a negative or no correlation between the number of spawning salmon and primary production in watersheds that have been impacted by timber harvest.

Much less is known about iteroparous fish that migrate from freshwater lakes to streams. Suckers (Catostomidae) are potamodromous fishes with the potential to influence stream ecosystems through their spring spawning migrations. Historically, suckers have run from the Great Lakes into its tributaries in huge numbers (longnose suckers: *Catostomus catostomus* and white suckers: *C. commersonii*); thousands of fish enter small streams while tens or hundreds of thousands arrive in larger tributaries. 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 (Klingler et al., 2003). Their eggs and fry are forage for many game fish and they have long supported economically and culturally important fisheries. However, in contrast to salmon, suckers spawn repeatedly throughout their life; relatively few carcasses are deposited as sources of nutrients.

This study examines how instream nutrient concentrations and ecosystem metabolism in oligotrophic streams of Michigan's Upper Peninsula vary with respect to land use and spawning migrations of potamodromous fishes. We quantified 1) which categories of watershed and riparian land use most influenced stream chemistry, 2) which aspects of watershed and riparian land use most influenced whole-stream metabolism, and 3) whether inputs of lake-derived material from sucker migrations affect stream nutrient concentrations and metabolism. By examining nutrient and carbon subsidies from both the surrounding landscape and migratory fishes, we sought to understand the relative importance of these alternative subsidy pathways in oligotrophic tributaries of the Great Lakes. Our monitoring of sucker migration also extends the study of subsidies from migratory fishes to include iteroparous native species.

Methods

Study sites

This study focused on streams located in northern Marquette County, Michigan, USA during April–August 2008 and 2009. Marquette County (8871 km²), located on the southern shore of Lake Superior, is sparsely populated (64,634 residents in 2010) with approximately 30% residing in Marquette, the largest city in the county, some 60 km from our sampling site on the Salmon Trout River. Despite a history of mining and logging in the county, most of the study area is currently forested.

Stream sites for land cover analysis were chosen based on reasonable accessibility by road, presence of cobble and riffle substrates, depths of 0.1–0.5 m, and the presence of downstream barriers to fish migrations to avoid confounding effects. In total, 26 sites on first- to fourth-order streams were selected for watershed analysis (Fig. 1). The fourth-order streams were the Salmon Trout River and the Yellow Dog River, which together drain most of the region. Five sites were within the Salmon Trout River watershed, 8 were within the Yellow Dog River watershed, and 13 sites were in smaller independent watersheds. Of the 26 watershed analysis sites, a representative subsample of 5 sites was selected for quantification of whole-stream metabolism. We also assessed the effects of fish migration by measuring chemistry and metabolism at two locations flanking an impassable dam. The upstream reach was also used for watershed analysis and was approximately 1 km above the dam which excluded migratory fishes; the downstream reach was approximately 4 km below the dam, where the stream could receive subsidies of lake-derived carbon and nutrients from spawning fishes. Though every attempt was made to choose analogous sites, the substrate downstream of the dam was dominated by sand rather than the cobble found upstream, and the river was deeper at the downstream site. More information on site selection and coordinates for all sites are available in Burtner (2009).

Land cover influence

We evaluated the influence of land cover on stream chemistry across all 26 sites. Watersheds were delineated using ArcGIS Version 9.3 and Arc Hydro Tools, Version 1.3 (Environmental Systems Research Institute, Inc., Redlands, CA) in conjunction with a digital elevation model of the region. Land use data were taken largely from the 1992 National Land Cover Dataset (NLCD). We analyzed only well-represented land-use classes from this region, including open water, agriculture, managed forest, and forest. Wetlands coverage was from the 1994 National Wetlands Inventory (NWI). NWI wetland classification was used instead of NLCD wetlands because Johnston et al. (2008) demonstrated that NWI-delineated wetlands more accurately predicted DOC concentrations. At the time of this study, there had been little land use change since the development of these land use maps and we qualitatively confirmed the accuracy of the dominant classes indicated for each site. To evaluate the influence of the riparian zone, we calculated land use percentages within a 10 m buffer around all upstream stream channels. Area and mean slope were also calculated for all watersheds and riparian zones.

Water samples were filtered (0.7 μm Whatman GF/F) and frozen until analysis for soluble reactive phosphorus (SRP; molybdate-ascorbic acid method), nitrate (NO_3; cadmium reduction method), ammonium (NH_4; phenol-hypochorite method), silica (Si; molybdate-oxalic acid-heteropoly blue method), chloride (Cl; ferric thiocynate method), and dissolved organic carbon (DOC; high temperature combustion method) according to methods detailed by Davis and Simmons (1979). Samples were collected once in June 2008. Additional samples for DOC were collected twice between April and August 2008 and twice between April and August 2009 and then averaged for each site.

Methods for measuring whole-stream metabolism were adapted from Marzolf et al. (1994), and were based on using diel oxygen changes to quantify ecosystem respiration (ER) and gross primary production (GPP). Oxygen fluxes were measured using the open-system, single-station method (Odum, 1956) using a logging sonde (YSI 6600, Yellow Springs, OH, USA) with a polarographic oxygen probe. The sonde was deployed for longer than 30 h at each site to estimate ER and GPP. The energy dissipation model (Tsivoglou and Neal, 1976) was used to correct ER and GPP to account for oxygen changes due to reaeration. The ratio of GPP to ER was also calculated (P:R).

Land use influences on stream chemistry were analyzed by computing Pearson correlation coefficients for each chemical compound with watershed and riparian area, mean slope, and percentages of land use. Land use percentages were arcsine-square-root-transformed.

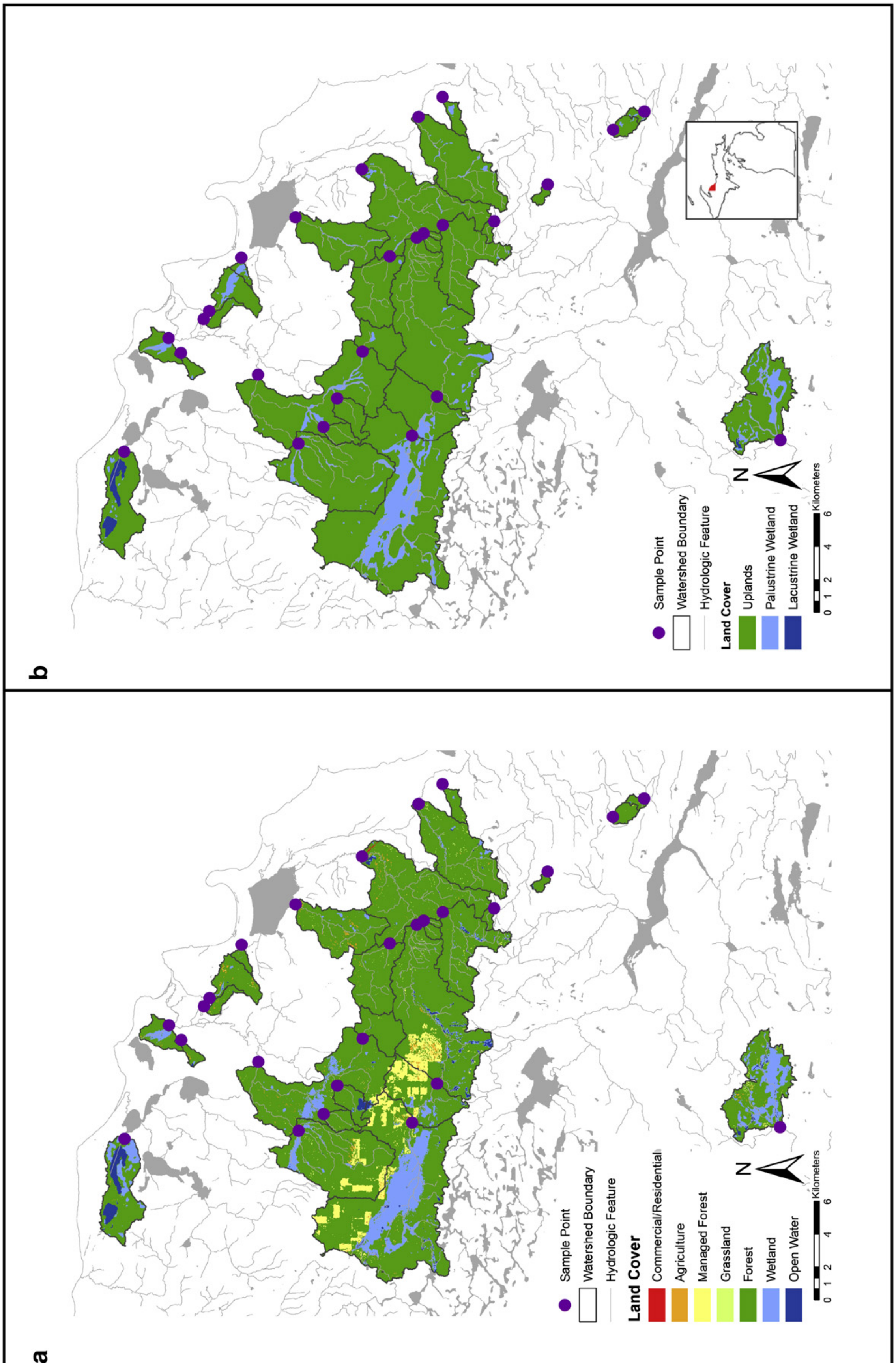

Fig. 1. Land cover from the National Land Cover Dataset (a) and the National Wetlands Inventory (b) for 26 sampling sites in northern Marquette County, Michigan, USA (inset) in 2008.

Managed forest was absent from half of the riparian zones and below 2% for all but one site and therefore was excluded from the riparian-scale analyses due to the low representation. We also calculated correlations between land use and stream metabolism parameters (GPP, ER, and P:R). The open water, managed forest, and agriculture classes were removed from the analysis of metabolism due to very low representation in the five focal watersheds.

Migratory fish influence

Fish migrations into the Salmon Trout River were monitored by placing back-to-back trap nets (5 cm mesh) in the lower reach immediately following spring snow melt in 2008 and 2009. This allowed separate censuses for all upstream and downstream migrating fishes. Fish were removed, measured, and released on the other side of the net daily. The full migration was captured in 2008 and a partial run was captured in 2009 due to adverse flow and weather conditions at the start of the run. The influence of the sucker migration on ecosystem functioning was assessed by comparing stream chemistry and metabolism above and below a barrier. SRP, NO_3, and NH_4 were measured daily at both upstream and downstream sites for 4 weeks during the sucker run (early-May through early-June) in 2008, and approximately weekly in 2009. Samples were analyzed as previously described, except that NH_4 in 2008 was quantified by fluorometry (Taylor et al., 2007). Paired *t*-tests were used to compare chemistry between the upstream and downstream sites.

To quantify fish effects on the stream ecosystem, whole-stream metabolism was measured upstream and downstream of the terminal dam at approximately weekly intervals during the 2009 sucker run. Metabolism was determined using the methods described earlier. Temporal patterns in GPP and ER were compared between upstream and downstream sites using general linear models. The influence of suckers was inferred from the interaction between time and site.

Results

Land cover influence

Total watershed area associated with the 26 sites ranged from 0.64 to 145.89 km^2 and riparian area ranged from 1587 to 1,433,095 m^2. Forest and wetland were the dominant land cover at both the watersheds and riparian spatial scales. Forest made up the majority of all watersheds (60–100%) and all but one riparian buffer (49–100%), while wetlands comprised up to 38% of watershed and 86% of riparian area. Managed forest was <11% of watershed area but was negligible in the riparian zone. Commercial and residential were a very small proportion of land cover with maximum watershed coverage of 0.17%

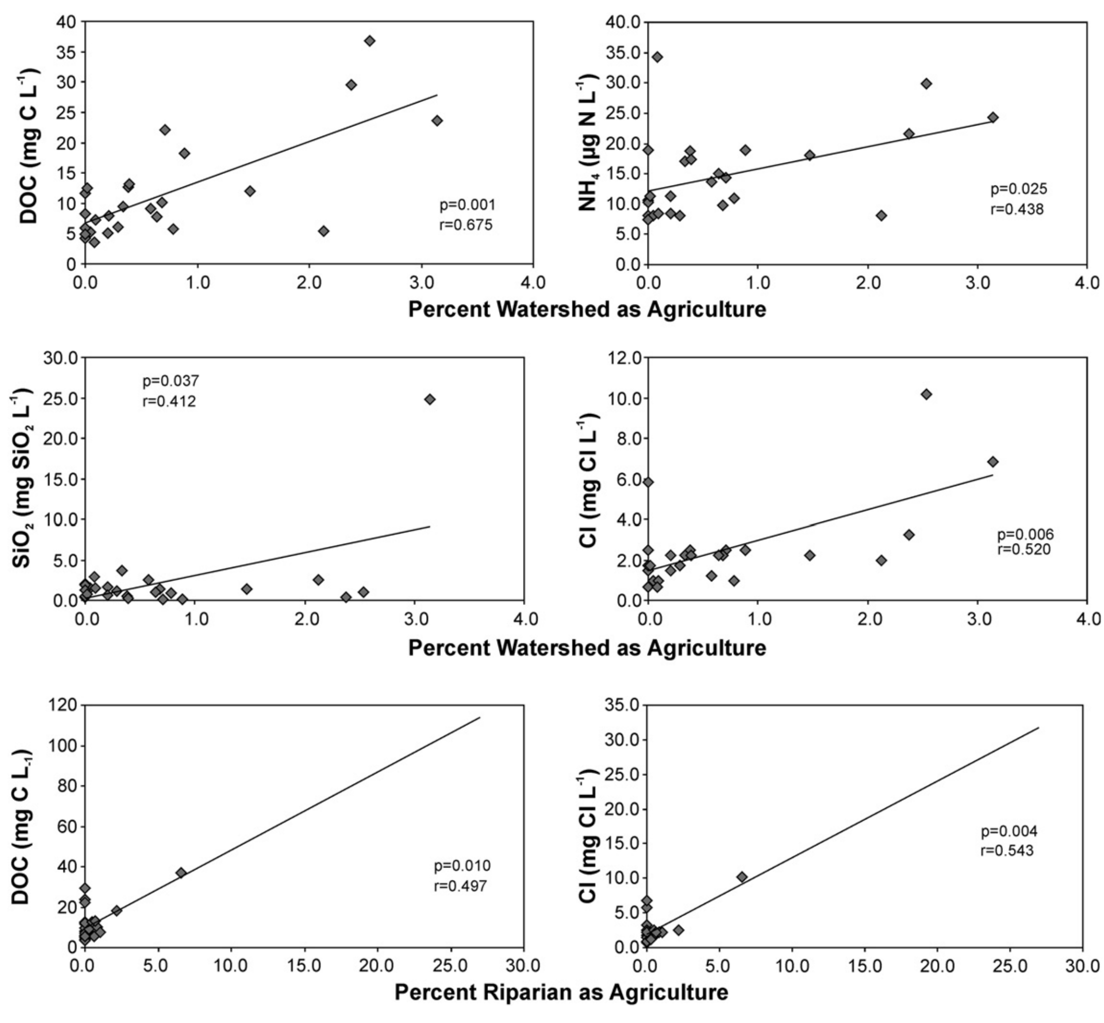

Fig. 2. The influence of agriculture on stream chemistry. Water quality data was collected at 26 streams in Marquette County, Michigan, USA in 2008. Pearson correlation coefficients (r) and significance (p) are shown from correlation analyses between water quality and land use parameters.

and maximum riparian coverage of 3.08%. Agriculture was also a small fraction of both the watershed (3%) and the riparian (6%) area.

At the watershed scale, agriculture was positively correlated with instream concentrations of DOC ($p<0.001$), NH_4 ($p=0.025$), Si ($p=0.037$), and Cl ($p=0.006$) (Fig. 2). Riparian-scale agriculture was also positively correlated with DOC ($p=0.010$) and Cl ($p=0.004$). The extent of riparian wetlands was correlated only with NO_3 ($p=0.006$), showing a negative association. Riparian forest was negatively correlated with DOC ($p=0.011$). Watershed and riparian area and slope were not correlated with any nutrients.

Metabolism of all 5 streams was dominated by ecosystem respiration; P/R ranged from 0.07 to 0.43. Both ecosystem respiration and primary production were significantly correlated with land cover. Ecosystem respiration and primary production were both strongly correlated with watershed area ($p=0.003$, $p=0.004$), the proportion of the watershed as managed forest ($p=0.021$, $p=0.026$), and with riparian area ($p=0.003$, $p=0.003$) respectively. Higher respiration rates and primary production were characteristic of larger watersheds having greater areas of managed forest in their riparian areas. The P/R ratio was not significantly related to watershed or riparian land cover.

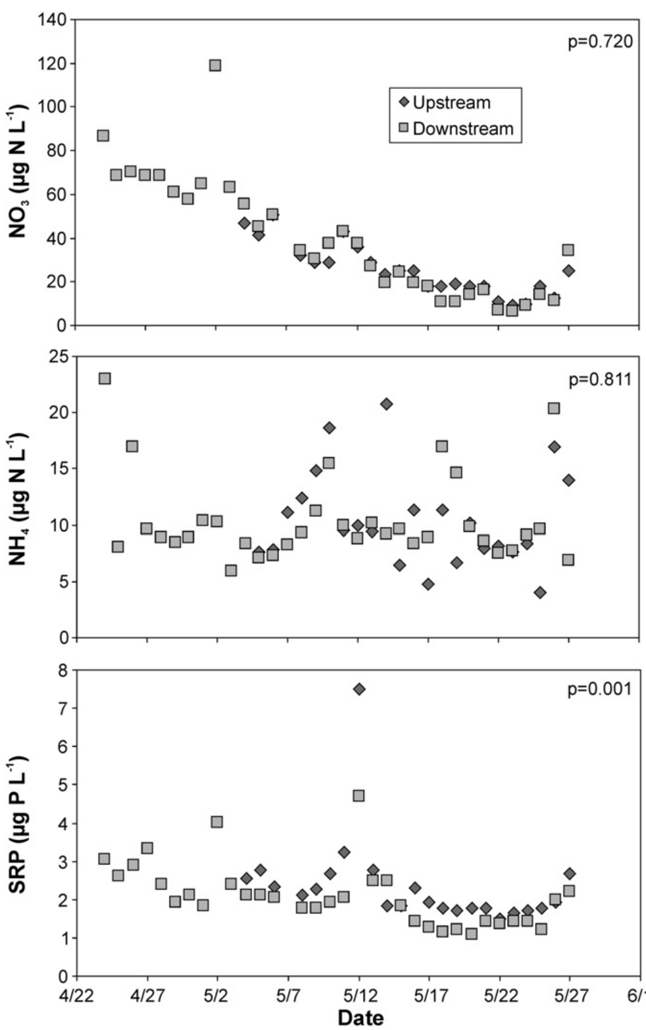

Fig. 3. Water chemistry during the 2008 sucker (*Catostomus spp.*) run in the Salmon Trout River, Marquette County, Michigan. Nitrate (NO3), ammonium (NH4), and soluble reactive phosphorous (SRP) are plotted upstream and downstream of a dam that serves as a barrier for sucker migration. Probability was estimated by paired *t*-test (n = 23).

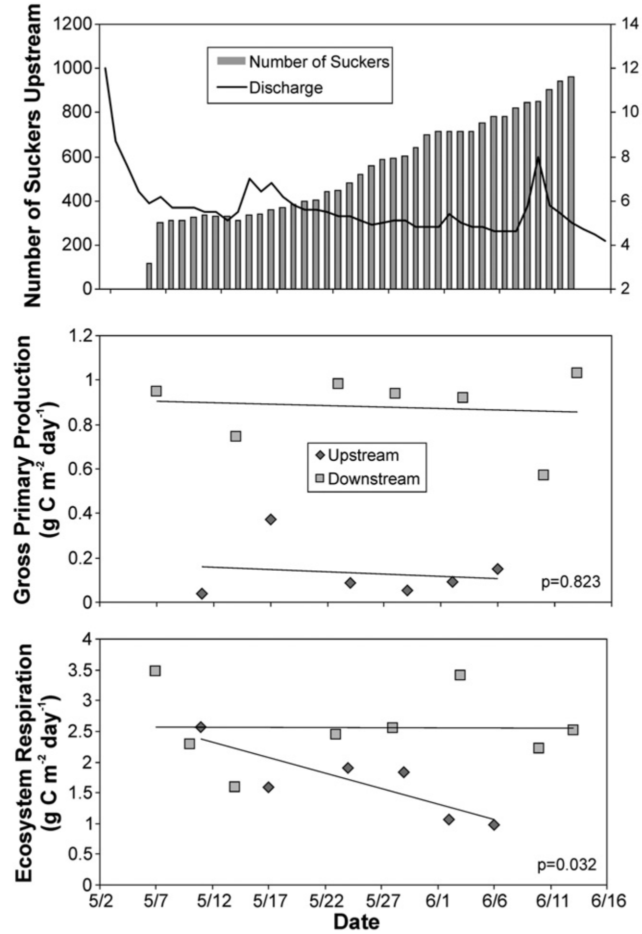

Fig. 4. Gross primary production and ecosystem respiration at two sites on the Salmon Trout River, MI, U.S.A. with the number of spawning suckers (*Catostomus spp.)* and discharge in 2009. Discharge data was downloaded from a USGS gaging station. Sites were located upstream and downstream of a dam that prevented fish passage. P values represent general linear models where the influence of suckers was tested using the interaction between time and site (n = 14).

Migratory fish influence

Sucker migrations differed between 2008 and 2009 in size, timing, and species composition. In 2008, 1447 longnose and white suckers were captured moving upstream, of which 89% were longnose suckers. This upstream run began April 30th and continued through May 15th. In 2009 a total of 1097 incoming suckers (40% were longnose), were collected from May 5th through June 12th.

Differences in nutrient concentrations and stream metabolism were detected upstream and downstream of the fish barrier during the sucker migration. In 2008 SRP was significantly greater at upstream locations ($p=0.001$; Fig. 3), counter to expectations based on fish-derived subsidies, and no differences were observed between upstream and downstream NO_3 ($p=0.720$) or NH_4 ($p=0.811$) concentrations. Similar trends were observed in 2009.

In 2009, gross primary production was quite stable above and below the dam during the sucker migration ($p=0.823$; Fig. 4). Despite the lack of temporal patterns at either location primary production was consistently about 0.6 g $O_2 m^{-2} d^{-1}$ higher at the downstream site (Fig. 4). However, over the course of the sucker migration, ecosystem respiration shifted disproportionately between the upstream and downstream reaches yielding a significant interaction between time and site ($p=0.032$; Fig. 4). Ecosystem respiration remained relatively constant in the downstream reach while the upstream reach experienced a continuous decrease in respiration over time.

Discussion

We assessed the carbon and nutrient inputs attributable to landscape variables and migrating fishes, thereby addressing the bi-directional input of nutrients from upstream terrestrial sources and downstream lacustrine sources. We found that dissolved nutrient concentrations were associated with land use, especially agriculture, and not with sucker-derived nutrients. In these heterotrophic ecosystems, both respiration and primary production were higher in larger watersheds with a greater proportion of managed forest. In addition, only ecosystem respiration was elevated by the presence of suckers. Thus, it appears that terrestrial land use exerts greater overall influence on stream chemistry and metabolism than sucker migrations in these oligotrophic tributaries of Lake Superior.

The transport of marine-derived nutrients into freshwater systems by spawning runs of anadromous fishes like salmon have been shown to substantially affect a number of ecosystem processes (Janetski et al., 2009). Introduced Pacific salmon, which now use many Great Lakes tributaries as spawning habitat, die after spawning and elevate total phosphorus, SRP, and periphyton biomass in some Lake Superior tributaries (Schuldt and Hershey, 1995). Though little studied, migrations of native suckers may play a seasonally-important role in stream dynamics in many Great Lakes tributaries where suckers constitute the majority of migratory fish biomass (Klingler et al., 2003).

Because suckers and most other potamodromous fishes are iteroparous, the nutrient subsidies provided are likely of lesser magnitude than those provided by their semelparous species such as salmon or lampreys (Flecker et al., 2010). Only two sucker carcasses were observed during the 2008 and 2009 sucker runs monitored for this study, indicating that the potential contribution of carcass decomposition is minor. Excretion and gamete release are more likely pathways by which sucker-derived nutrients could have influenced ecosystem respiration. The average female sucker deposits >10% of her biomass as eggs, yet only approximately 1% of eggs are exported to lakes as larvae (R. Papke, P.B. McIntyre, and J.D. Allan, unpublished data). The remaining eggs may provide an important food resource for invertebrates and fishes, thereby contributing to ER.

The temporal shift in ER observed only in the presence of migratory suckers was intriguing. Though the consistent pattern of higher GPP on sandy substrates downstream of the dam than on the rocky substrates above the dam was likely attributable to differences in substrate or other physical characteristics, this is unlikely to explain the fluctuations in ER. Instead, we tentatively interpret the lack of decline in ER in the downstream reach as an effect of sucker subsidies. At the time when respiration began to drop at the downstream reach, nutrient inputs from the watershed may also have been declining due to less runoff, as indicated by decreasing stream discharge (Fig. 4). However, labile nutrients or carbon from suckers could have elevated ER below the dam even as ecosystem respiration naturally dropped at the upstream reach throughout the study period. Though we did not observe enhanced nutrient or DOC concentrations during the fish migration, rapid microbial use of such high-quality subsidies could explain both the lack of concentration changes and observed enhancement of ER downstream of the dam. However, further work will be needed to confirm this interpretation.

Land use influenced stream ecosystem condition, as evidenced by elevated concentrations of dissolved organic carbon, ammonium, silica, and chloride where agricultural land use was present. Agriculture's effect on stream chemistry is well documented, from the mid-Atlantic (Jones et al., 2001), to Midwestern prairies (Hunsaker and Levine, 1995), to the Great Lakes (Johnson et al., 1997; Sliva and Williams, 2001). However, in all these studies, the agriculture present was both widespread and high-intensity. The extent of agriculture in this study was a modest maximum of 3.1% of watershed area and was limited to hay, market gardens, hobby farms, and a honey farm. Unlike many agricultural landscapes, the soils in this region are shallow, rocky, and poorly drained and unlikely to store, buffer, and absorb nutrients. These soils may provide a quick path for nutrient-rich runoff into streams. As a result, even small-scale, low-impact agriculture practices in this region appear to affect stream chemistry and ecosystem processes.

The relationship between watershed area and whole-stream metabolism is often complicated by the relationship between watershed area and stream order. The river continuum concept (Vannote et al., 1980) hypothesized that rivers are heterotrophic in the headwaters and become autotrophic as the river becomes larger. All of the streams in this study were heterotrophic, which was expected as they were all small and well-shaded. Though both gross primary production and ecosystem respiration were positively correlated with watershed and riparian area, P/R was not correlated as would have been expected. This suggests that the gradual shift from heterotrophy to autotrophy that occurs over the length of the river is likely non-linear across the narrow spectrum of streams that we studied.

This ecosystem-based project provides a foundation to understand how streams are influenced by bi-directional inputs from upstream terrestrial sources and fish migrations from downstream lakes. Dissolved nutrients responded to several allochthonous sources but not to sucker-derived nutrients. Ecosystem respiration and primary production responded similarly to watershed and riparian area and managed forest, yet only ecosystem respiration responded to the presence of suckers. In this mostly forested landscape both land use and sucker subsidies impacted stream chemistry and metabolism; however, the relationships may be complicated in systems that are under more anthropogenic stress. Understanding the linkages between allochthonous nutrient sources and stream chemistry and functioning will aid in predicting the consequences of anthropogenically-driven changes on low-order streams.

Acknowledgments

Funding for this study was provided by the Huron Mountain Wildlife Foundation. Supplemental support was provided by Wayne State University, The University of Michigan and the D. H. Smith Fellowship. We thank the Michigan Department of Natural Resources for the loan of the nets, the NOAA Great Lakes Environmental Research Laboratory for providing access to analytical equipment, and Dr. Kerry Woods and Wayne Thorpe for logistical arrangements at the Huron Mountain Club. Our gratitude also goes to Tom Johengen, Brian Roberts, Troy Zorn, Michelle Lelli, Bradley Sisson, Cory VonAchen, Jacqueline Fenner, Sander Robinson, Duane Gossiaux, and Vijayavel Kannappan for laboratory and field support.

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