Native Fish Migrations Deliver Nutrient

Subsidies to Great Lakes Tributaries

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ABSTRACT

Fish migrations can deliver materials and energy against stream currents and provide important

subsidies to stream ecosystems. There is an extensive literature on Pacific salmon, which are

semelparous, showing that marine-derived nutrients are incorporated into all stream and riparian

trophic levels where salmon migrations occur, and that these nutrients can spur productivity. In

contrast, there is little research on the role of iteroparous fishes. I investigated the effects of

iteroparous sucker (Catostomidae) migrations on nutrient dynamics, algal growth, and caddisfly

(Limnephilidae: *Limnephilus* spp.) growth in a small, oligotrophic Lake Michigan tributary, using

experimental barriers to establish reaches with and without a sucker migration. Soluble reactive

phosphorus and ammonium became elevated during the sucker migration at treatment reaches relative

to reference reaches while nitrate dynamics did not differ between treatments. Algal and caddisfly

growth were higher in reaches receiving a sucker migration. *Limnephilus* in enclosures with a sucker

carcass became rapidly enriched in δ^{15}N and δ^{13}C indicating assimilation of sucker materials. Stable

isotope data from the field suggest assimilation of sucker N but not C, but this result could not be

confirmed statistically due to gaps in the data. This study suggests that iteroparous fish migrations can

provide important nutrient subsidies to stream ecosystems. Suckers are restricted from much of their

historic spawning range by anthropogenic barriers; my results suggest that restoring connectivity in the

Great Lakes Region would restore this important process to a state more closely resembling natural

conditions.

ACKNOLEDGEMENTS

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INTRODUCTION

The movement of materials and nutrients across ecosystems is a ubiquitous phenomenon critical to the

maintenance of community structure and ecosystem productivity (Polis et al. 1997). Rivers generally

transport materials and nutrients in a single direction; however, fish can deliver nutrients and energy

against the current as they migrate upstream to spawn (Hall 1972), and there is increasing recognition of

the importance of external resource sources (Wipfli and Baxter 2010). The role of Pacific salmon

(*Oncorhynchus* spp.) in delivering marine-derived nutrients to stream ecosystems has received

substantial attention. Salmon-derived nutrients are incorporated into all stream trophic levels including

algae, macroinvertebrates, and fish (Hicks et al. 2005, Claeson et al. 2006). Studies have found that

Pacific salmon migrations increase primary production (Wipfli et al. 1998) and macroinvertebrate

growth, standing stock, and production (Wipfli et al. 1998, Chaloner and Wipfli 2002, Walter et al. 2006,

Lessard et al. 2009).

Marine-derived nutrients delivered by salmon also reach the terrestrial ecosystem. The assimilation of

marine-derived nitrogen by terrestrial vegetation is well documented (Ben-David et al. 1998, Bilby et al.

2003, Bartz and Naiman 2005, Wilkinson et al. 2005). Terrestrial insects, particularly Diptera, utilize fish

carcasses and incorporate marine-derived nitrogen (Hocking et al. 2009). Christie and Reimchen (2008)

showed that songbird densities in the riparian corridor were higher in reaches receiving salmon

migrations. Vertebrate scavengers and predators feed on salmon as they migrate upstream and after

they die (Hilderbrand et al. 1999). Thus, marine-derived nutrients delivered by migrating salmon are

incorporated into all trophic levels in streams and riparian zones and represent an important source of

energy and nutrients.

Nutrients delivered by migrating fish can enter the stream food web via excretion, gametes, and

carcasses. Many studies on Pacific salmon recognize the potential for these three pathways, but

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because Pacific salmon are semelparous, dying in the stream after spawning once, their primary influence is often attributed to the large biomass of carcasses within the stream channel.

In addition to fertilization effects, however, Pacific salmon excavate large redds while spawning that are a substantial disturbance and have been shown to decrease abundance, standing stock, richness, and diversity of macroinvertebrates (Moore et al. 2004, Lessard and Merritt 2006, Moore and Schindler 2008, Honea and Gara 2009, Lessard et al. 2009). There are disturbance and fertilization effects associated with salmon migrations, and it has been posited that environmental context will determine the predominance of one versus the other.

In contrast to the extensive research on the role of semelparous migrations in stream ecosystems, and despite the fact that a large majority of fish migrations are iteroparous (Flecker et al. In Press), little attention has been paid to whether iteroparous migrations provide material subsidies. Durbin (1979) calculated potential nutrient contributions from anadromous alewife migrations, and more recently, Walters et al. (2009) demonstrated incorporation of marine-derived nutrients at all trophic levels in a stream receiving a spawning alewife migration but found no change in nutrient concentrations or algal accumulation. I know of no other studies on the potential fertilization effects of iteroparous migrations; thus, there is a paucity of studies that have examined the influence of iteroparous migrations on nutrient levels, algal growth, and macroinvertebrate growth, in spite of the great potential for transfer of materials during these migrations.

Sucker (Catostomidae) migrations present an excellent opportunity to deepen our understanding of how migrations by iteroparous fishes influence stream ecosystems. Suckers represent an enormous, iteroparous migration out of the Great Lakes into streams to spawn, with 10^3-10^4 migrants entering small streams and 10^5-10^6 breeding in large rivers (Klingler et al. 2003). Suckers are widespread and migrate into a wide variety of streams to spawn. This enables studies on the influence of iteroparous

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migrations along gradients of migration size, stream size, and background nutrients. Also, there are

three key aspects of white sucker (*Catostomus commersonii*) and longnose sucker (*C. catostomus*) life

history that increase the probability of net nutrient and energy contributions: spawning adults do not

feed during the migration, they are broadcast spawners and so do not disturb the substrate substantially

during spawning (Walton 1980), and larvae migrate out of the stream immediately following emergence

with minimal feeding in their natal habitat (Walton 1980). These traits minimize the likelihood of

nutrient and material exports, increasing the potential magnitude of subsidies.

Fish migrations should influence stream ecosystems when fish biomass is high relative to stream size,

background nutrient and energy levels are low, and there is a mechanism for transfers from the

spawning migration to the stream food web (Flecker et al. In Press). The first two criteria are met for

many sucker migrations; however, it is less clear whether nutrients from the migrations can enter the

food web. Three pathways exist for the transfer of nutrients delivered by fish migrations: excretion,

gametes, and carcasses. For semelparous migrations, in which fish die after spawning once, carcasses

represent a huge contribution of materials (Gende et al. 2002). For iteroparous migrations, in which

most fish leave the spawning habitat after spawning and return in subsequent years, carcasses may still

represent an important source of nutrients because some fish die during the migration. However, it is

likely that the relative contributions of excretion and gametes are higher for iteroparous migrations than

for semelparous migrations. The magnitude of these sources and the efficiency with which they are

transferred to the stream food web should determine the degree to which sucker migrations will

influence stream ecosystems.

The role of iteroparous migrations is also important from a management perspective. In spite of a

growing literature on stream barriers, there is substantial uncertainty surrounding their effects on fish

assemblages (Harford and McLaughlin 2007). Perched culverts and low-head dams, in addition to larger

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dams, prevent the passage of suckers upstream (Klingler et al. 2003), potentially blocking an important nutrient delivery. Dams and road-stream crossings are ubiquitous throughout North America, and likely exclude suckers from much of their historic spawning habitat in the Lake Michigan basin. It is important that we understand the way that suckers interact with their spawning streams, so that we can recognize the implications of anthropogenic limitation of the spawning distribution of suckers.

The objectives of this study are to determine whether nutrients from a sucker migration are incorporated into the food web, and to examine how nutrient concentrations, algal growth, and insect growth respond to a sucker migration in a small, oligotrophic stream receiving a relatively large run of spawning white and longnose suckers.

METHODS

Wilsey Bay Creek (45.703483 N, 86.933509 W), a second order tributary to Lake Michigan in Michigan's Upper Peninsula, was the focus of this study. Data were collected between April 18, 2009 and June 6, 2009. Mean discharge for the study period was 0.46m^3/sec, mean wetted channel width was 3.6m, and mean depth was 0.35m. Approximately 7,500 white and longnose suckers (*Catostomus commersonii* and *C. catostomus*) migrated into the stream in 2009; there were much smaller migrations of *Esox lucius*, *Amia calva*, *Lota lota* and *Ameiurus melas*, representing less than 5% of the biomass present during the study (P.B. McIntyre and J.D. Allan, unpublished data).

Double mesh barriers were installed just after the initiation of the sucker migration to establish reaches with and without a sucker migration. A total of around 100 suckers were observed upstream of the barriers; however, thousands of suckers were observed below the barriers including many just downstream, so there was a dramatic dichotomy in exposure to the sucker migration between the reaches upstream and downstream of the barriers. Six sampling reaches 30m in length were established: two reference reaches upstream of the barrier and four treatment reaches downstream. All reaches were sampled on the same day weekly over six weeks.

Nutrient Dynamics

Water samples were collected weekly for dissolved nutrient concentrations. Samples were filtered (Whatman GF/F, 0.7 µm pore size), refrigerated, and analyzed within 48hrs for NH_4 concentrations using fluorometric methods (Taylor et al. 2007) or frozen for subsequent analysis of soluble reactive phosphorus (SRP) and NO_3 using standard colorimetric methods. Mixed models for SRP, NO_3, and NH_4 were run using time, treatment, and their interaction as factors. Slice analysis (SAS Institute Inc. 2008) was performed when the interaction effect was significant to test the effect of time on each treatment and the effect of treatment on each date.

Algal Accumulation

Ceramic tiles (4.8x4.8cm) were placed at each of the six sampling reaches on April 18, 2009. Ten tiles were collected from each reach on June 4, 2009. Tiles were kept frozen in darkness until extraction. Chlorophyll a was extracted for 24hrs with 90% buffered ethanol at room temperature and analyzed using fluorometry; samples were then acidified to correct for phaeopigements. A one-way ANOVA was used to test for differences between sites with a planned contrast between treatment and reference reaches.

Macroinvertebrate Growth and Assimilation of Lake-Derived Nutrients

Macroinvertebrate samples were collected weekly from submerged stream vegetation along 1m of stream bank using a D-frame dipnet for a standardized interval (30 seconds). No specific location was sampled twice over the course of the study. Samples were sorted at 5x magnification; *Limnephilus* were identified under a microscope following Merritt et al. (2008). Head capsule width (HCW) was measured using digital photographs at 40x magnification and ImageJ 1.42 software (CV=0.4%). HCW was converted 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). All individuals from two or three samples were measured per reach on each date; a total of 2,212 individuals were measured with a mean of 63 per reach on each date.

Two samples of 6 *Limnephilus* individuals each were selected haphazardly from reaches each week for stable isotope analysis. Gastrointestinal tracts and cases were removed, and all six individuals were combined into a single sample due to the small size of the organisms; samples were homogenized prior to analysis. Samples were frozen until they were oven dried (60°C, 48hrs). Carbon and nitrogen isotopic ratios were determined by mass spectrometer by Cornell University Stable Isotope Laboratory.

Assimilation Experiment

Limnephilus were placed in enclosures (47x32x30cm plastic tubs fitted with a 230cm^2 mesh opening at the upstream and downstream ends to allow for current) in Little River (45.8432 N, 86.8011 W), which was selected because it contained a similar invertebrate fauna to Wilsey Bay Creek including abundant *Limnephilus* but did not receive a sucker run in 2009. All boxes were filled with the sand, gravel, and cobble that occurred immediately beneath their location to a depth of at least 5cm. Five of the boxes received a sucker carcass to serve as a potential source of nutrition. *Limnephilus* individuals were assigned randomly to the boxes and two groups of five were retained to represent the baseline isotope ratios. Five individuals were collected on days 5, 7, and 10 of the experiment from each box for isotope analysis. A flood on day 10 terminated the experiment. Isotope samples were prepared and analyzed using the same methods as above. A repeated measures ANOVA was used to assess differences in *Limnephilus* isotope signatures between enclosures with and without a sucker carcass.

RESULTS

Nutrient Dynamics

SRP discharge became elevated at treatment sites in the middle of the sucker migration and returned to base levels at the end, while reference sites changed little over the course of the run. A mixed model comparing SRP discharge between treatments over time revealed significant effects of time ($P < 0.0001$), treatment ($P < 0.0001$), and the interaction between time and treatment ($P = 0.011$). Slice analysis revealed that time had a significant effect on treatment reaches ($P < 0.0001$) but no significant effect on reference reaches ($P = 0.643$). Additionally treatment had a significant effect only on the second and third sampling dates (Fig 1a, Table 1).

Similarly, NH_4 discharge was similar at treatment and reference reaches at the beginning of the season, diverged in the middle, and converged at the end of the season (Fig 1b, Table 1). A mixed model revealed significant time ($P < 0.001$), treatment ($P = 0.0089$), and interaction ($P = 0.0007$) effects. Slice analysis showed significant time effects for treatment ($P < 0.0001$) and reference ($P < 0.0001$) reaches and a significant treatment effect on the third sampling date ($P < 0.0001$).

Qualitatively, the pattern was similar for NO_3, although it was less pronounced (Fig 1c). However, the mixed model revealed a significant time ($P < 0.0001$) and treatment ($P = 0.0082$) effect but no significant interaction effect ($P = 0.4278$). Slice analysis was not performed for NO_3 since there was no significant interaction effect.

Algal Accumulation

A one-way ANOVA revealed a significant difference in chlorophyll a concentration among sites ($P < 0.001$) and a planned contrast between treatments showed significantly higher chlorophyll a concentrations at sites exposed to the sucker migration ($P < 0.001$, Fig 2).

Preliminary analysis revealed high correlations between chlorophyll a concentration on tiles and many stream variables (i.e., NO_3, NH_4, SRP, light, and temperature), preventing use of regression methods to resolve which candidate drivers best explained the spatial pattern. Instead, I made qualitative comparisons of univariate linear regressions of chlorophyll a against potential drivers (Fig 3). There were significant positive relationships between chlorophyll a accumulation and light, NO_3 discharge, and SRP discharge, a significant negative relationship between chlorophyll a and temperature, and no significant relationship between chlorophyll a and NH_4. Treatment reaches had higher nutrient discharge and light and lower temperature than reference reaches.

Macroinvertebrate Growth and Assimilation of Lake-Derived Nutrients

The first stable isotope data were collected after suckers had been in the stream for around two weeks. $\delta^{15}N$ for *Limnephilus* in reaches exposed to the sucker run were enriched over reference reaches throughout the season with the biggest difference occurring mid-season (Fig 4). $\delta^{13}C$ values increased at treatment and reference reaches and the relative difference did not change over the course of the sucker run (Fig 4). The presence of sucker carcasses at three date-site combinations, including two references, caused aberrant spikes in the data. Exclusion of these data points prevented analysis by repeated measures ANOVA due to loss of replicate data points for isotope data from field samples. Stable isotope data from prior to the onset of the sucker migration were not available.

A mixed model showed that time, location, and the interaction between time and location had a significant effect on *Limnephilus* mass ($P < 0.0001$, $P = 0.0107$, and $P < 0.0001$, respectively). Further, slice analysis (SAS Institute Inc. 2008) revealed that there was no site effect on the first sampling date, 18 April, 2009 ($P = 0.9823$); however, there was a significant site effect on 30 April ($P < 0.0001$) and 7 May ($P < 0.0001$) and a near significant difference on 14 May ($P = 0.0579$). *Limnephilus* began to pupate

around 14 May and mean mass decreased at all sampling locations after 14 May, so later dates were excluded from this analysis.

A one-way ANOVA of 5th instar mass among sampling locations across all dates showed a significant difference between locations (P < 0.001), and a planned contrast between treatments revealed significantly higher 5th instar mass at reaches exposed to a sucker run versus reference reaches (P < 0.001, Fig 5). Additionally, there was a signficant positive correlation between *Limnephilus* δ^{15}N and 5th instar mass (R^2=0.318, P = 0.004, Fig 6). Note that these data do not represent two measurements on the same individuals but separate samples collected on the same date at the same location.

Assimilation Experiment

Sucker tissue had a mean δ^{15}N value of 13.2 (n=3, SD=0.189) and a mean δ^{13}C value of -20.9 (n=3, SD=0.450).

In enclosures, *Limnephilus* with access to a sucker carcass rapidly became enriched in both δ^{15}N and δ^{13}C (Fig 7). Repeated measures ANOVAs revealed that treatment, time, and the interaction between treatment and time had a significant effect on both δ^{15}N and δ^{13}C (All P-values < 0.001). Bonferroni adjusted post-hoc pair-wise comparisons revealed that there was no significant difference in *Limnephilus* δ^{15}N or δ^{13}C between enclosures with and enclosures without a sucker carcass at the start of the experiment, but they diverged on all dates thereafter.

There was a significant linear relationship between δ^{15}N and δ^{13}C values for *Limnephilus* in enclosures (Fig 8a, R^2=0.895, P < 0.0001) and a nearly significant, but very weak relationship for *Limnephilus* collected in the field (Fig 8b, R^2=0.058, P = 0.055); this relationship accounted for substantially more of the variation in the enclosure data.

DISCUSSION

Sucker migrations have the potential to influence stream ecosystems via nutrient subsidies. My results suggest that sucker migrations influence nutrient dynamics, algal growth, and caddisfly growth. Caddisflies in enclosures rapidly assimilated sucker-derived N and C, indicating direct feeding on sucker carcasses. In the field, caddisflies appear to assimilate sucker-derived N but not C.

Nutrient Dynamics

NH_4 and SRP became significantly elevated at treatment sites relative to reference sites over the course of the sucker migration, whereas there was no significant elevation of NO_3 (Fig 1). Given the comparable nutrient levels at treatment and reference reaches at the beginning and end of the study, when few suckers were in the system, the elevated nutrient levels at treatment locations strongly suggest nutrient contributions from the migration. NH_4 is the primary form of nitrogen excreted by freshwater fishes (McIntyre et al. 2008) and is the initial product of remineralization of N from decomposing carcasses and eggs. Studies have reported a range of nutrient responses to fish migrations. A study on anadromous, iteroparous alewives in a small Atlantic tributary saw no increases in nutrient concentrations (Walters et al. 2009); however many studies on Pacific salmon have observed elevated nutrient levels associated with migrations (Naiman et al. 2002). Elevated ambient nutrient levels at reaches receiving a sucker migration indicate contributions greater than the stream's uptake capacity.

Algal Growth

Correlations among light, temperature, N, and P make it difficult to parse the driving forces behind the increased algal growth at reaches exposed to the sucker migration; however, evidence of nitrogen limitation at the study site (P.B. McIntyre and J.D. Allan, unpublished data) suggests that the elevated nutrient levels during the sucker migration could play a role in the increased algal growth. Temperature exhibits a negative relationship with algal growth (Fig 4) and therefore is unlikely to drive the observed

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difference. This is almost certainly a spurious correlation given the well documented positive relationship between algal growth and temperature (Allan and Castillo 2007). The co-occurrence of the highest light levels with the highest nutrient increases at downstream sites provides ideal conditions for increased primary production. Increases in epilithic algal growth have been documented for Pacific salmon migrations in Great Lakes tributaries (Schuldt and Hershey 1995) and in their native range (Wipfli et al. 1998). Additionally, algal growth increased during a simulated alewife migration (Durbin et al. 1979). My results indicate that algal growth may respond to increased nutrient availability during sucker migrations.

Macroinvertebrate Growth and Assimilation of Lake-Derived Nutrients

Isotopic enrichment of *Limnephilus* in enclosures with a sucker carcass indicates the assimilation of sucker-derived carbon and nitrogen. Thus, when sucker carcasses are readily available, *Limnephilus* utilize them as a food resource. Carcasses observed in the field were rapidly colonized by *Limnephilus, Asynarchus,* other Trichoptera, Leptophlebiid mayflies, and snails indicating that this finding holds in the field. Importantly this experiment demonstrates the isotopic enrichment of *Limnephilus* exposed to sucker carcasses, enabling clearer interpretation of field data.

δ^{15}N at locations receiving a sucker migration responded similarly to that of *Limnephilus* in enclosures with a sucker carcass, although the presence of carcasses in reference reaches on two dates inhibited the planned statistical analyses. Also the lack of stable isotope data prior to the arrival of suckers makes it difficult to interpret the differences in δ^{15}N on the first sampling date. Elevated δ^{15}N at reaches receiving a sucker migration relative to reference reaches on the first date may represent rapid assimilation of sucker N by *Limnephilus*, as was observed in enclosures, or it may represent naturally existing gradients in δ^{15}N. It is likely that the increases in δ^{15}N over the first half of the sampling period represent assimilation of sucker N.

The coincident enrichment of carbon isotopes at reference and treatment reaches suggests a seasonal source or dietary shift in carbon isotope ratios, rather than the assimilation of lake-derived carbon. Seasonal algal carbon enrichment beginning with spring snowmelt and peaking at summer's end has been observed in streams in the western U.S. (McCutchan and Lewis 2002), and ontogenetic diet shifts have been implicated in changing carbon isotope ratios (France 1996). Flow variation also may influence algal carbon fractionation (Singer et al. 2005), and steadily falling stream discharge over the sampling period aligns with the reported negative relationship between algal δ^{13}C and flow . Given the multiple possible explanations for δ^{13}C enrichment and the constant difference between reaches with and without a sucker migration, there is no evidence that *Limnephilus* assimilated lake-derived carbon. Macroinvertebrate assimilation of lake-derived nitrogen but not carbon was reported previously for a chinook salmon migration in a Lake Superior tributary (Schuldt and Hershey 1995).

The strong linear relationship between carbon and nitrogen enrichment in enclosures suggests a direct feeding pathway from the sucker carcasses to the caddisflies. In contrast, there was a very weak relationship between carbon and nitrogen enrichment in the field and thus a decoupling of lake-derived carbon and nitrogen, suggesting an indirect pathway of lake-derived nitrogen to caddisflies via algae, microbes, or fungi.

Final instar *Limnephilus* were significantly larger in reaches exposed to a sucker migration (Fig 8), but there was no significant difference among sites at the beginning of the sucker migration. These results, in conjunction with the significant positive relationship between growth and the incorporation of lake-derived nitrogen (Fig 9), suggest that sucker migrations increase *Limnephilus* growth rates and final body size. Although I do not have adequate density estimates to specifically calculate production, it is possible that increases in growth led to increases in production of *Limnephilus*. However, it is difficult to

draw conclusions about secondary production from the growth of a single species, because the effect of fish migrations on macroinvertebrates can vary across taxa (Chaloner and Wipfli 2002).

The implications of increased caddisfly growth are twofold. First, increased female body size is related to higher fecundity across diverse insect taxa (Honek 1993). Using a Trichoptera specific transformation (Svensson 1975), I calculate that individual female fecundity would increase by an average of 10.5% for the size increase observed at our study site. Second, aquatic insect emergence can be an important source of energy and nutrients for terrestrial food webs (Nakano and Murakami 2001). If increased growth rates resulted in increased production, sucker migrations likely increased the transfer of energy and nutrients to terrestrial food-webs via insect emergence.

The onset of *Limnephilus* pupation coincided with observed decreases in mean *Limnephilus* mass across all sites and decreases in $\delta^{15}N$ at sites with a sucker migration. Seasonal decreases in mass at emergence have been reported for numerous aquatic insect taxa (Svensson 1975, Petersson 1989, Sweeney et al. 1995) and explained by trade-offs between individual state and reproductive or environmental time constraints (Rowe and Ludwig 1991). An alternative explanation for the observed decrease in size is that size selective predation altered the *Limnephilus* size distribution (Peckarsky 1982). Thus the observed decreases likely represent a removal of large individuals from the population through either pupation or predation, and the decrease in the population mean reflects a shift in the make-up of the population itself rather than size decreases by individual insects. Therefore it is logical to exclude the data after the peak mean size from growth analyses, since they represent only a small subset of the population sampled on previous dates.

It appears that larger individuals that pupate earlier or are removed by predation have assimilated more lake-derived nutrients. This indicates that utilization of lake-derived nutrients is not uniform and may be partitioned temporally due to different hatching or development times or spatially due to varying

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exposure to sucker nutrients, which could be explained by the patchiness of eggs and carcasses as resources or differing exposure to mineralized nutrients due to flow patterns.

Nutrient subsidies by iteroparous migrations

Three potential pathways exist for materials delivered by fish migrations: excretion, carcasses, and gametes. In studies on Pacific salmon, there has a been a great deal of focus on the role of carcasses since Pacific salmon (with the exception of steelhead) die en masse after spawning (Naiman et al. 2002, Schindler et al. 2003).

Because suckers are iteroparous, returning to lakes after spawning and spawning again in subsequent years, the potential for fertilization via carcasses is smaller than for semelparous migrations. However, many suckers do perish during the spawning migration. Many of the carcasses decompose in the stream and are rapidly colonized by macroinvertebrates; additionally, raccoons, black bears, coyotes, bald eagles, great blue herons, crows, and seagulls have been observed utilizing carcasses as a resource (P.B. McIntyre, personal observation). In addition, eggs represent a potentially large source of nutrients and energy from sucker migrations. Eggs comprise an average of 12% of female biomass and only around 1% of eggs are exported as larvae (R. Papke, P.B. McIntyre, J.D. Allan, unpublished data). Excretion may also play a role given its immediate availability in inorganic form but represents a much smaller total mass than the other sources.

Significant nutrient and energy subsidies should occur when: migration biomass is large relative to stream size, background nutrient and energy levels are low, and effective transfer mechanisms exist (Flecker et al. In Press).   The effect of sucker migrations on nutrient dynamics and stream productivity is likely governed by migration size and environmental context. The low background nutrient levels and high sucker biomass relative to stream discharge at our study site make conditions ideal for fertilization by the sucker migration. I illustrate that, under the right conditions, suckers are an important source of

nutrients. However, their degree of importance likely varies greatly with environmental context and migration size.

Semelparous migrations have received considerable attention over the last few decades, and their role in delivering nutrient subsidies is well documented (Naiman et al. 2002). In contrast, the potential delivery of material subsidies by iteroparous migrations has received little attention. Recent work on iteroparous alewives highlighted the potential role of excretion and documented the incorporation of nutrients delivered by an iteroparous migration into the food web (Post and Walters 2009, Walters et al. 2009); however, I know of no studies to date that illustrate influence of nutrient additions by an iteroparous migration on primary or secondary production. This study demonstrates that iteroparous migrations can influence stream ecosystems via nutrient subsidies.

Management Implications

Suckers are bottom-dwelling fishes incapable of making the fantastic acrobatic leaps that salmon are renowned for. Thus, low-head dams, perched culverts, and other small barriers can prevent upstream migration (Klingler et al. 2003). Such barriers, in addition to larger dams, are widespread and likely exclude suckers migrating out of the Great Lakes from the vast majority of potential spawning habitat. This may be particularly influential in streams with large spawning migrations relative to stream size and low background nutrient levels, where suckers have the largest potential to influence production and other ecosystem processes. While numerous considerations must contribute to decisions about stream barrier removal or improvement, suckers likely deliver an important nutrient subsidy in many streams and increased connectivity could restore this process to stream reaches upstream of barriers, enhancing ecosystem productivity and restoring a process to a state more closely resembling natural conditions.

TABLE 1. Differences between mean SRP and NH4 discharge for reaches receiving a sucker migration (μ_S) and those without a migration (μ_{ref}) and the significance of slice analysis testing for treatment effects on each day. * indicates significance at the 0.05 level.

|	18-Apr	30-Apr	7-May	14-May	21-May	28-May	4-Jun
SRP (mg/sec)							
μ_S-μ_{ref}	0.04	0.52	0.76	0.25	0.25	0.24	-0.01
P-value	0.777	0.001*	<0.001*	0.095	0.100	0.114	0.919
NH$_4$ (mg/sec)							
μ_S-μ_{ref}	-1.50	-0.12	8.05	1.64	2.49	-0.50	0.10
P-value	0.281	0.928	<0.001*	0.240	0.079	0.716	0.945
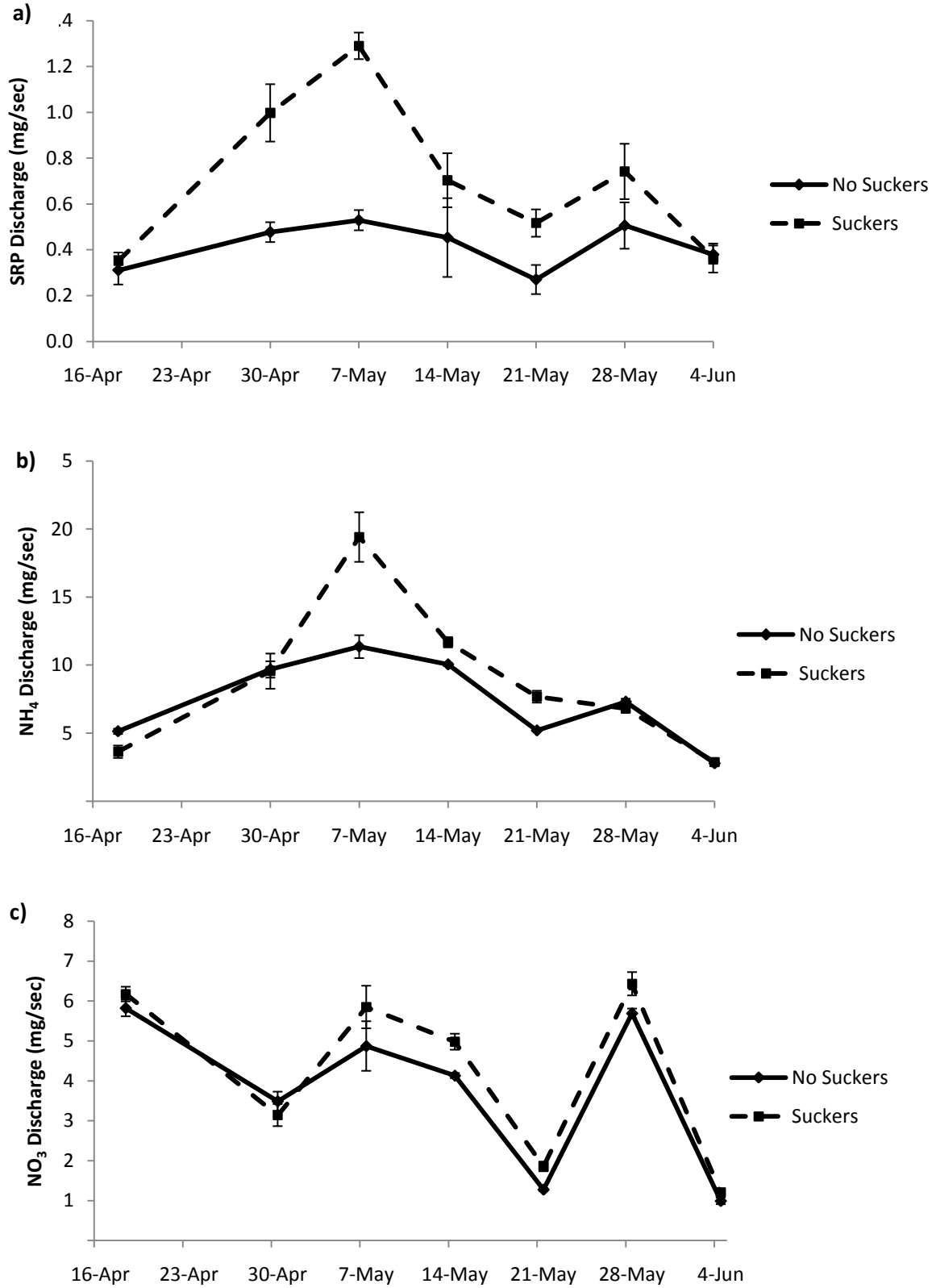
FIG 1. Comparison of **a)** soluble reactive phosphorus, **b)** NH_4, and **c)** nitrate discharge between treatment and reference reaches over the course of the sucker migration. Error bars represent SE.
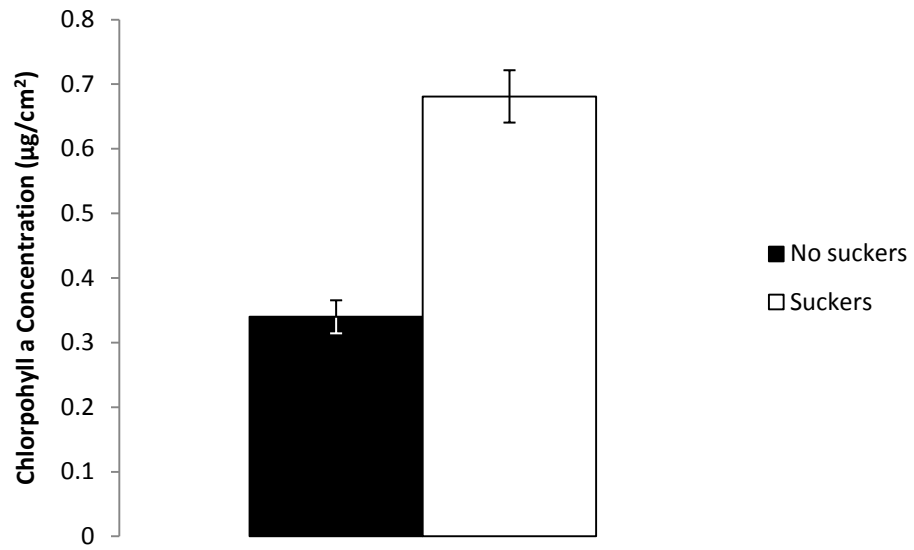
FIG 2. Differences in algal accumulation between treatment and reference reaches. Reaches that received a sucker migration had significantly higher chlorophyll a concentrations than reference reaches.
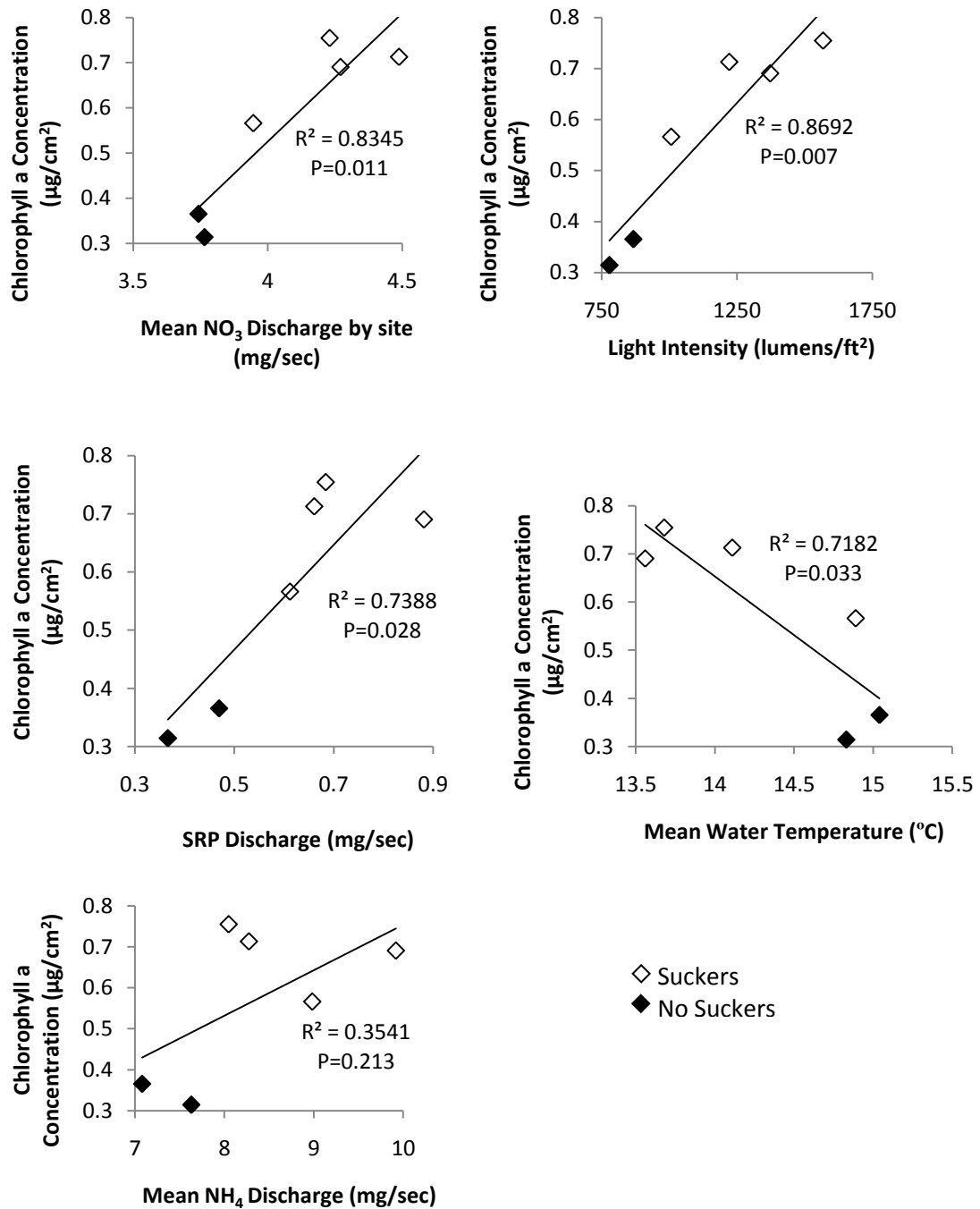
FIG 3. Linear regressions between chlorophyll a and potential drivers. Light, temperature, SRP, and NO_3 were significantly correlated with chlorophyll a (note the apparent negative association with temperature).
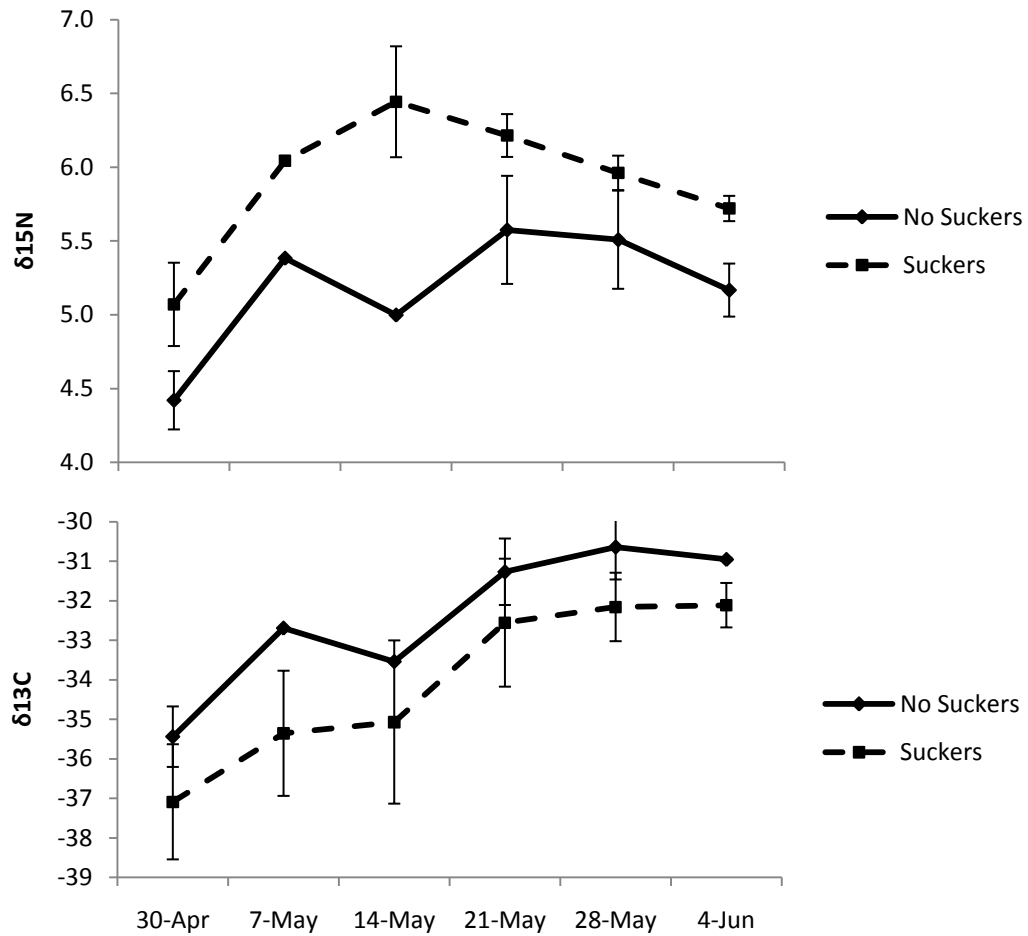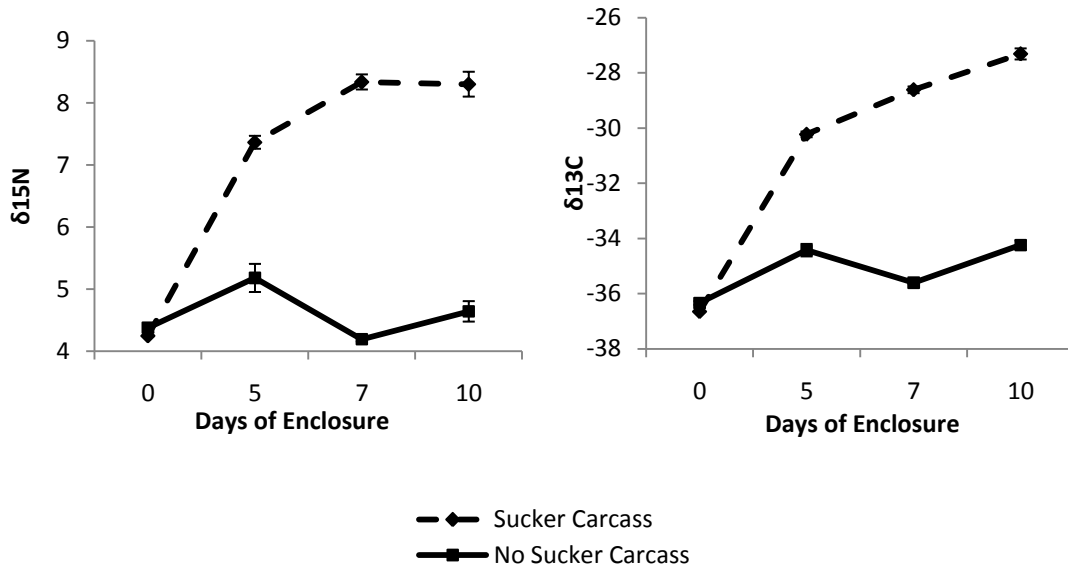
FIG 4. C and N stable isotope ratios over the course of the sucker migration. δ^{15}N for *Limnephilus* exposed to the sucker migration was enriched relative to references at the initiation and the largest difference occurred in the middle of the season. Relative δ^{13}C values remained similar over the course of the season.
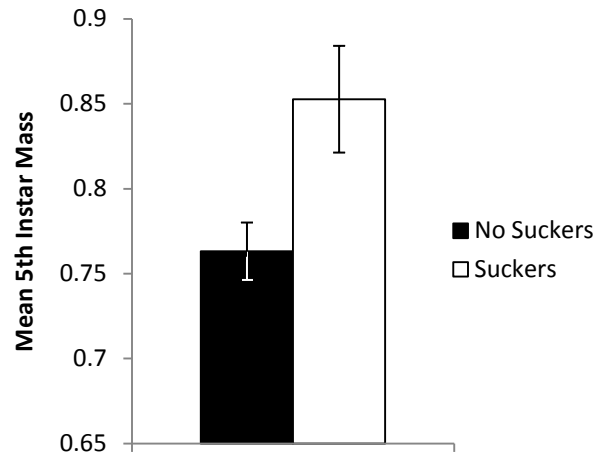
FIG 5. Mean *Limnephilus* 5th instar mass at treatment and reference reaches. *Limnephilus* 5th instar mass was significantly higher at reaches that were exposed to a sucker run versus reference reaches ($P < 0.001$). Error bars represent SE.
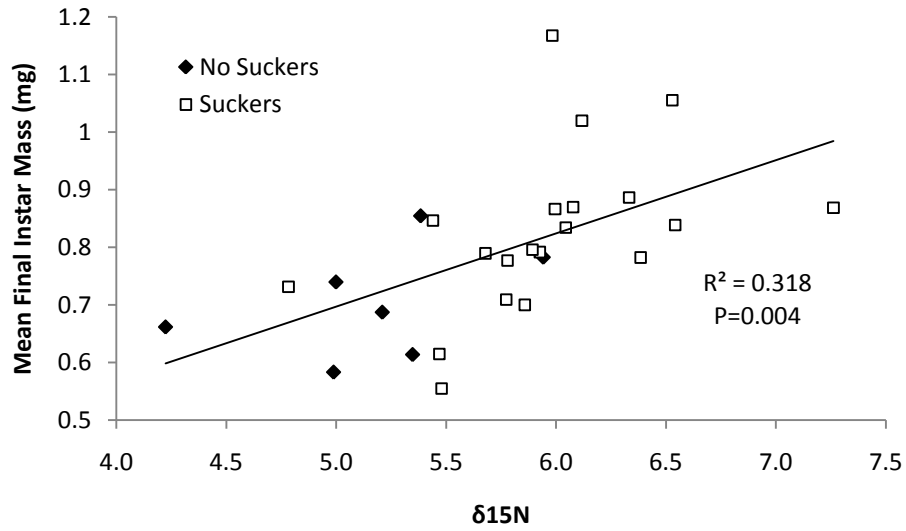
FIG 6. Relatonship between $\delta^{15}N$ enrichment and size in *Limnephilus*. *Limnephilus* 5th instar mass was positively correlated with $\delta^{15}N$ values. (Note: all data contribute to regression; symbols are for illustrative purposes only)

FIG 7. Changes in C and N stable isotope ratios for *Limnephilus* in enclosures with or without a sucker carcass over time. *Limnephilus* enclosed with a sucker carcass became enriched in $\delta^{15}N$ and $\delta^{13}C$ while references did not change significantly (repeated measures ANOVA). Error bars represent SE.
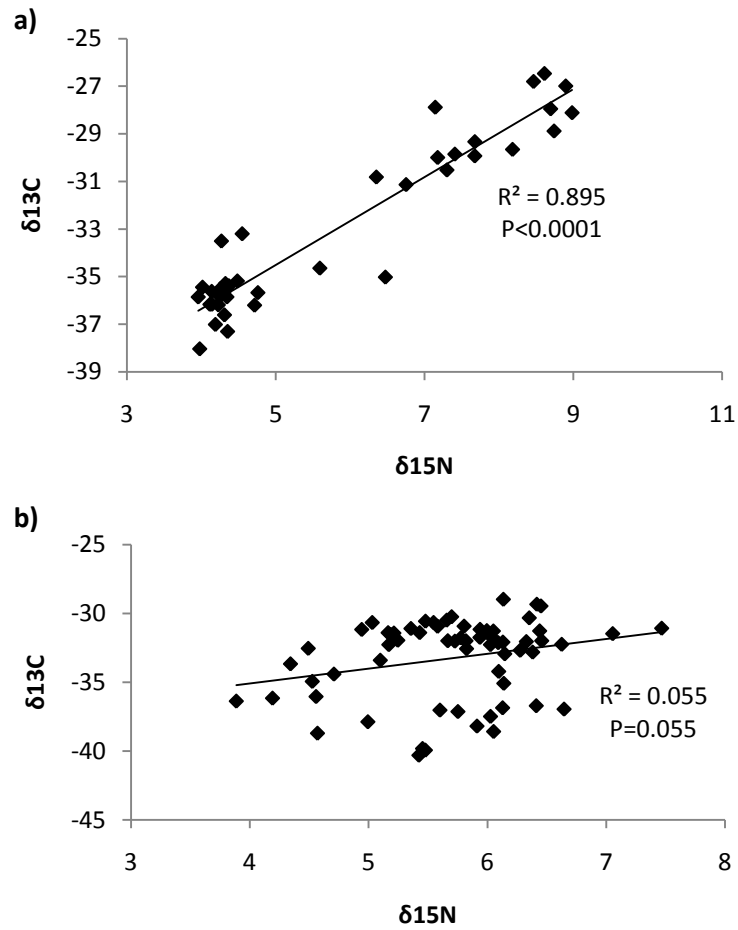
FIG 8. Relationship between C and N stable isotope ratios in enclosures and in the field. **a)** In enclosures, there was a strong linear relationship between *Limnephilus* δ^{15}N and δ^{13}C values. **b)** In the field, there was a very weak linear relationship between *Limnephilus* δ^{15}N and δ^{13}C values.

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