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   - **How to use it**
     - Highlight a word or sentence.
     - Click on the Replace (Ins) icon in the Annotations section.
     - Type the replacement text into the blue box that appears.

2. **Strikethrough (Del) Tool** – for deleting text.

   - **How to use it**
     - Highlight a word or sentence.
     - Click on the Strikethrough (Del) icon in the Annotations section.

3. **Add note to text Tool** – for highlighting a section to be changed to bold or italic.

   - **How to use it**
     - Highlight the relevant section of text.
     - Click on the Add note to text icon in the Annotations section.
     - Type instruction on what should be changed regarding the text into the yellow box that appears.

4. **Add sticky note Tool** – for making notes at specific points in the text.

   - **How to use it**
     - Click on the Add sticky note icon in the Annotations section.
     - Click at the point in the proof where the comment should be inserted.
     - Type the comment into the yellow box that appears.
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   Inserts an icon linking to the attached file in the appropriate place in the text.

   **How to use it**
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   - Click on the proof to where you’d like the attached file to be linked.
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   - Select the colour and type of icon that will appear in the proof. Click OK.

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   **How to use it**
   - Click on one of the shapes in the Drawing Markups section.
   - Click on the proof at the relevant point and draw the selected shape with the cursor.
   - To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
   - Double click on the shape and type any text in the red box that appears.
Life history traits and spawning behavior modulate ecosystem-level effects of nutrient subsidies from fish migrations

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Abstract. Migratory animals can have profound impacts on ecosystem structure and function. In streams, salmon are well known for their contrasting influences on primary productivity through nutrient delivery, which enhances potential productivity, and substrate disturbance during nest building, which reduces algal biomass and primary production. However, most migratory fish species neither disturb the substrate significantly nor die en masse after spawning, hence their influence on ecosystems may differ from that observed in salmon streams. To determine the influence of nutrient subsidies from migrations of iteroparous fish whose broadcast spawning does not disturb the substrate substantially, we compared nutrient limitation, nutrient concentrations, and stream metabolism during spawning migrations of suckers (Catostomus spp.) in Lake Michigan tributaries with and without migration barriers. Although suckers deliver both nitrogen and phosphorus as eggs and waste excretion, only nitrogen concentrations were elevated during the migration (NH4-N rose 44% relative to sites without a sucker run). Nutrient diffusing substrates demonstrated P-limitation during the migration at sites spanning a wide range of sucker abundance, suggesting that high demand for likely masked P inputs from fish. Time series analyses indicated that gross primary production (GPP) increased with sucker excretion, but not with egg deposition after accounting for abiotic conditions. In contrast, egg deposition, but not excretion, was associated with a slight increase in ecosystem respiration (ER), suggesting that sucker gametes provide labile carbon that contributes to ER. The effects of suckers contrast with ecosystem responses to salmon migrations, which elevate ER but have mixed effects on GPP. This disparity reflects the fact that suckers fertilize streams without attendant disturbance effects. Our results suggest that basic differences in life history and behavior of migratory fish determine the direction and magnitude of their ecosystem effects. As a result, broad trait-based predictions of the ecosystem role of migratory fishes may become possible as more species are studied.

Key words: Catostomus catostomus; Catostomus commersonii; migration; nutrient subsidy; stream metabolism; trait-based.

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INTRODUCTION

Animal migrations can link disparate ecosystems by transferring materials and creating new food web interactions, resulting in large and lasting impacts on ecosystem dynamics and productivity (Bauer and Hoye 2014). The role that particular species play in material transport depends on behavioral and life history traits (Marczak et al. 2007, Flecker et al. 2010), suggesting that a
trait-based framework could be useful for predicting the ecosystem role of species. As migrations are threatened across the globe (Humphries and Winemiller 2009, Robinson et al. 2009), such a framework would provide a basis for inferring the ecosystem impacts of species losses.

Migratory fish deliver nutrients and energy that subsidize food webs in their spawning grounds (Varpe et al. 2005, Janetski et al. 2009). These materials can arrive in the form of carcasses, gametes, or waste products, and the balance among these different pathways depends strongly on a species’ life history strategy (Childress and McIntyre 2015). Species that die en masse after spawning (i.e., semelparous fishes) deposit many carcasses, whereas species that spawn multiple times (i.e., iteroparous fishes) do not. For instance, semelparous Pacific salmon are famous for contributing large quantities of nutrients to their spawning grounds via carcasses and waste excretion, which can enhance productivity (Janetski et al. 2009). There is also mounting evidence that iteroparous species can deliver substantial quantities of nutrients as gametes and waste during their migrations (Walters et al. 2009, Childress and McIntyre 2015), but their influence on ecosystem functioning remains uncertain.

Oviposition behavior is another aspect of life history variation that could mediate the effects of migratory fishes on recipient ecosystems. Most migratory fish species simply broadcast their gametes across the substrate with minimal disturbance, but Pacific salmon perturb large areas of the stream bed while building nests. The bioturbation created by salmon spawning has major impacts on stream biota and processes (Moore and Schindler 2008, Harding and Reynolds 2015).

Current understanding of how fish migrations affect ecosystem dynamics is largely based on Pacific salmon, whose semelparous life history can result in enormous nutrient additions even as their nest digging balances or even reverses net effects on primary productivity (Holtgrieve and Schindler 2011). Thus, the relative effects of disturbance and nutrient addition on gross primary production (GPP) depend on the substrate size, which governs susceptibility to disturbance (Freeman et al. 2003, Holtgrieve and Schindler 2011, Levi et al. 2013). In contrast to their context dependent effects on GPP, salmon consistently enhance ecosystem respiration (ER) by exposing or adding organic matter along with nutrients during spawning. GPP and ER are fundamental components of carbon cycling and serve as integrative metrics of the influence of fish migrations on stream ecosystems. The goal of this study was to quantify ecosystem responses to fish with different life history and oviposition behavior than salmon, thereby broadening the understanding of how fish traits affect the ecosystem-level influence of migratory species.

Suckers (Catostomidae) provide an ideal opportunity to test the applicability of findings from salmon to iteroparous species that do not disturb the substrate when spawning. Sucker species migrate to spawn annually in most streams across North America, and often reach high densities on their spawning grounds. They are broadcast spawners, spreading their adhesive eggs across the substrate with minimal digging (Walton 1980, Page and Johnston 1990). In Great Lakes tributaries, migrations range in size from hundreds to thousands of fish in small streams and up to a million in large rivers (Klingler et al. 2003, Burtnor et al. 2011, Childress et al. 2015). These migrations can deliver nutrients that enhance concentrations substantially above background levels (Childress and McIntyre 2015), leading to increased algal and invertebrate growth (Childress et al. 2014). However, the effects of suckers on whole-stream metabolism remain unknown.

Here we compare nutrient dynamics, algal nutrient limitation, and whole-stream metabolism among nearby streams that receive a wide range of sucker migration sizes. Our objective was to use nutrient limitation patterns to infer how nutrient subsidies are likely to affect GPP and interpret temporal patterns of GPP and ER rates in terms of input pathways of sucker-derived nutrients. By selecting streams with and without barriers to spawning migrations of iteroparous longnose suckers (Catostomus catostomus) and white suckers (Catostomus commersonii), we took advantage of existing spatial differences in order to focus on temporal dynamics of fish, nutrients, and metabolism. We hypothesized that sucker migrations enhance stream GPP but have no effect on ER, in contrast to ecosystem responses to salmon. Increased GPP during sucker migrations is expected because of fertilization in the absence of substrate disturbance. No change in ER is predicted due to the lack of both carcass
inputs and release of benthic organic matter by substrate disturbance, though nutrient inputs could enhance microbial capacity to metabolize the available organic material. To place our results in a broader context, we synthesize the effects of migratory fishes on stream metabolism with respect to differences in life history and orientation behavior, yielding a simple predictive framework that links fish traits with ecosystem responses.

**Methods**

**Site characteristics**

We studied fish migrations and ecosystem dynamics in Lake Michigan tributaries in Door County, Wisconsin. The study area contains a mix of coniferous and hardwood forest and agricultural land use. The study streams (Table 1) were all in low-gradient and second-order, featuring sand- and silt-dominated pools alternating with short cobble-bottomed riffles. Sampling occurred during spring conditions as temperatures were rising and discharge fluctuated as snow pack melted off (Fig. 1).

**Sucker migration dynamics**

To determine the timing and size of sucker migrations, we installed trap nets in two streams, Lily Bay Creek and Hibbard Creek, in 2012 and 2013. From 26 March to 20 May 2012, we deployed a single net facing upstream that spanned 80% of the stream, which we used to determine the timing but not the magnitude of the migration. Nets were checked daily and all fish were sexed, counted, and released to continue their migration. These nets captured both incoming and outgoing migrants, and all incoming migrants were marked with a dorsal fin clip to enable identification of recaptures. In 2013, two trap nets spanning the entire stream were installed from 16 April to 29 May to catch all incoming and outgoing migrants separately, providing robust data on the magnitude and timing of the migration. Incoming migrants were again marked. Field observations indicated that the first fish arrived roughly 2 d before nets were installed, and all out-migrating fish without a fin clip were assumed to have entered in equal numbers on those 2 d. Nets were deployed only in these two streams due to labor limitations; though population estimates are not available elsewhere, suckers were first observed in all other streams within 4 d of the first captures in the nets, and our later observations indicated similar duration of the migration season across sites.

**Nutrient subsidy**

Spring nutrient dynamics were assessed by repeatedly sampling across a large suite of sites with and without a sucker migration every 2 d (Table 2). All streams in the study area have sucker migrations in the spring, but three sampling sites were located above fish barriers (impassible road culverts) to serve as a reference for conditions without sucker migrations. In two of the reference sites, barriers were located <200 m from the stream mouth and the third was ~1 km upstream. Migrations of longnose

Table 1. Study stream attributes. Nutrient concentrations are means over the course of the study. Italics indicate streams with a lake upstream in the watershed.
Fig. 1. Seasonal dynamics of (a) migrating suckers, (b) temperature, (c) discharge, and (d) light in four study streams during the 2013 sampling period.

Table 2. Details of where/when measurements were taken during this study. X denotes sites/years in which measurements were taken.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Sucker migration</th>
<th>Nutrient dynamics 2012</th>
<th>Nutrient dynamics 2013</th>
<th>Nutrient limitation 2013</th>
<th>Metabolism 2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish Creek (downstream)</td>
<td>Present</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Fish Creek (reference)</td>
<td>Absent</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Fisher Creek</td>
<td>Absent</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Heins Creek (downstream)</td>
<td>Present</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Heins Creek (reference)</td>
<td>Absent</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Hibbard Creek</td>
<td>Measured</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Lily Bay Creek</td>
<td>Measured</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Reibolds Creek</td>
<td>Present</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Shivering Sands Creek</td>
<td>Present</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Whitefish Bay Creek</td>
<td>Present</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>
and white suckers ranged from <500 to >10,000 individuals among the sites. Sampling was conducted before, during, and after the sucker migration in 2013 (April 6 to June 5), but 2012 sampling was only during and after the migration (March 22 to May 23) because the migration was unusually early due to warm temperatures. Samples were collected at the same location in the thalweg of each stream on each sampling day and were filtered (Whatman GF/F 0.7 μm) in the field and analyzed for ammonium (NH₄-N) within 48 h of collection using fluorometry (Holmes et al. 1999, Taylor et al. 2007) or frozen for subsequent analysis of nitrate (NO₃-N) and soluble reactive phosphorus (SRP) by standard colorimetric methods (APHA 1998).

Changes in NH₄-N and SRP associated with the sucker migration were evaluated using linear mixed effect (LME) models. Sucker migration phenology was measured in just two streams as described above and was assumed to be identical in all streams for this analysis. To test for a sucker effect on NH₄-N and SRP, we considered suckers to be present throughout the period when >5% of the migrating population was present in both of the streams where fish were intensively monitored. LME models included sucker accessibility (i.e., whether a site received a sucker migration or not), sucker presence on a particular day (i.e., temporal variation within accessible streams), and their interaction as predictors. Presence was used to represent the time dynamic in this analysis because abundance estimates were not available for most of the streams. To account for the non-independence of measurements from the same stream and the 2-yr, each stream and the 2-yr were represented by a random intercept term. A significant interaction between accessibility and sucker presence was interpreted as an indication of divergence between reference and accessible streams when suckers were present. Nutrient data were In-transformed to meet the assumption of normality.

**Nutrient limitation**

For there to be a plausible mechanistic link between sucker-derived nutrients and GPP, nutrients must limit algal growth. Thus, we evaluated nutrient limitation of periphyton using nutrient diffusing substrates (NDS; Tank et al. 2007) deployed in all eight study streams for 20 d (16 April–May) in 2013 during the sucker run. In streams with migration barriers, experiments were conducted downstream in accessible reaches (Table 2). Plastic containers were filled with agar amended with nitrogen (0.5 M NH₄Cl), phosphorus (0.5 M KH₂PO₄), nitrogen and phosphorus (0.5 M NH₄Cl + 0.5 M KH₂PO₄), or no nutrients. A frilled glass disk separated the agar from the water column, and served as the algal growth substrate. Three randomized complete blocks of NDS were secured to each of two metal bars (n = 6 per treatment), which were placed ~2 m from each other on the stream bottom. After collection, disks were kept frozen in darkness until extraction of chlorophyll a in 90% pH-buffered ethanol (24 h, 20 °C). Extracts were analyzed by fluorometry, including an acidification step. NDS washed out in two streams, so results are available from six sites (Table 2). The effect of nutrient amendments on chlorophyll a accrual was evaluated using two-way factorial ANOVAs of the effects of N and P. We interpreted significant main effects as evidence of primary limitation and a significant N·P interaction in the presence of a single primary effect as evidence of secondary limitation (Tank et al. 2007).

**Whole-stream metabolism**

We measured whole-stream metabolism in reaches of four streams simultaneously from 6 April to 5 June 2013. Lily Bay Creek and Hibbard Creek received spawning migrations of ~10,000 suckers (mixture of longnose and white). Fish Creek and Fisher Creek had impassable barriers <300 m from their mouths, and we measured metabolism in the upstream reaches to serve as reference sites to document stream metabolism in the absence of suckers.

Water level was logged every 6 min in each stream using a HOBO® U20 (Onset Computer Corporation, Bourne, Massachusetts, USA) and converted to discharge using a power-function relationship established across a range of water levels (all R² > 0.97; Appendix S1). Discharge measurements at the logger and ~400 m upstream at two of the study reaches indicated loss of ~3% of the water within the reaches. Broad-spectrum light energy, which is highly correlated with photosynthetically active radiation (Long et al. 2012), was
recorded every 5 min at a representative location on the stream bottom of each site using a HOBO® UA-002 Pendant. All sites had trees in the riparian zone that reduced light penetration to the stream.

We estimated stream metabolism on a daily time step using a single-station open-channel method (Odum 1956) from diel fluctuations in dissolved oxygen (DO) concentration. Focal reaches were selected to maximize homogeneity of flow, substrate, and channel dimensions. Dissolved oxygen and temperature were recorded at 10 min intervals using HOBO® U26 (Onset Computer Corporation) loggers. Changes in DO concentration result from the production of oxygen through gross primary production (GPP), consumption through ecosystem respiration (ER), and exchange with the atmosphere. To estimate atmospheric exchange, the reaeration coefficient (K) was estimated using average daily water velocity, depth, and discharge (Raymond et al. 2012, equation 7). Gas exchange was then adjusted for stream temperature using Schmidt numbers (Wanninkhof 1992) and multiplied by mean depth to obtain gas transfer velocity. After accounting for gas exchange, respiration rate was estimated as the average rate of change in DO during the night, when GPP is negligible. GPP was then estimated as the difference between net daytime oxygen change and ER after accounting for atmospheric exchange. Metabolism estimates were checked using a Bayesian metabolism model that simultaneously fits parameters for gas exchange, primary production, and respiration (Holtgrieve et al. 2010), which yielded qualitatively similar results. Bayesian models did not converge on dates with low variability in oxygen concentrations due to lack of information; therefore, we present only the results from the Odum (1956) method.

To determine the influence of seasonal dynamics and the fish migration on stream metabolism, we fit separate time series models for GPP and ER in each stream. Models included known drivers of stream metabolism (temperature, discharge, temperature-discharge interaction, light (GPP model only); Mulholland et al. 2001, Demars et al. 2011, Roberts et al. 2011), a temporal autocorrelation parameter, sucker excretion of SRP, and sucker egg deposition. GPP was also included as a predictor in ER models because algal growth often provides labile carbon fueling microbial activity. Daily excretion of SRP by suckers was estimated using an individual-level model that accounts for temperature and body size (Childress and McIntyre 2015). SRP was selected rather than NH₄ because our NDS experiments indicated that P is most limiting for algal accrual, but excretion of SRP and NH₄ were strongly correlated ($R^2 = 0.89$, $P < 0.001$). Daily egg deposition was estimated using a body size-ovary mass relationship from our study system (Childress and McIntyre 2015) coupled with emigration date for each female. In contrast to the nutrient analysis, we used daily estimates of sucker inputs because stream-specific measurements were available for both sucker sites. Finally, to test for a spurious effect of suckers due to correlation with some unmeasured seasonal variation not included in the model, we included the average sucker excretion and egg deposition of the two sucker streams within predictive models of metabolism for reference streams. All predictors were z-score standardized prior to analyses.

All statistical analyses were conducted using R v3.2.1 (R Core Team 2015).

**Results**

*Nutrient subsidy*

The presence of suckers was associated with an average increase in NH₄ concentrations of 44% across streams and years, with median concentrations increasing from 11 to 18 μg-NH₄-N·L⁻¹, while reference sites remained at baseline concentrations throughout the season (Fig. 2). The LME model showed that the presence of suckers increased NH₄ significantly (interaction between treatment and sucker run: $t = 3.07$, $P = 0.002$; Appendix S2). There was an additional seasonal pattern at some sites; NH₄ concentrations during the first 2 weeks of sampling in 2013 were elevated in all four streams with a lake upstream (Table 1), but fell rapidly as ice melted off the lakes prior to the sucker migration. This pattern was not observed in 2012 because sampling began after ice-off. In contrast to NH₄, there was no apparent increase in SRP concentrations during the sucker migration (LME, interaction between treatment and sucker run: $t = -0.625$; Appendix S2). There was also no relationship between suckers and NO₃, which varied widely among
streams (50–2000 μg-NO₃-N L⁻¹) and closely tracked discharge during the spring melt with no evidence of sucker influence (LME, interaction of sucker presence and treatment: t = 0.39).

**Nutrient limitation**

Nutrient diffusing substrate experiments demonstrated a positive algal response to P additions in all streams (Fig. 3; see Appendix S3 for full ANOVA results). Additionally, algal accrual exhibited co-limitation by N and P in three streams. In another stream, algae exhibited additive, but separate positive effects of N and P.

**Whole-stream metabolism**

GPP and ER exhibited large seasonal swings in all four study streams. Both GPP and ER were elevated during the sucker migration (Fig. 4); however, these metabolic changes also coincided with changes in abiotic conditions (Fig. 1). In the time series models predicting GPP variation within a site, sucker excretion had a significant positive effect and egg deposition had no effect after accounting for important effects of temperature, discharge, and light (Table 3). In reference streams where suckers were absent, fitting the effect of sucker abundances elsewhere provided no evidence of a spurious correlation. In contrast to GPP patterns, ER did not respond to sucker excretion, but egg deposition was associated with a small but significant increase in ER (Table 3). Variability in ER within sites over the course of the season was strongly associated with changes in temperature, discharge, and GPP.

**Discussion**

Our results demonstrate that suckers can elevate nutrient concentrations leading to increased GPP during spawning. Additionally, sucker egg deposition was associated with a
Fig. 3. Chlorophyll a growth on nutrient diffusing substrata amended with no nutrients (C), nitrogen (N), phosphorus (P), or both N and P (NP). P-values from a 2-way ANOVA testing for the effects of N, P, and their interaction are listed below the corresponding stream; significant effects are bolded. Error bars represent ±1 SE. NDS were deployed in reaches with a sucker migration in all streams with the exception of Fisher Creek; see Table 1 for complete site and sucker migration details.

Fig. 4. Spring dynamics of (a) gross primary production and (b) ecosystem respiration in reference (black/gray lines) and sucker (colored lines) sites. Colors indicate sucker abundance; blue represents the absence of suckers, and increasingly yellow colors indicate high abundance. Statistical results are in Table 2.

slight increase in ER. These findings lengthen the chain of ecosystem changes that can be causally attributed to iteroparous migratory fish (Walters et al. 2009, Childress and McIntyre 2015). Importantly, our results contrast with evidence that salmon increase ER, but often diminish GPP during spawning (Holtgrieve and Schindler 2011, Levi et al. 2013). Suckers are
Table 3. Coefficients for time series models testing the effect of suckers on stream metabolism while accounting for abiotic conditions. Italicized streams received a sucker migration. Average sucker abundance from the sucker streams was included as a predictor in models for reference streams as a test for a spurious effect of suckers. The first order autoregressive term is called ar1. Positive coefficients indicate a positive relationship between GPP or ER and the predictor. Standard errors are in parentheses and bold indicates coefficients that are significantly different from zero (95% CI). Predictors were z-score standardized prior to analysis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Lily Bay Creek</th>
<th>Hibbard Creek</th>
<th>Fish Creek</th>
<th>Fisher Creek</th>
</tr>
</thead>
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<tr>
<td>Gross primary production</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ar1</td>
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<td>0.24 (0.13)</td>
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<td>0.05 (0.12)</td>
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<td>0.07 (0.03)</td>
<td>0.06 (0.04)</td>
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<td>Ecosystem respiration</td>
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<tr>
<td>ar1</td>
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<td>0.09 (0.13)</td>
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<td>0.89 (0.12)</td>
<td>0.91 (0.1)</td>
<td>0.92 (0.1)</td>
</tr>
</tbody>
</table>

widespread and often abundant in freshwaters across North America, indicating that the ecosystem influence of fish migrations is not limited to coastal rivers where diadromous salmon and eulachons spawn.

Nutrient diffusing substrates demonstrated that the addition of nutrients enhanced algal accrual at all sites, hence nutrient inputs from migrating suckers have the potential to increase algal growth (see also Childress et al. 2014). Suckers deliver large quantities of both N and P to their spawning grounds in the form of excretion and eggs; our previous work showed that suckers deposited >30% more P than was exported as SRP in the spring of 2013 in Lily Bay Creek (Childress and McIntyre 2015). Because the sucker nutrients were delivered during the time we assessed nutrient limitation, sucker nutrient additions may have eased P-limitation (Ruegg et al. 2011) but clearly did not eliminate it. The N:P ratio of sucker nutrient inputs is 13.4:1 (Childress and McIntyre 2015), quite close to the Redfield ratio, suggesting that sucker inputs are unlikely to tip the balance between N- and P-limitation substantially (Hillebrand and Sommer 1999). Data on nutrient limitation were only available for one site without a sucker migration, so no generalizations about nutrient limitation at sucker vs. non-sucker sites is possible. However, the reference site exhibited only P-limitation, similar to many sites with a sucker run, suggesting that P input is the most likely pathway for fish migrations to affect GPP in the study region. Our finding that sucker migrations increase nutrient availability is consistent with previous studies on suckers and other migratory fish. Although the list of studied taxa is still relatively short, anadromous species such as Pacific salmon (Janetski et al. 2009) and alewife (West et al. 2010), as well as entirely freshwater migrants such as suckers (Childress and McIntyre 2015), directly contribute nutrients to their spawning grounds. Importantly, our results demonstrate that suckers consistently increase nutrient availability across a range of migration sizes, showing that their effect is not limited to a few streams with exceptionally large migrations (Childress et al. 2014, Childress and McIntyre 2015).

High background nutrient levels can overwhelm fish inputs, obviating their effects (Marczak et al. 2007, Flecker et al. 2010). Across Great Lakes tributary streams, the strength of
nutrient limitation, and therefore the potential
link between suckers and ecosystem productivity,
is likely to increase from south to north because
agricultural inputs are more prevalent around
the southern lakes (Han et al. 2009). Our study
watersheds in northern Lake Michigan include a
mix of forest and agriculture, and background N
concentrations were as high as 2 mg NO₃-N L⁻¹.
Nonetheless, fish had a measureable effect on
NH₄. In contrast, background SRP was relatively
low, and did not exhibit a response to sucker mi-
gurations. The significant elevation of NH₄ but not
SRP during the migration, in spite of substantial
inputs of both N and P (Childress and McIntyre
2015), suggests a higher demand--supply ratio
for P than for N. Increased nutrient concentra-
tions at the stream mouth represent excess or
regenerated nutrients, thus P uptake by algae
and microbes apparently masked the presence of
fish-derived P inputs.

The delivery of limiting nutrients via excretion
appears to be responsible for the observed in-
crease in GPP during the sucker migration. The
effect of excretion, but not eggs on GPP is likely
due to excretion directly supplying nutrients in
usable form, whereas nutrients in eggs must be
mineralized before uptake by primary produc-
ers. The fish effect on GPP was overlaid on strong
algal responses to shifting abiotic conditions
during the spring (Figs. 1 and 3). Spring is a high-
ly productive and dynamic season in temperate
streams because temperatures are rising and ri-
parian vegetation does not yet shade the stream
(Roberts et al. 2011). Spring fish migrations,
which include many clupeids as well as suckers,
coincide with these conditions, increasing nutri-
ent availability at a time when other conditions
are primed to support algal growth. Thus, it is
impressive that GPP showed a significant re-
sponse to sucker excretion despite background
variability associated with seasonal changes in
light, temperature, and discharge.

In contrast to GPP, ER showed a small increase
associated with sucker egg deposition but not
excretion. Eggs may have increased ER through
provisioning of labile carbon to the microbial
community, in addition to providing limiting nu-
trients. Fish eggs are energy-rich and only 0–13%
of sucker eggs survive to become emigrating lar-
vae (Childress et al. 2015); most eggs decompose
or are preyed upon in the stream, contributing
to ER. Release of milt by males would also co-
incide with egg inputs, and could be a factor in
ER. The effect of sucker gametes on ER is likely
concentrated in spawning habitat, which may ex-
plain the difference in the observed effect in our
two study streams. More suckers were observed
spawning in the metabolism study reach in Lily
Bay Creek, which is a shorter stream and has
fewer spawning locations. Overall, the contribu-
tion of eggs was associated with a slight increase
in ER, but the influence of seasonal changes in
temperature and discharge was much larger.
Higher GPP was also associated with higher ER,
which may indicate an indirect link between
excretion of nutrients and ER mediated by new
algal production.

Our elucidation of a small increase in ER and
larger increase in GPP during sucker migrations
differs strongly from the increased ER, but variable
effects on GPP associated with salmon spawning
These discordant results are likely driven by dif-
fences in spawning behavior and biomass depo-
sition. Salmon create a major disturbance to their
spawning streams as they excavate nests (Moore
and Schindler 2008). In contrast, suckers are gen-
erally broadcast spawners (Page and Johnston
1990) that do not disturb substrates during spawn-
ing. The finding that salmon can increase GPP
when disturbance effects are minimized on large
rocky substrates (Levi et al. 2013) accords with the
hypothesis that differences in spawning behavior
between suckers and salmon contribute to dispar-
ities in ecosystem responses. Additionally, suck-
ers deposit materials primarily through excretion
and gametes (Childress and McIntyre 2015) while
salmon leave behind carcasses as well. Salmon
shed much of their energy and carbon before dy-
ning because no reserves are needed for the future
(Hood et al. 2007), whereas suckers and other iter-
oporous species must retain energy for emigration
and subsequent bouts of reproduction. Thus, al-
though suckers and salmon both deliver nutrients,
it appears that fertilization is the dominant effect
of sucker migrations, while disturbance during
salmon migrations typically depresses GPP and
elevates ER in conjunction with inputs of labile
carbon (Holtgrieve and Schindler 2011).

As the range of migratory fish species studied in
an ecosystem context grows, it is becoming clear
that environmental context is a major determinant
of the ecological influence of migratory fish. Ecosystem characteristics such as background nutrient concentrations, ecosystem size, light availability, and substrate size can predetermine whether an ecosystem will respond to a fish migration. For example, if nutrients do not limit primary production, then the addition of fish nutrients will not spur an increase in GPP (Marczak et al. 2007, Flecker et al. 2010). As an example of the influence of ecosystem size from this study, Lily Bay Creek and Hibbard Creek had similar size sucker migrations, but Hibbard Creek GPP responded only half as strongly, likely because it had twice the discharge to dilute inputs from suckers. With the stage set by the environmental context, fish life history and behavior can then mediate the overall ecosystem response to fish migrations.

Migratory fish life history and behavior determine both the magnitude of material inputs and the strength of disturbance associated with spawning. Thus, ecosystem responses to fish migrations represent a complex balance between boosting rates through nutrient and energy subsidies and constraining GPP while boosting ER through substrate disturbance (Fig. 5). The size of material contributions is influenced by parity, body size, reproductive investment, phenology, migration size, and larval mortality. For example, iteroparous species will have more modest per capita material contributions each year than semelparous species, even though their aggregate inputs via gametes or excretion can be substantial (Durbin et al. 1979, Walters et al. 2009, Childress and McIntyre 2015). Spawning behavior interacts with environmental conditions to determine the ecological outcome; broadcast spawning fish would be expected to have a constant effect on GPP over a gradient of substrate sizes, whereas the effect of nest building species can range from positive on large substrates to strongly negative on small substrates (Janetski et al. 2009, Ruegg et al. 2012, Bellmore et al. 2014). Some life histories inherently limit the influence of migratory fish on ecosystem processes. For example, amphidromous gobies both spawn and achieve most of their growth in streams, but have a brief oceanic larval stage (McDowall 2009). Because young are tiny when they enter marine waters and remain small when they return to streams, their movements between ecosystems result in minimal nutrient transfer.

Fig. 5. Conceptual figure depicting how variability in substrate disturbance and nutrient delivery alter the per capita influence of fish migrations on (a) gross primary production and (b) ecosystem respiration with examples of the role of particular species groups. Nutrient contributions depend on mortality rate, body size, fecundity, and excretion rates, and the effects of nutrient addition are dependent on nutrient limitation. Disturbance of the substrate is determined by the extent to which spawning is associated with bioturbation for nest building. Gobies refer to amphidromous gobies, which have an oceanic larval phase, but because they both grow and spawn in freshwaters, they do not contribute substantial nutrients.

Development of a trait-based, predictive understanding of ecosystem responses to fish migrations requires additional studies of a broader range of species with different combinations of
life history and behavioral attributes. Suckers provide an informative contrast to Pacific salmon in two key life history traits: parity and spawning behavior, building on insights from anadromous clupeids (Durbin et al. 1979, Walters et al. 2009) and sea lamprey (Nislow and Kynard 2009, Hogg et al. 2014). To further disentangle disturbance and life history effects, studies on species with other trait combinations are needed to populate the full trait-space, but our initial framework provides testable hypotheses. For example, steelhead rainbow trout are iteroparous but disturb the substrate like other Pacific salmon, so we would expect them to depress GPP and boost ER as they disturb substrates, but provide smaller nutrient contributions to fuel autotroph and heterotroph activity. This is just one example of how the diversity of migratory fishes provides fodder for trait-based predictions of ecosystem-level responses.

Our results from suckers spawning in Great Lakes tributaries reveal that stream productivity can be enhanced by iteroparous fish migrations even against a backdrop of agricultural N loading. Ultimately, life history and environmental context may often be linked because ecosystem characteristics such as the predictability and magnitude of disturbance influence life history evolution in fishes (Winemiller and Rose 1992). In the case of sucker migrations, we find that differences in background nutrients and discharge among streams can moderate ecosystem responses, but that an iteroparous life history does not prevent fish from affecting stream metabolism. To the contrary, the combination of excreting P and minimal substrate disturbance enable suckers to boost GPP while only weakly affecting ER. The ubiquity of iteroparous, migratory fishes in the world’s river systems suggests that important effects on ecosystem dynamics may be widespread and can perhaps be predicted through trait-based analyses for abundant species.

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