

Nutrient Subsidies from Iteroparous Fish Migrations Can Enhance Stream Productivity

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ABSTRACT

Migratory animals often transfer nutrients between ecosystems, enhancing productivity in the subsidized system. Most research on nutrient subsidies by migratory fishes has focused on Pacific salmon, whose semelparous life history is unusual among migratory fishes. To test whether iteroparous species can provide ecologically important nutrient inputs to stream ecosystems, we experimentally blocked the migration of suckers (*Catostomidae*) midway up an oligotrophic tributary of Lake Michigan. Comparing reaches upstream of the barrier to downstream reaches containing thousands of breeding fish, we found that suckers elevated phosphorus and nitrogen concentrations three- to five-fold. Algal accrual was doubled and caddisflies grew 12% larger in subsidized reaches relative to reference reaches. An enclosure experiment demonstrated that caddisflies with access to a fish carcass rapidly became enriched in ¹⁵N and ¹³C, and experimental carcass additions were rapidly colonized by high densities of caddisflies.

However, under natural conditions below the experimental barrier, caddisflies became enriched in ¹⁵N but not ¹³C, indicating that fish-derived nutrients entered the stream food web primarily through indirect pathways rather than direct consumption of carcasses or gametes. At pupation, an average of 18% of caddisfly tissue N below the barrier was sucker-derived. In comparison to our focal stream, a reference stream with few suckers showed no seasonal or longitudinal patterns in nutrients and stable isotopes. These results demonstrate that iteroparous fish migrations can spur productivity via nutrient subsidies, despite low mortality rates. Thus, concerns about negative ecosystem-level consequences of blocking migrations of semelparous fishes are also applicable to iteroparous species when migrations are large.

Key words: migratory fish; nutrient subsidy; *Catostomus*; stable isotope; *Limnephilus*; caddisflies; nitrogen; phosphorus.

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INTRODUCTION

The exchange of materials and nutrients across ecosystem boundaries is a ubiquitous phenomenon critical to the maintenance of community structure and ecosystem productivity (Polis and others 2004; Baxter and others 2005). Biota can play a key role in these transfers, and in some cases individual species can have a large influence on resource availability in the recipient ecosystem. The ecological

importance of biotic transfers is contingent on characteristics of both species and ecosystems (Marczak and others 2007).

Fish migrations can constitute a major source of cross-ecosystem nutrient subsidies, and the role of Pacific salmon (*Oncorhynchus* spp.) in delivering marine-derived nutrients to stream ecosystems has been a longstanding focus of ecological research (Juday and others 1932). There is a large body of literature documenting salmon-delivering nutrients (Naiman and others 2002; Tiegs and others 2011), which are incorporated by algae (Verspoor and others 2010), macroinvertebrates (Bilby and others 1996), fish (Reichert and others 2008), and terrestrial consumers (Hilderbrand and others 1999). In contrast to the enrichment effects, salmon also disturb the stream benthos during spawning, which can decrease algal and macroinvertebrate standing stocks (Moore and Schindler 2008) and gross primary production (Holtgrieve and Schindler 2011). The disturbance associated with salmon spawning often outweighs the enrichment effect of marine-derived nutrients (Verspoor and others 2010; Levi and others 2013), and the net effect depends strongly on the environmental context of the recipient ecosystem (Holtgrieve and others 2010; Ruegg and others 2012).

Pacific salmon offer a fascinating model for assessing nutrient subsidies from fishes; however, their semelparous life history is unusual among the world's migratory fish species (Flecker and others 2010). There have been few strong tests of whether nutrients delivered by iteroparous species are large enough to be ecologically important. Broadly speaking, nutrients delivered by migrating fish can enter the stream food web via three pathways: excretion by live fish, gametes deposited during reproduction, and carcasses of deceased breeders. Salmon carcasses have long been viewed as the primary pathway for nutrient inputs (Juday and others 1932). However, eggs have also been highlighted as an important pathway (Bilby and others 1998; Moore and others 2008), and there is increasing evidence for the importance of excretion by live fish in generating nutrient subsidies (Tiegs and others 2011). Thus, even in fishes that do not die en masse, there is still potential for nutrient subsidies. For instance, anadromous alewives transfer marine-derived nitrogen (N) and phosphorus (P) to inland lakes (West and others 2010) and streams (Durbin and others 1979; Browder and Garman 1994; Walters and others 2009).

Dams, culverts, and other anthropogenic barriers have severely restricted the migration routes available to fishes (Liermann and others 2012;

Januchowski-Hartley and others 2013). As a result, they have altered the distributions of migratory species with large ecological consequences (Freeman and others 2003). Discussion of these impacts often focuses on coastal areas with anadromous species, but there are many more migratory fish species that complete their life cycle entirely within freshwater (Flecker and others 2010). The vast majority of these migratory species are iteroparous, hence determining the ecological role of iteroparous fish migrations can inform barrier management decisions across a broad range of ecosystems.

In this study, we evaluate the potential for iteroparous suckers (Catostomidae) to provide nutrient subsidies during their annual breeding migrations. Suckers have five characteristics that make them an interesting group for the study of nutrient subsidies. First, most sucker species are iteroparous; in our study region, breeders range in age from 3 to 14+ years. Second, they are potamodromous, meaning that their migrations occur entirely within freshwater. Third, at least one migratory species of this family is found in most rivers and lakes across North America, thus results may be relevant to many continental freshwaters. Fourth, spring migrations of suckers often involve huge numbers of individuals moving into streams and rivers; 10^2 – 10^4 migrants spawn in small tributaries of the Great Lakes, whereas 10^5 – 10^6 breed in large rivers (for example, Klingler and others 2003). The sheer number of breeders may enable suckers to influence ecosystem processes even if per capita effects are low. Finally, suckers are broadcast spawners, thus migrations are not likely to have a disturbance effect that offsets the effects of nutrient enrichment.

To assess the ecosystem-level influence of suckers, we experimentally blocked the upstream movement of suckers in two oligotrophic streams; one had a large sucker migration, whereas the other had few suckers and served as a reference site. We measured the dynamics of nutrient concentrations, algal growth, and insect growth throughout the course of the migration. We used stable isotopes, which have often been used to demonstrate nutrient subsidies from anadromous fish (Naiman and others 2002; Walters and others 2009), to trace whether shifts in nutrient availability were derived from suckers. We also conducted ancillary experiments to quantify the rate of isotopic change in consumers feeding directly on a fish carcass and to assess use of carcasses by insects in the field. This combination of field experiments and isotopic tracers yields a strong test of the

potential importance of iteroparous, potamodromous migrants to stream ecosystems.

METHODS

We monitored the dynamics of the sucker migration and ecosystem responses in Wilsey Bay Creek (45.7035N, 86.9335W, hereafter Wilsey) and Martin Creek (45.7906N, 86.8099W, hereafter Martin), second-order tributaries to Lake Michigan in Michigan's Upper Peninsula, in April–June 2009. Mean discharge for the study period was 0.46 m³/s for Wilsey and 0.24 m³/s for Martin, mean wetted channel widths were 3.6 and 4.6 m, and mean depths were 0.35 and 0.16 m, respectively. The riparian area of both streams is dominated by grasses, alders, and cedars. The substrate of both streams is dominated by sand alternating with shorter reaches of cobbles and bedrock. In the region, peak flows generally occur in spring after snowmelt with lows in late fall. Background concentrations of dissolved inorganic nitrogen (DIN) were 8.0 µg-N/l in Wilsey and 9.2 µg-N/l in Martin, and background soluble reactive phosphorus (SRP) concentrations were 0.8 and 1.4 µg-P/l, respectively. Background concentrations were also low in Wilsey in 2008 (9.2 µg-N/l and 1.9 µg-P/l). Approximately 10,000 white and longnose suckers (*Catostomus commersonii* and *C. catostomus*) migrated into Wilsey in 2009, comprising around 10,500 kg of sucker biomass. Fewer than 500 suckers migrated into Martin, so data from that site serve as a reference point for interpreting longitudinal gradients and temporal dynamics observed in Wilsey.

Suckers are iteroparous, broadcast spawners and do not feed during their approximately 2 week spawning migration. Larvae emigrate from the stream soon after absorbing the yolk (Walton 1980), and thus do not export stream nutrients. Concurrent migrations of *Esox lucius*, *Ameiurus melas*, *Amia calva*, *Lota lota*, and *Oncorhynchus mykiss* collectively amounted to less than 5% of sucker biomass during the study (P.B. McIntyre and J.D. Allan, unpublished data). The time course of the migration in Wilsey was documented by catching incoming and outgoing fish using paired trap nets spanning the width of the stream with separate entries facing upstream and downstream. Fish were counted daily and released on the other side of the nets. Our frequent observations in Martin indicated synchrony with the Wilsey migration, but we estimated migration size using visual observations along the length of the stream rather than netting fish because the stream mouth is relatively inaccessible and our previous observations indicated a small migration.

Sucker Exclusion Experiment

To create stream reaches without migratory suckers, we installed mesh barriers (plastic fencing with 2 × 2 cm openings) 2.3 km (Wilsey) and 1.1 km (Martin) upstream of the stream mouths soon after the migration began. Although roughly 100 suckers were observed above the barriers in Wilsey, our manipulation created a large contrast in the potential subsidy from the thousands of suckers observed below the barrier compared to a modest number upstream. A beaver dam acted as a natural barrier roughly 1 km upstream of the experimental barrier in Wilsey; hence suckers were excluded from approximately 31% of the available spawning habitat. The mean fish densities created by our barrier (~0.95/m²) were similar to those observed in 2008 (~0.92/m²) when the beaver dam alone blocked the stream. To measure the effects of the barrier, we established six sampling reaches (30 m long, >200 m between) in each stream; two were upstream of the barrier, and four were downstream. Each reach was sampled weekly from the beginning to end of the sucker run (seven sampling dates).

To assess fish effects on nutrient availability, water samples were collected weekly for analysis of dissolved nutrient concentrations. Samples were filtered (Whatman GF/F, 0.7 µm), then refrigerated for quantification of ammonium (NH₄) within 48 h by fluorometry (Taylor and others 2007) or frozen for later colorimetric analysis of SRP and nitrate (NO₃). Discharge fell by an order of magnitude during the study, but differed by less than 2% between upper and lower reaches in each stream. Because falling discharge could dramatically alter the effect of a given level of subsidy on nutrient concentrations, we converted measured concentrations into nutrient discharge fluxes using daily discharge estimates from stream gauges at the bottom of each stream. Nonetheless, temporal and spatial patterns of nutrient dynamics were qualitatively and statistically similar between nutrient discharge and concentration metrics.

To evaluate the influence of suckers on algal growth, ceramic tiles (4.8 × 4.8 cm) were placed in each sampling reach in Wilsey and Martin; five were collected weekly, and ten were collected on the final date. Tiles were kept frozen in darkness until extraction of chlorophyll *a* in 90% buffered ethanol (24 h, 20°C). Extracts were analyzed by fluorometry, including an acidification step. Chlorophyll data were natural-logarithm transformed. At each site, HOBO pendants[®] (<http://www.onsetcomp.com>) were used to record temperature

every 10 min and relative light availability (based on broad-spectrum luminosity) every minute on two cloudless days. Average temperature and light were calculated for each site to evaluate their influence on algal growth.

To determine fish effects on macroinvertebrate growth in Wilsey, weekly samples were taken from submerged grasses along stream banks at three locations in each reach using a D-frame dipnet for a standardized time (30 s) and bank length (1 m). Specific locations were sampled only once to minimize depletion effects. Taxa were identified following Merritt and others (2008). Our analyses focus on a sand-cased caddisfly *Limnephilus* sp., which was the most abundant taxon throughout the study period. Examination of gut contents revealed mostly detritus with some algae. We measured head capsule width (HCW) using digital photographs (40 \times) and ImageJ 1.42 software (CV = 0.004, n = 10 duplicates), and converted HCW to dry mass using an established relationship for the genus: Dry Mass (mg) = $0.821 \times \text{HCW (mm)}^{4.065}$ (Johansson and Nilsson 1992). A total of 2,212 individuals were measured with a mean of 63 individuals per reach on each date. Insect growth was not evaluated in Martin.

Two additional sets of six *Limnephilus* were collected from each reach on each date for stable isotope analysis. Gastrointestinal tracts and cases were removed, and all six individuals were combined into a single sample. Samples were oven-dried (60°C, 48 h), homogenized, and subsampled (1.2 mg) into tin capsules for analysis of stable isotope ratios of carbon (C) and N at the Cornell University Stable Isotope Laboratory. Results were expressed using standard $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ notation (Fry 2006), and trout tissue standards throughout the sample runs showed high precision ($\delta^{15}\text{N}$: SD = 0.11‰, n = 25; $\delta^{13}\text{C}$: SD = 0.04‰, n = 25). The first stable isotope data were collected after suckers had been in the stream for approximately 2 weeks. The presence of sucker carcasses near insect sampling sites at three date-reach combinations in Wilsey, including two upstream reaches, was associated with enriched outliers that were excluded from analyses. One other sample was also excluded because its $\delta^{13}\text{C}$ was greater than 2 SD lower than any other sample. In Martin, *Limnephilus* were not collected in five reach-date combinations due to scarcity.

Linear mixed models (LMM) were used to test effects of location (upstream or downstream of the barrier), date, and their interaction on nutrients, algal accumulation, caddisfly size, and stable isotope ratios using reach as a random effect. A

significant interaction between location and date indicates that reaches above and below the barrier behaved differently over the course of the migration. If this interaction was significant, planned contrasts between locations on each date were carried out. The LMM approach was chosen to account for site-specific differences that were not related to the sucker migration, to account for repeated measurements at individual sites, and to ensure that the model was robust to missing data.

The first *Limnephilus* pupae were observed in Wilsey on 14 May, and mean mass subsequently decreased at all reaches; data from after 14 May were excluded from the LMM. Linear regression was used to evaluate relationships between insect size and $\delta^{15}\text{N}$. To link nutrient inputs to algal growth, which is N-limited based on nutrient-diffusing substrate assays (P.B. McIntyre, unpublished), we used multiple linear regression with light, temperature, NH_4 , and NO_3 concentrations as predictors. Two-source, one-isotope linear mixing models with error terms (Phillips and Gregg 2001) were used to calculate proportion of N derived from suckers. Isotope ratios at each site on the first sampling date were used as baselines, and the isotope ratio of sucker tissues plus a fractionation rate of 3.4‰ (Post 2002) was used as the second end-member. The assumed fractionation rate is at the high end of the observed range (McCutchan and others 2003), thereby yielding a conservative estimate of the proportion of N derived from sucker inputs.

Isotope Assimilation Experiment

To calibrate interpretation of shifts in stable isotope ratios of *Limnephilus* exposed to the sucker migration, we conducted an isotope assimilation experiment in a separate stream. Little River (45.8432N, 86.8011W) lacked any fish migration but contained a similar invertebrate fauna to our focal sites. *Limnephilus* were placed in flow-through enclosures [47 \times 32 \times 30 cm plastic tubs with mesh (1 \times 1 mm) walls at the front and back] on the stream bottom. All enclosures were provided with a substrate of mixed sand, gravel, and cobbles from the streambed, and half of them received one fresh sucker carcass (n = 5) whereas the remainder did not (n = 5). Thirty *Limnephilus* from Little River were randomly assigned to each enclosure. Initial stable isotope ratios were determined from two sets of five individuals, and five individuals were collected from each enclosure after 5, 7, and 10 days. A flood on day 10 terminated the experiment. Samples were processed as described earlier.

Repeated measures ANOVA was used to test effects of carcass addition, time, and their interaction on *Limnephilus* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Carcass Addition Experiment

To evaluate whether *Limnephilus* directly utilize sucker carcasses, nine fresh white sucker carcasses were secured to the stream bottom in Wilsey. Carcasses were placed downstream of all sampling sites to avoid contamination. The number of *Limnephilus* visible on the carcasses was recorded daily for a period of 9 days. Prior to introducing the carcasses, six Surber samples were taken haphazardly from the same area to establish a *Limnephilus* density on the streambed.

All statistical analyses were conducted using R 2.15.1 (R Development Core Team 2012).

RESULTS

Nutrient Availability and Uptake

Concentrations of SRP and NH_4 were low on the first sampling date in both Wilsey and Martin. Downstream reaches in Wilsey had elevated NH_4 in the middle of the sucker migration, then returned to initial levels at the end, whereas upstream reaches in Wilsey and both upstream and downstream reaches in Martin changed little (Figure 1). In Wilsey, SRP showed the same pattern of elevated levels in downstream reaches mid-season, whereas upstream and downstream reaches in Martin did not diverge. Temporal variation in NO_3 was less clearly tied to the sucker migration but showed peaks in Wilsey on the first and penultimate sampling dates that were associated with rain events. Low NO_3 concentrations under base flow conditions early in the season did not increase downstream during the migration (Figure 1C). There was a significant interaction between time and location for SRP (LMM: $F_{6,24} = 5.15$, $P = 0.002$) and NH_4 (LMM: $F_{6,24} = 6.13$, $P < 0.001$) in Wilsey with peak differences on the first sampling date after the maximum abundance of suckers in the stream (Table 1). In contrast, there was no significant interaction for SRP ($F_{6,24} = 1.42$, $P = 0.25$) or NH_4 ($F_{6,24} = 1.62$, $P = 0.19$) in Martin. There was no significant interaction between location and time for NO_3 in Wilsey ($F_{6,24} = 1.03$, $P = 0.431$) or Martin ($F_{6,24} = 0.82$, $P = 0.57$).

Algae grew much faster in downstream reaches of Wilsey, whereas there was no clear pattern in Martin (Figure 2). On the final sampling date, downstream Wilsey reaches that were exposed to nutrients from migrating suckers had twice the

chlorophyll *a* (mean = $0.68 \mu\text{g}/\text{cm}^2$, SD = 0.08) observed in upstream reaches (mean = $0.34 \mu\text{g}/\text{cm}^2$, SD = 0.04). There was a significant interaction between location and time for Wilsey (LMM: $F_{5,20} = 5.42$, $P = 0.003$) but not Martin ($F_{5,20} = 1.26$, $P = 0.32$), with contrasts showing significantly higher chlorophyll *a* at downstream Wilsey reaches on the final three dates. Multiple regression predicting chlorophyll *a* from light, temperature, NO_3 , and NH_4 ($R^2 = 0.99$, $P = 0.016$) indicated significant positive relationships with NO_3 ($P = 0.023$) and NH_4 ($P = 0.036$) concentrations when accounting for the positive relationships with light ($P = 0.007$) and temperature ($P = 0.080$). Spatial correlation among predictors was high (R^2 range 0.27–0.86); N and light increased but temperature decreased with distance downstream.

Macroinvertebrate Growth and Nutrient Sources

Sucker muscle was substantially enriched in ^{15}N ($\delta^{15}\text{N}$ mean = 13.2‰ , SD = 0.2, $n = 3$) and ^{13}C ($\delta^{13}\text{C}$ mean = -20.9‰ , SD = 0.45, $n = 3$) relative to initial values for caddisflies (mean = 4.9‰ , SD = 0.57; mean = -36.5‰ , SD = 2.5). In Wilsey, $\delta^{15}\text{N}$ of *Limnephilus* in reaches exposed to the sucker run was higher than in upstream reaches throughout the study, with the greatest difference occurring mid-season (Figure 3; Table 1). In contrast, *Limnephilus* in Martin were slightly enriched in $\delta^{15}\text{N}$ in the upstream reach, with modest increases over time and similar rates of change in upstream and downstream reaches. There was a significant interaction between location and time for $\delta^{15}\text{N}$ in Wilsey (LMM: $F_{5,46} = 2.42$, $P = 0.050$), but not for Martin (LMM: $F_{5,34} = 0.25$, $P = 0.935$). At the onset of pupation, caddisflies in downstream reaches were composed of an average of 18 ± 3 (SE) percent sucker-derived N (Figure 3). A marginally significant interaction between location and time for *Limnephilus* mass suggests differential growth rates above and below the barrier in Wilsey (LMM: $F_{1,43} = 3.22$, $P = 0.080$). Final-instar *Limnephilus* larvae exposed to the sucker migration were 12% larger on average than those in upstream reaches (Figure 4). $\delta^{13}\text{C}$ values increased in all reaches of both streams during the sucker run (Figure 3), but there was no interaction between location and time in Wilsey ($P = 0.464$) or Martin ($P = 0.609$). Across all reach-date combinations in Wilsey, there was a significant positive correlation between *Limnephilus* $\delta^{15}\text{N}$ and 5th instar mass ($R^2 = 0.317$, $P = 0.002$, Figure 4B).

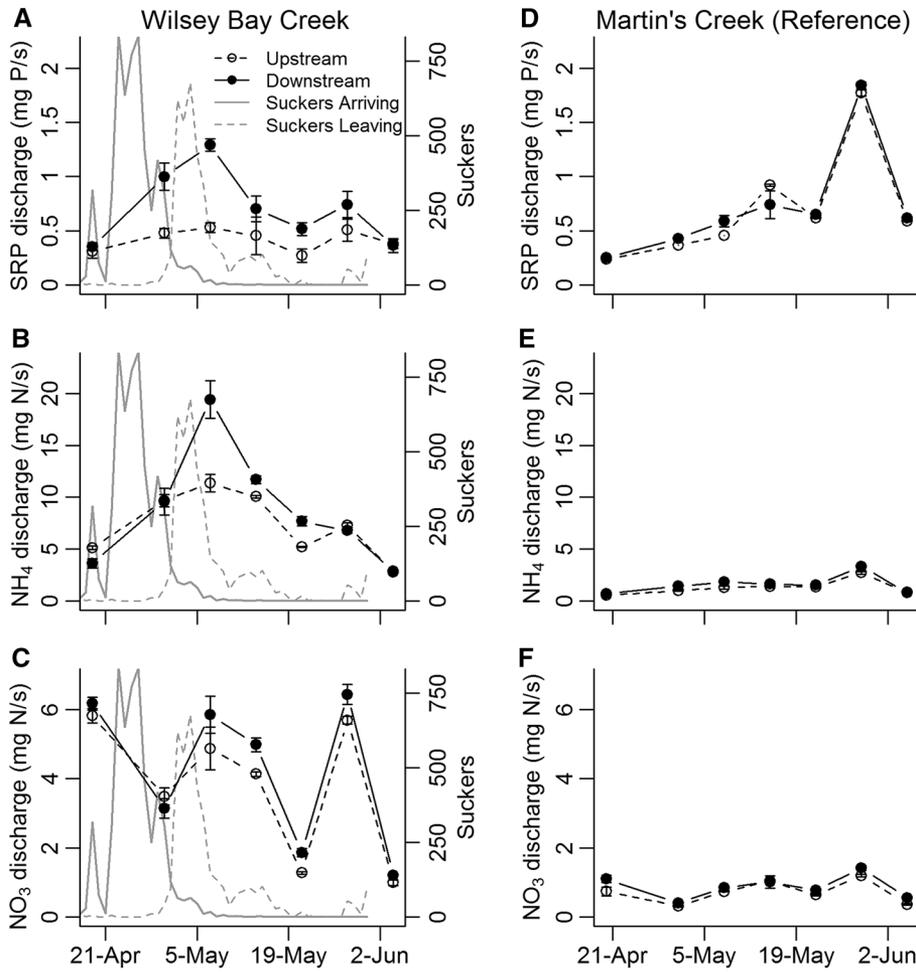


Figure 1. Comparison of discharge flux of SRP, NH₄, and NO₃ between upstream and downstream reaches during the sucker migration in A–C Wilsey and D–F Martin. Nutrients became elevated during the sucker migration at downstream reaches in Wilsey which had a large sucker run, whereas nutrients did not differ between upstream and downstream reaches in Martin, which had few suckers. Daily fish counts are represented as lines to reduce clutter. Bars represent one SE.

Table 1. Results of Post-hoc Comparisons for LMM with Significant Interaction Between Location and Date, Indicating a Sucker Effect

| | 18-Apr | 30-Apr | 7-May | 14-May | 21-May | 28-May | 4-Jun |
|---|--------|--------------|--------------|--------------|--------------|--------------|--------------|
| SRP | | | | | | | |
| $\mu_{down}-\mu_{up}$ | 0.04 | 0.52 | 0.76 | 0.25 | 0.25 | 0.24 | -0.01 |
| <i>P</i> -value | 0.789 | 0.023 | 0.006 | 0.159 | 0.164 | 0.179 | 0.923 |
| NH₄ | | | | | | | |
| $\mu_{down}-\mu_{up}$ | -1.5 | -0.12 | 8.05 | 1.64 | 2.49 | -0.5 | 0.1 |
| <i>P</i> -value | 0.334 | 0.932 | 0.004 | 0.296 | 0.142 | 0.732 | 0.948 |
| Chlorophyll <i>a</i> | | | | | | | |
| $\mu_{down}-\mu_{up}$ | NA | 0.03 | -0.1 | 0.15 | 0.26 | 0.3 | 0.34 |
| <i>P</i> -value | NA | 0.716 | 0.281 | 0.114 | 0.029 | 0.018 | 0.011 |
| <i>Limnephilus</i> $\delta^{15}N$ | | | | | | | |
| $\mu_{down}-\mu_{up}$ | NA | 0.53 | 0.87 | 1.52 | 0.7 | 0.45 | 0.55 |
| <i>P</i> -value | NA | 0.135 | 0.056 | 0.010 | 0.068 | 0.172 | 0.113 |

Values are differences in mean SRP and NH₄-N discharge, chlorophyll *a* concentration, and *Limnephilus* $\delta^{15}N$ and mass between reaches receiving a sucker migration (μ_{down}) and those without a migration (μ_{up}), and bold font indicates significance of contrasts between locations at the 0.05 level.

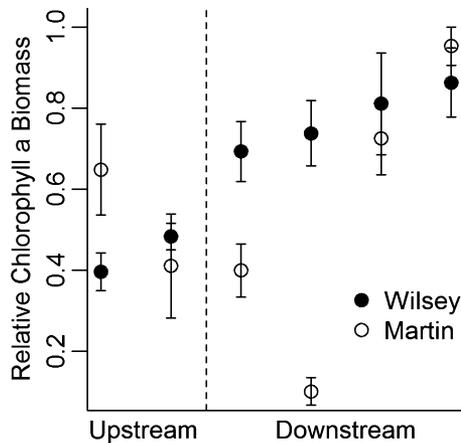


Figure 2. Algal biomass across sampling sites standardized using the maximum value per day per stream. The dotted line represents an experimental barrier which excluded suckers from upstream reaches. Error bars represent standard error among sampling dates at a given site. Downstream sites show elevated chlorophyll *a* biomass in Wilsey (large sucker migration), but there is no pattern in Martin (few suckers).

Isotope Assimilation Experiment

In the isotope assimilation experiment, *Limnephilus* with direct access to a sucker carcass rapidly became enriched in both ^{15}N and ^{13}C (Figure 5), and rmANOVA indicated significant interactions between treatment and time for both $\delta^{15}\text{N}$ ($F_{3,18} = 21.33$, $P < 0.001$) and $\delta^{13}\text{C}$ ($F_{3,18} = 28.65$, $P < 0.001$). Planned contrasts indicated no significant difference in *Limnephilus* $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ between treatments at the start of the experiment ($P > 0.46$), but caddisflies in the carcass treatment became enriched in ^{15}N and ^{13}C on all subsequent dates (all $P < 0.001$).

There was a tight positive relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for *Limnephilus* from the isotope assimilation experiment ($R^2 = 0.895$, $P < 0.001$). In contrast, *Limnephilus* collected from Wilsey during the sucker exclusion experiment showed a weak, marginally significant positive relationship ($R^2 = 0.052$, $P = 0.057$) and those from Martin showed a weak positive relationship ($R^2 = 0.242$, $P < 0.001$) between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Figure 6).

Carcass Addition Experiment

Experimentally placed sucker carcasses were colonized within 1 day (Figure 7), and mean density after one or more days was 933 individuals/m² (SD = 820) compared to a background density of 194 individuals/m² (SD = 50) on the streambed ($n = 6$ samples). The maximum density on a carcass reached 3,454 individuals/m².

DISCUSSION

Our experimental manipulations provide clear evidence that sucker migrations can transfer lake-derived nutrients into their breeding streams, benefiting multiple trophic levels. These results show that substantial contributions to stream food webs by migratory fishes are not limited to semelparous or anadromous species. Stable isotope data from *Limnephilus* in both the barrier and isotope assimilation experiments, combined with algal growth data, demonstrate that effects on production dynamics are linked across trophic levels; migrating fish provide limiting nutrients that are rapidly taken up by microbes and algae, then transferred to animals.

The temporal pattern of nutrient discharge fluxes strongly suggests that fish drove most of the observed nutrient dynamics. Although upstream and downstream reaches showed similar dissolved N and P levels at the beginning and end of our monitoring in Wilsey, both nutrients showed peaks only in the downstream reaches at the height of the migration. NH_4 and SRP concentrations increased three to fivefold in downstream sites when the suckers were present. In contrast, there was no difference between upstream and downstream reaches in Martin, where the sucker migration was an order of magnitude smaller. Shifts in N were driven by NH_4 rather than NO_3 , presumably because NH_4 is the primary N compound excreted by live fishes (McIntyre and Flecker 2010) and released from decomposing carcasses and eggs (Claeson and others 2006).

To place these sucker-driven nutrient pulses into a broader context, we can compare them to background nutrient yield and inputs from rainfall during the same season. Rainfall events are a major source of nutrients to tributaries throughout the Lake Michigan basin (Robertson 1997; Han and others 2009), and we collected water samples at the downstream site in Wilsey Bay Creek in 2008 (collected daily; two events) and 2009 (collected every second day; one event) from April to June. These rainfall events generated clear pulses of nutrients; however, in each year, the nutrients associated with the sucker migration based on our upstream–downstream comparison were 6 to 33 times (DIN) and 13 to 25 times (SRP) the magnitude of yield driven by rainfall.

In addition, the sucker nutrient pulses were 3.5 to 4 times (DIN) and 1 to 1.5 times (SRP) as large as upstream nutrient inputs summed over the sampling period. Thus, fish-derived nutrients represent a major source of limiting nutrients during the late

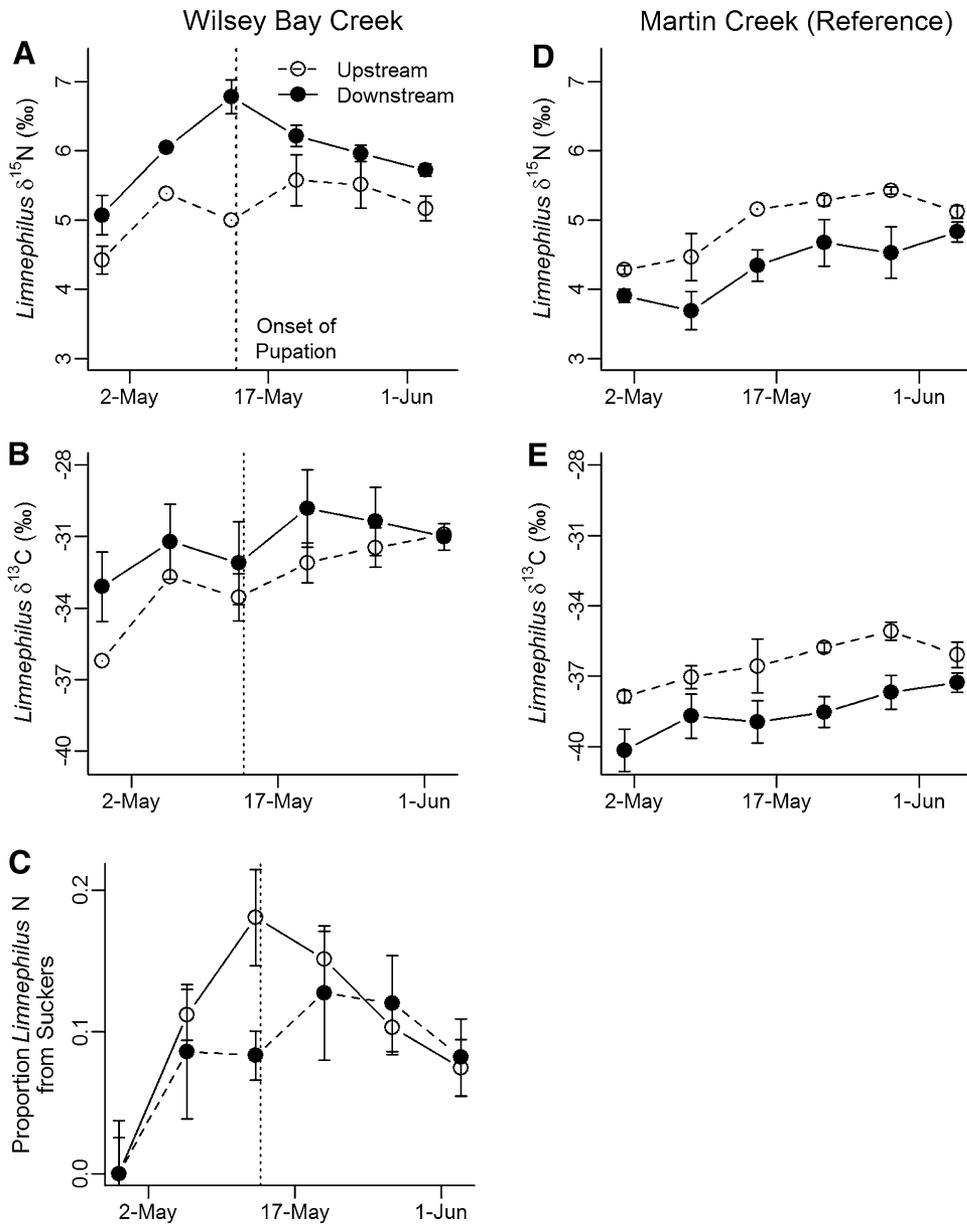


Figure 3. **A** $\delta^{15}\text{N}$ for *Limnephilus* caddisflies exposed to the sucker migration was enriched, with the largest difference occurring mid-migration. **B** $\delta^{13}\text{C}$ values remained relatively similar over the course of the migration. **C** The proportion of total *Limnephilus* N derived from suckers peaks at around 20%. The first sampling date was used as the baseline on a reach-by-reach basis; however, suckers had been in the stream for over 2 weeks, so estimates are conservative. **D–E** Upstream and downstream reaches showed similar dynamics for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in Martin, which had a small sucker migration.

spring compared to other external sources. Because suckers are iteroparous, only a small proportion of the nutrients from the sucker become available in the stream, mostly as eggs (~17% of female body mass; P.B. McIntyre and J.D. Allan, unpublished data) and excretion. Based on published whole fish nutrient contents of catostomids (McIntyre and Flecker 2010) combined with biomass estimates, the sucker nutrient pulses represent 3% of P and 11% of N contained in the suckers. Nonetheless, sucker nutrients dominated stream flux during the migration.

Algal biomass accumulated faster in downstream reaches in Wilsey, suggesting that primary producers utilized the nutrients from the migratory

fish. As expected based on nutrient-diffusing substrate experiments in both streams (P.B. McIntyre, unpublished data), algal growth was positively associated with NO_3 and NH_4 concentrations, and this held true even after accounting for higher light levels downstream. In addition, there was no longitudinal pattern associated with the barrier in Martin, suggesting that fish rather than inherent longitudinal gradients were responsible for upstream–downstream differences in Wilsey. Although algal accrual on tiles is not necessarily representative of the entire primary producer community, the low nutrient levels in these streams are likely to limit primary production more broadly.

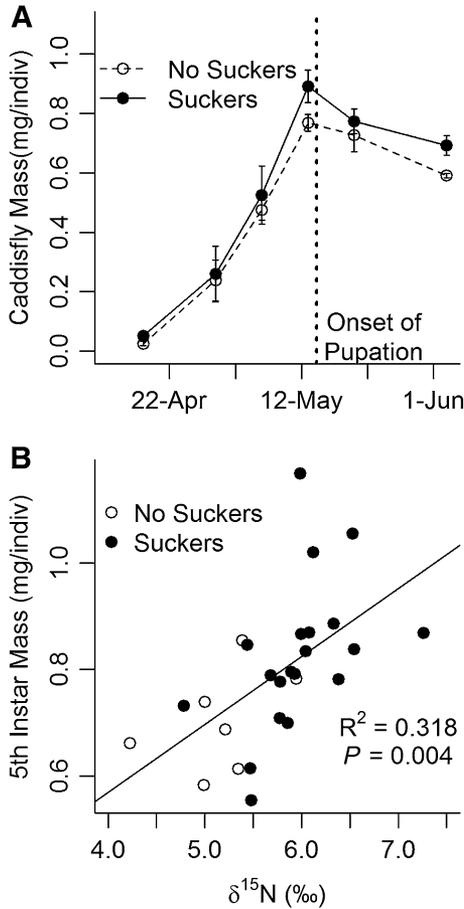


Figure 4. **A** Mean mass of *Limnephilus* during the sucker migration. Decreasing sizes after the onset of pupation is due to removal of the largest individuals from the population. *Error bars* represent one SE. **B** *Limnephilus* 5th instar mass was positively correlated with $\delta^{15}\text{N}$. Note that all data contribute to regression; *symbols* are for illustrative purposes only.

Our stable isotope data demonstrate unequivocally that nutrient subsidies from suckers were incorporated into the stream food web. Under both natural and enclosure conditions, *Limnephilus* caddisflies were able to rapidly acquire N derived from fish. Lack of comparable isotope patterns in *Limnephilus* from Martin Creek suggests that the patterns are not due to seasonal or longitudinal differences. In addition, our field observations show that when sucker carcasses are available, *Limnephilus* exploit them as a food resource. Experimental carcass additions were colonized rapidly; *Limnephilus* reached an average of four times background density after 24 h, and one carcass had 18 times background density. Moreover, natural carcasses were also rapidly colonized by *Asynarchus* and other Trichoptera, leptophlebiid mayflies, planorbid snails, isopods, and amphipods.

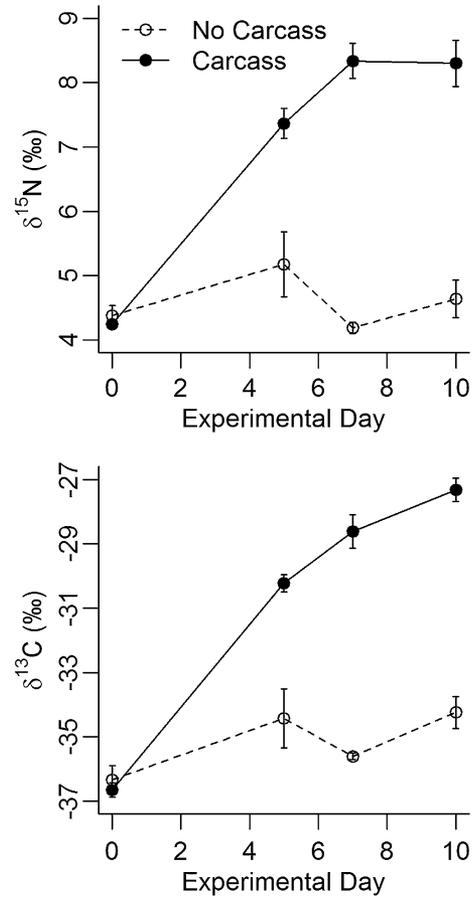


Figure 5. Changes in C and N stable isotope ratios for *Limnephilus* caddisflies in enclosures with or without a sucker carcass over time. Sucker tissue had a $\delta^{15}\text{N}$ value of 13.2 and $\delta^{13}\text{C}$ value of -20.9 . *Error bars* represent SE.

Thus, the full suite of primary consumers in spawning streams utilizes sucker carcasses when available, and preliminary analyses of snails, isopods, and mayflies show that all taxa become enriched in ^{15}N during the sucker migration. We suspect that our initial *Limnephilus* $\delta^{15}\text{N}$ data already reflect rapid assimilation of sucker-derived N—as observed in the enclosure experiment—such that our estimates of sucker N assimilation are conservative, because we used this first sampling date as the reference point for interpreting subsequent enrichment. Even so, it appears that 18% of the caddisfly N at metamorphosis was sucker-derived.

In contrast to N, *Limnephilus* $\delta^{13}\text{C}$ showed small, consistent increases in upstream and downstream reaches of both Wilsey and Martin. These parallel patterns suggest a seasonal or diet-based driver rather than caddisfly assimilation of sucker-derived C. Carbon fractionation by algae is decreased at low flows (Finlay and others 1999), so falling stream

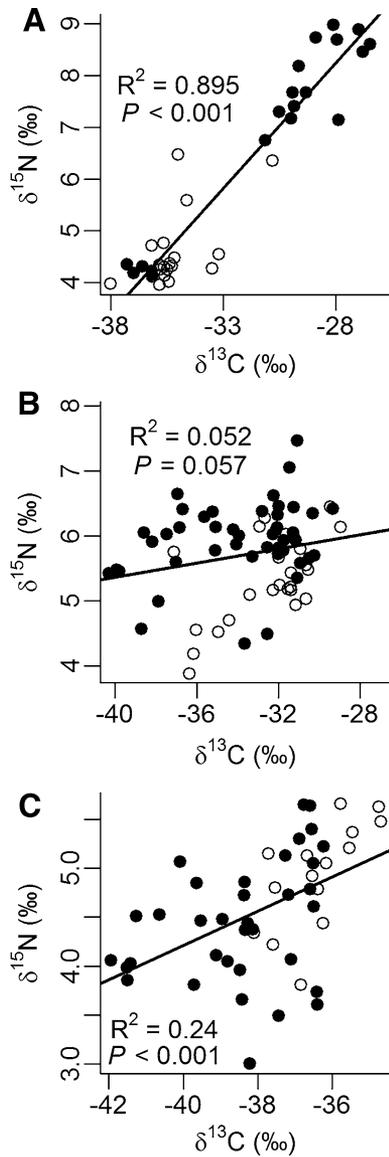


Figure 6. Relationship between C and N stable isotope ratios of *Limnephilus* caddisflies in experiments with (filled markers) and without (open markers) access to nutrients from migratory suckers. **A** In enclosures, there was a strong linear relationship between *Limnephilus* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values driven by access to a sucker carcass. **B** In Wilsey, *Limnephilus* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were weakly related, if at all. **C** In Martin, there was a weak relationship between *Limnephilus* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

discharge over the sampling period could have driven flow-based shifts in periphyton $\delta^{13}\text{C}$.

The disparate shifts in N and C isotopes in Wilsey contrast with the parallel shifts in our isotope assimilation experiment and seasonal changes in Martin, suggesting that indirect pathways are the dominant mode by which sucker-derived nutrients enter natural food webs. Though we observed

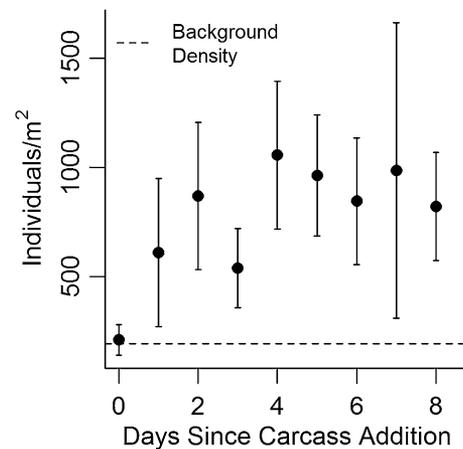


Figure 7. *Limnephilus* caddisfly colonization of carcasses secured to the stream bottom. Error bars represent SE.

Limnephilus and other invertebrates feeding on the few available sucker carcasses, the isotope assimilation experiment showed that direct consumption results in strong isotopic enrichment of both C and N. The small, parallel shifts in N and C isotope ratios in Martin suggest seasonal patterns. Free-ranging caddisflies below the barrier in Wilsey showed a decoupling of C and N, becoming differentially enriched only in N. Thus, we hypothesize that nutrients were taken up by algae and/or microbes prior to assimilation by caddisflies, and that direct feeding on carcasses plays a minor role in nature.

Increased growth rates and final size of *Limnephilus* below the barrier suggest that the sucker migration provides a substantial benefit to consumers. Although the statistical significance of growth differences was marginal, the ecological implications are important. We do not have adequate density estimates to calculate secondary production; however, increases in *Limnephilus* growth likely led to higher net insect production. Increased caddisfly growth could have at least two further implications. First, fecundity increases with female body size in insects (Honek 1993), so the observed increase in size in subsidized reaches is likely accompanied by higher fecundity. *Limnephilus* fecundity is also influenced by food quality (Jannot 2009), hence any direct feeding on sucker eggs or carcasses could provide a further boost compared to a diet of detritus and algae. Second, increased larval growth could enhance the biomass of stream insects contributing to riparian food webs. Although emerging insects transfer a very small proportion of the nutrients delivered by migratory salmon to terrestrial ecosystems (Francis and others 2006), export of stream insects is often an important source of energy and nutrients for

nearby terrestrial food webs (Nakano and Mura-kami 2001; Epanchin and others 2010). Thus, stream fertilization by suckers could have benefits that carry over into the riparian zone.

Interestingly, the onset of *Limnephilus* pupation coincided with observed decreases in mean *Limnephilus* larval mass across all reaches and decreases in $\delta^{15}\text{N}$ in reaches exposed to a sucker migration. Seasonal decreases in mass at emergence have been reported for numerous aquatic insect taxa (for example, Petersson 1989) and are explained by maximizing fecundity given individual growth state and reproductive or environmental time constraints (Rowe and Ludwig 1991). The coincident decreases in $\delta^{15}\text{N}$ and size suggest that large individuals with high $\delta^{15}\text{N}$ derived from greater access to sucker-derived subsidies are able to pupate first, which could arise from patchy distribution of the subsidy within the reach or individual variation in the capacity to utilize the subsidy.

Many of our results parallel the enrichment responses observed for anadromous fishes and contrast with reductions in algal and macroinvertebrate productivity driven by salmon disturbance. The increased nutrient availability echoes patterns observed in studies of Pacific salmon (Epanchin and others 2010) and clupeids (Durbin and others 1979; Browder and Garman 1994, but see Walters and others 2009). The observed increases in algal and macroinvertebrate growth are consistent with salmon studies that minimize disturbance effects (for example, carcass additions) (Janetski and others 2009). The evidence of similar nutrient enrichment from migrations of suckers and other fishes suggests that nutrient subsidies can arise from major migrations of both semelparous and iteroparous fishes, and hence subsidies may be more widespread than currently recognized.

Significant nutrient and energy subsidies should occur when migration biomass is large relative to stream size, background nutrient levels are low enough to limit ecosystem productivity, and effective transfer pathways exist (that is, the materials are accessible to resident biota) (Flecker and others 2010). Thus, the effect of sucker migrations on nutrient dynamics and stream productivity is likely governed by migration size and environmental context, as has been recognized for salmon (Tiegs and others 2012) and clupeids (Durbin and others 1979; Walters and others 2009). The low background nutrient levels and high sucker biomass relative to stream discharge in Wilsey make conditions ideal for fertilization by the sucker migration. In contrast, the comparatively small sucker

run in Martin was apparently insufficient to affect nutrient and algal dynamics. Determining critical thresholds of migrations size and ecosystem context represents an important area for future research.

Several aspects of sucker life history increase the probability of net nutrient and energy contributions to stream ecosystems. First, spawning adults do not feed during the migration, so they are unlikely to export nutrients when the fish leave the system. Second, suckers are broadcast spawners that do not disturb the substrate substantially during spawning (Walton 1980; Page and Johnston 1990). In contrast, by digging large redds, salmon reduce periphyton and macroinvertebrates while increasing export of seston (Moore and others 2004; Moore and Schindler 2008). Third, larvae migrate out of the stream shortly after absorbing their yolk (Walton 1980). Therefore, out-migration of sucker larvae does not represent an export of stream nutrients, but rather a simple return of imported nutrients back to the lake ecosystem. These characteristics of migratory suckers both minimize the likelihood of nutrient and C exports from streams and favor retention of inputs.

The logistical challenges of fish exclusions and permit constraints prevented us from replicating the barrier experiment in multiple streams with large sucker migrations. Despite the fact that our reach-scale observations in Wilsey were pseudoreplicates where reaches were non-randomly distributed with respect to the sucker migration, our results provide strong evidence that the sucker migration drove the observed patterns. Nutrient levels in Wilsey were similar upstream and downstream before and after the migration, but diverged sharply during the migration. Comparable temporal and longitudinal patterns of nutrients, stable isotopes, and algal growth were not observed in a reference stream with a small sucker migration (Martin). The observed ^{15}N enrichment of insects downstream of the barrier in Wilsey strongly suggests sucker-derived nutrients; $\delta^{15}\text{N}$ of aquatic invertebrates generally decreases during spring (Woodland and others 2012). Thus, we interpret the observed patterns of nutrients, algae, and insects downstream of the barrier in Wilsey as evidence of how large sucker migrations can affect small streams. Though the sucker migration into Wilsey is large relative to other nearby streams, it is by no means uniquely large. Much larger numbers of catostomids move through high-order tributaries but strive to reach smaller headwater streams before spawning (for example, Klingler and others 2003), such that the influence of their subsidies may be felt most strongly in low-order headwaters

that are comparable to small, direct tributaries like Wilsey.

Migrations of semelparous fishes have received considerable attention in the nutrient subsidy literature, and their ecological influence is remarkable. Our work on suckers in the Great Lakes shows that iteroparous, potamodromous species can also provide important nutrient subsidies to stream ecosystems. Given the widespread distribution of suckers and other iteroparous species, subsidies from migratory fishes are probably much more common than has been documented. Thus, we reiterate earlier calls to expand research on the range of taxa and ecosystems in which significant nutrient subsidies might occur (Flecker and others 2010). This type of research is particularly pressing because anthropogenic barriers like dams and road culverts have dramatically reduced access to migratory spawning grounds for fishes in the Great Lakes basin (Januchowski-Hartley and others 2013) and around the world (Liermann and others 2012; Pracheil and others 2013). At the same time that such barriers continue to be constructed in some regions (for example, Ziv and others 2012), barrier removals are on the rise in other regions (Stanley and Doyle 2003). The growing evidence that natural nutrient inputs from fish migrations enhance ecosystem productivity indicates that restoring ecological connectivity will benefit efforts to conserve both species and ecosystems and raises further concerns about the construction of new barriers whose impacts may extend well beyond fishes themselves.

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