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# Nutrient recycling by caddisflies alleviates phosphorus limitation in case periphyton

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**Abstract:** Selective feeding and differential nutrient excretion by aquatic invertebrates plays a substantial role in nutrient recycling. Grazing larvae of the caddisfly *Glossosoma intermedium* construct a portable case for protection that also serves as a good substrate for periphyton colonization because it is constantly fertilized by larval excreta. We tested whether case periphyton was nutrient enriched compared to streambed periphyton and whether selective feeding by caddisfly larvae on case periphyton facilitates P remineralization. We measured total N, total P, and N:P in stream water and streambed cobble periphyton in 3 western Wisconsin streams. We collected larvae and measured N and P content and N:P of case periphyton, *G. intermedium* body, and *G. intermedium* excretion products. Cobble periphyton N:P at 2 streams suggested P limitation ( $368 \pm 109$  and  $50 \pm 10$ ), but case periphyton N:P at those streams did not ( $11 \pm 3$  and  $11 \pm 0.8$ , respectively). Neither cobble nor case periphyton N:Ps suggested P limitation at the 3<sup>rd</sup> stream. Measured excretion N:P was more similar to the excretion N:P predicted for caddisfly grazing on case periphyton than for caddisfly grazing on cobble periphyton. Our results suggest that larval excretion alleviated P limitation of case periphyton and that case periphyton may serve as an important dietary resource for the grazing caddisfly larvae. Feeding on this P-rich case periphyton promotes P remineralization in P-limited, lotic ecosystems.

**Key words:** *Glossosoma intermedium*, consumer-driven nutrient recycling, stoichiometry, lotic ecosystem, caddisfly, Driftless Area

In aquatic ecosystems, periphyton is the primary food resource for benthic grazers (Wallace and Webster 1996). The nutrient composition of periphyton is flexible and can be altered by benthic consumers through consumption of organic nutrients and excretion of inorganic nutrients (Frost et al. 2002, Hillebrand et al. 2002, 2008, Liess and Hillebrand 2006). Small-scale nutrient inputs via differential N or P excretion by invertebrates can lead to changes in periphyton N:P and to patches of N- or P-rich periphyton in an otherwise N- or P-poor periphyton mat (Pringle et al. 1988, Hillebrand et al. 2004, Evans-White and Lamberti 2006, Ings et al. 2010). Most research on consumer-driven nutrient recycling (CNR) by aquatic invertebrates has focused on mobile grazers (but see Ings et al. 2010). However, sessile invertebrates or portable-cased grazers, such as caddisflies, often excrete their waste repeatedly at the same location and could cause stronger spatial patchiness in periphyton nutrient ratios than mobile grazers do (Ings et al. 2010, 2012).

*Glossosoma intermedium*, a caddisfly that constructs a portable larval case for protection, inhabits many midwestern streams at high densities, ( $>6600$  individuals [ind]/m<sup>2</sup>; Cavanaugh et al. 2004) and is considered a keystone herbi-

vore (Kohler and Wiley 1992). When densities of *Glossosoma* peak, they exert strong top-down grazing pressure on cobble periphyton (Kohler 1992). Under conditions of high interspecific competition, *G. intermedium* shifts its foraging behavior and increasingly grazes on the periphyton colonizing the dorsal case surfaces of conspecific larvae where algal growth is greater than on cobbles (Cavanaugh et al. 2004).

Excretion by cased invertebrates can affect the nutritional composition of periphyton on their cases (Pringle 1985, Ings et al. 2010). The structure of *G. intermedium* cases may promote case periphyton fertilization because gaps between case particles allow diffusion of nutrients in excreta (Bergey and Resh 1994). N- and P-rich periphyton also colonize the tubes of tube-dwelling chironomids (Pringle 1985). The larvae of *Tinodes waeneri* exhibit gardening behavior and fertilize the periphyton on their retreats with excreta. This garden serves as a nutritious food resource for the larvae (Ings et al. 2010) and can alleviate nutrient limitation (Kahlert and Baunsgaard 1999). Case grazing by *G. intermedium* may be a similar strategy to alleviate P limitation in P-limited streams.

The extent of case-periphyton fertilization depends on the nutritional composition of larval excreta. In general,

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aquatic invertebrate consumers are relatively homeostatic in their body nutrient composition, i.e., their nutrient composition does not change as resource quality changes (Cross et al. 2005). Invertebrates need constant proportions of N and P for growth and differentially excrete remaining nutrients. Therefore, grazer body N:P and food N:P directly affect grazer excreta N:P (Elser and Urabe 1999). The elemental imbalance between the grazer and its food can be estimated as the difference between resource N:P and consumer body N:P. The elemental imbalances indicate the identity of the limiting nutrient and help to predict the N:P recycling ratio (Elser and Hassett 1994). A positive N:P imbalance (resource N:P > grazer N:P) suggests that grazer growth is P-limited (Elser and Hassett 1994, Liess et al. 2009). The imbalance can then be used to predict the N:P of excreta, i.e., the N:P recycling ratio (Liess et al. 2009). Because *G. intermedium* inhabits P-limited streams, it is expected to excrete as little P as possible in an attempt to retain the limiting nutrient (Sterner and Elser 2002).

Our objectives were to estimate the nutrient ratios of stream water, cobble periphyton, *G. intermedium* larvae and excreta, and case periphyton to better understand the feedback between *G. intermedium* CNR and its periphyton resource. We hypothesized that caddisfly excreta decrease P limitation in case periphyton. Based on this hypothesis, we had 2 predictions: 1) excretion N:P is lower than stream-water N:P; and 2) case periphyton N:P is lower than cobble periphyton N:P. We also hypothesized that *G. intermedium* larvae exhibit nutritional homeostasis with respect to body N:P, and that recycled N:P would depend on whether case or cobble periphyton were consumed. This hypothesis led to 2 additional predictions: 3) larval N:P does not differ among sites, despite differing periphyton N:P among sites and 4) excretion N:P is similar to predicted excretion N:P for case-grazing caddisflies, indicating that case grazing is common.

## METHODS

### Study area

We studied 3 coldwater streams in the Driftless Area of southwestern Wisconsin (USA) between November 2010 and February 2011. The Driftless Area was unglaciated throughout the most recent glacial period (Pleistocene Epoch) (Tenorio and Drezner 2006). This region of Wisconsin has extensive karst topography with many natural, spring-fed streams. We sampled 3 spring-fed streams, Coon Creek (CC), Spring Coulee Creek (SC), and Timber Coulee Creek (TC), 3 times when *G. intermedium* densities were high (>1000 ind/m<sup>2</sup>) (Cavanaugh et al. 2004).

### Sample collection

We collected *G. intermedium* larvae, excreta, and cases, and cobble periphyton and stream water at 1 transect each in CC, SC, and TC on 3 different occasions ( $n = 9$  [3/date/stream]). We randomly chose 1 of 6 transects in a riffle at

each site on each sampling date. We collected 3 cobbles from the transect and 10 *G. intermedium* larvae from each cobble. We extracted the larvae from their cases, placed the cases in vials containing filtered (Whatman GF/F; Maidstone, UK) stream water, and stored them on ice for transportation to the laboratory. We rinsed the larvae with filtered stream water and placed them in incubation vials containing 40 mL of filtered stream water (10 larvae/vial). We placed the vials in the stream and incubated the larvae for 2 h in situ to collect excreta. All larvae survived the incubation and egested little to no fecal matter. We also incubated vials containing only filtered stream water as controls. After the incubation, we removed the larvae from the incubation vials and placed them in vials containing fresh, filtered stream water. We placed all vials containing excreta on ice for transportation to the laboratory, where we immediately placed cases and larvae individually in a drying oven at 60°C for 48 h and then stored them in a desiccator prior to analysis.

We collected periphyton from a circular area (9.6 cm<sup>2</sup>) on each cobble by brushing with a modified tube sampler (Steinman 1992). We mixed the periphyton with 100 mL of filtered stream water and stored it in 500-mL Nalgene<sup>®</sup> bottles for transportation to the laboratory where we filtered the water (Whatman GF/F). We placed the filters in a drying oven at 60°C and stored them in a desiccator.

### Nutrient analyses

Water from incubation vials containing *G. intermedium* excreta and water from control streamwater vials underwent simultaneous total N (TN) and total P (TP) persulfate digestion (APHA 2005), followed by analyses for NO<sub>3</sub><sup>-</sup> via the Cd reduction and soluble reactive P (SRP) via the ascorbic acid-molybdate methods. We estimated N and P in *G. intermedium* excreta (mg P mg<sup>-1</sup> dry mass [DM] d<sup>-1</sup> and mg N mg<sup>-1</sup> DM d<sup>-1</sup>) by calculating the difference between the mean control sample (filtered stream water) N and P concentration and the incubation water N and P concentration.

We used hydrochloric acid TP digestion for solids followed by SRP analysis (APHA 2005) to measure the concentration of P in *G. intermedium* body tissue. Prior to analysis, we weighed whole *G. intermedium* larvae and used larvae ranging from 0.40 to 3.8 mg DM. We used the same methods to measure TP concentrations of cobble periphyton per unit surface area of filter segments (6-mm filters) and of case periphyton per unit case mass (14.4–74.6-mg clusters of upper-case particles). We used a Costech<sup>®</sup> (Valencia, California) CHN elemental analyzer to measure TN concentration (moles/mg DM) of *G. intermedium* larvae, cobble periphyton, and case periphyton and total C (TC) concentration for larvae and cobble periphyton. We used single, dried larvae (separate from their cases) ranging from 0.42 to 3.75 mg DM to measure TN and TC concentration in larval tissue. We used clusters of

Table 1. Equations used to calculate consumer–resource N:P imbalance (1) and predicted excretion N:P for cobble and for case periphyton used as food resource with either positive (2) or negative (3) resource imbalance.  $N:P_{imb}$  = the difference between resource N:P and larval N:P,  $N:P_{resource}$  = N:P of cobble or case periphyton,  $N:P_{larvae}$  = N:P of *G. intermedium* larvae,  $N:P_{recycled}$  = N:P recycled by *G. intermedium* larvae,  $L$  = maximum P assimilation efficiency = 0.8.

Number	Equation	Imbalance condition
1	$N:P_{imb} = N:P_{resource} - N:P_{larvae}$	—
2	$N:P_{recycled} = (N:P_{resource} - L[N:P_{larvae}]) / (1 - L)$	$N:P_{imb} > 0$
3	$N:P_{recycled} = N:P_{resource}(1/L) / (1 - L)(N:P_{cobble\ or\ case}) / N:P_{larvae}$	$N:P_{imb} \leq 0$

upper-case particles weighing between 6.36 and 59.88 mg DM to measure TN concentration in case periphyton. We measured TN of cobble periphyton by analyzing 6-mm-diameter segments of filters containing dried periphyton.

#### Resource imbalances and predicted recycled N:P

We calculated N:P imbalances between *G. intermedium* larvae and cobble periphyton and *G. intermedium* larvae and case periphyton according to Elser and Hassett (1994) (Table 1). Then we calculated predicted N:P recycling ratios of *G. intermedium* larvae based on cobble periphyton as food resource and based on case periphyton as food resource. We used equations published by Sterner (1990) and assumed a constant P assimilation efficiency of 0.8 (Frost et al. 2006, Liess et al. 2009).

#### Statistical analyses

We ran all analyses in SPSS (version 20; SPSS, Inc., Armonk, New York) and set  $\alpha$  at 0.05. We used a 1-way repeated measures analysis of variance (rmANOVA) with time as a treatment factor and N:P of cobble periphyton, case periphyton, larvae, excreta, and stream water as dependent variables to test whether replicate measurements varied over time within a stream. We used  $t$ -tests to compare *G. intermedium* excretion N:P with streamwater N:P and paired  $t$ -tests to compare case periphyton N:P with cobble periphyton N:P within each site.

We used a 1-way multivariate analysis of variance (MANOVA) with stream as the treatment factor and larvae and cobble periphyton N:P, C:N, or C:P as response variables to compare larval and cobble periphyton N:P among streams. We used subsequent multiple-comparison tests to identify specific differences in N:P, C:N, or C:P of cobble periphyton or larvae among streams.

We used a  $t$ -test to compare resource imbalances of cobble and case periphyton and 1-way ANOVA with post hoc comparisons to compare predicted excretion N:P with cobble periphyton consumption, predicted excretion N:P with case periphyton consumption, and realized excreted N:P at each site.

#### RESULTS

Sampling date did not affect N:P of stream water, cobble periphyton, *G. intermedium* larvae, excreta, or case periphyton in CC, SC, or TC (CC:  $F = 1.180$ ,  $df = 2$ ,  $p = 0.333$ ; SC:  $F = 0.619$ ,  $df = 2$ ,  $p = 0.569$ ; TC:  $F = 1.047$ ,  $df = 2$ ,  $p = 0.374$ ). Therefore, data from all sampling dates were pooled for further analyses.

Stream water N:P differed among sites, but excretion N:P was consistently lower than stream water N:P. Excretion N:P at CC (mean  $\pm$  SE,  $27 \pm 8$ ), SC ( $26 \pm 4$ ), and TC ( $41 \pm 11$ ) was significantly lower than stream water N:P ( $214 \pm 20$ ,  $346 \pm 36$ , and  $129 \pm 14$ , respectively;  $p < 0.0001$ ,  $p = 0.012$ , and  $p < 0.001$ , respectively; Fig. 1A). TC stream water had the highest P concentration ( $0.036 \pm 0.004$  mg/L; Table 2) and the lowest N:P ( $129 \pm 14$ ; Fig. 1A). CC and SC had similar stream water P concentrations ( $0.016 \pm 0.01$  and  $0.018 \pm 0.003$ , respectively; Table 2) but differed in streamwater N:P ( $214 \pm 20$  and  $346 \pm 36$ , respectively; Fig. 1A).

Cobble and case periphyton N:P differed at 2 of the 3 streams (Fig. 1B). At CC and SC, cobble periphyton N:P ( $368 \pm 109$  and  $50 \pm 10$ , respectively) suggested P limitation ( $N:P > 32$ ; Kahlert 1998). However, case periphyton N:P at CC ( $11 \pm 3$ ) and SC ( $11 \pm 0.8$ ) were lower than cobble periphyton N:P (CC:  $t = 3.309$ ,  $df = 6$ ,  $p = 0.016$ ; SC:  $t = 3.933$ ,  $df = 7$ ,  $p = 0.006$ ) and did not suggest P limitation. At TC, cobble and case periphyton N:P were similar ( $t = 1.404$ ,  $df = 7$ ,  $p = 0.203$ ), and neither cobble nor case periphyton N:P ( $43 \pm 18$  and  $13 \pm 7$ , respectively) suggested P limitation.

*Glossosoma intermedium* appeared to maintain a constant elemental composition among streams despite differences in cobble periphyton N:P (1-way MANOVA;  $F = 2.903$ ,  $df = 4$ ,  $p = 0.034$ ). Larval N:P did not differ among streams (multiple comparison test;  $F = 2.135$ ,  $df = 2$ ,  $p = 0.144$ ), but cobble periphyton N:P did ( $F = 6.679$ ,  $df = 2$ ,  $p = 0.006$ ). Cobble periphyton N:P differed between CC and TC ( $p = 0.004$ ) and between CC and SC ( $p = 0.006$ ), but not between TC and SC ( $p = 0.932$ ) (Fig. 1B). Stream did not affect cobble periphyton or larval C:N or C:P ( $F = 2.100$ ,  $df = 4$ ,  $p = 0.100$  and  $F = 1.078$ ,  $df = 4$ ,  $p = 0.381$ , respectively; Fig. 2A, B).

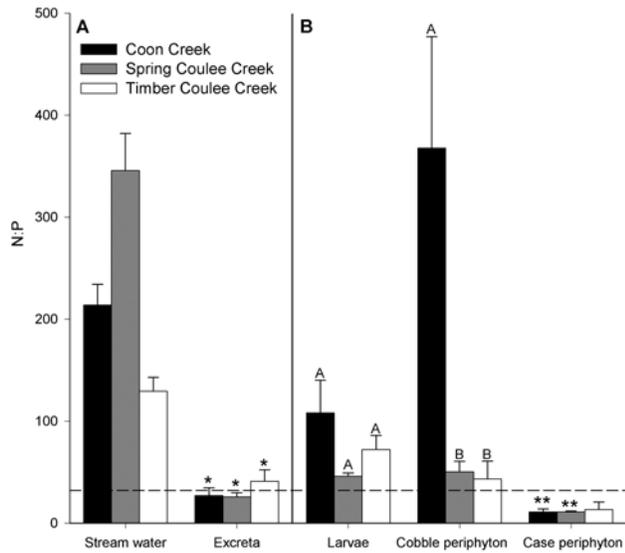


Figure 1. Mean ( $\pm$  SE) molar N:P for all response variables (stream water, larval excreta, larvae, cobble periphyton, and case periphyton) at Coon Creek, Spring Coulee Creek, and Timber Coulee Creek. A.—Comparison of stream water N:P to excretion N:P within each stream. \* indicates excreta bars differ from stream water bars within streams. B.—Comparison of larval N:P and cobble periphyton N:P among streams and comparison of cobble periphyton N:P to case periphyton N:P within each stream. Larvae and cobble periphyton bars with the same letter are not different among streams. \*\* indicates case periphyton bars differ from cobble periphyton bars within streams. Periphyton with N:P > 32 (indicated by the dashed line) is considered P-limited.

The nutritional imbalances between *G. intermedium* larvae and their periphyton resources supported conclusions based on the stoichiometry of cobble and case periphyton. At CC and SC, cobble periphyton was P limiting, whereas case periphyton was not, and neither periphyton resource was P limiting at TC. At CC and SC, predicted N:P imbalances for consumption of cobble periphyton were posi-

tive ( $291.5 \pm 135.4$  and  $7.7 \pm 12.5$ , respectively), suggesting that the resource is P-limited, especially at CC (Fig. 3A). However, predicted imbalances for consumption of case periphyton were negative ( $-96.9 \pm 29.3$  and  $-35.0 \pm 3.2$ , respectively) and were significantly lower than predictions for consumption of cobble periphyton ( $t = 2.946$ ,  $df = 12$ ,  $p = 0.012$  and  $t = 3.234$ ,  $df = 11$ ,  $p = 0.008$ , respectively; Fig. 3A). At TC, predicted imbalances for consumption of cobble and case periphyton were negative ( $-28.9 \pm 22.6$  and  $-57.5 \pm 15.7$ , respectively) and did not differ ( $t = 0.970$ ,  $df = 14$ ,  $p = 0.348$ ; Fig. 3A).

Stream affected predicted and realized excretion N:P ( $F = 9.588$ ,  $df = 22$ ,  $p = 0.001$  and  $F = 9.108$ ,  $df = 15$ ,  $p = 0.003$ , respectively; Fig. 3B). At CC and SC, realized excretion N:P differed from predicted excretion N:P ( $27 \pm 8$  and  $26 \pm 4$ , respectively) for consumption of cobble periphyton ( $1710 \pm 589$ ,  $p = 0.002$ ;  $205 \pm 45$ ,  $p = 0.013$ ; respectively), but not for consumption of case periphyton ( $111 \pm 29$ ,  $p = 0.974$ ;  $46 \pm 3$ ,  $p = 0.920$ , respectively; Fig. 3B). At TC, realized and predicted excretion N:P for cobble and case periphyton consumption did not differ ( $41 \pm 11$ ,  $144 \pm 57$ , and  $85 \pm 34$ , respectively;  $F = 1.704$ ,  $df = 24$ ,  $p = 0.205$ ) (Fig. 3B).

**DISCUSSION**

*Glossosoma intermedium* excreta decreased P limitation in case periphyton. At all 3 streams, excretion N:P was lower than stream water N:P. At 2 of 3 streams, case periphyton N:P was lower than cobble periphyton N:P (accepting hypothesis 1). Larval N:P did not differ among the streams despite differences in cobble periphyton N:P, indicating homeostatic regulation of body nutrient composition in *G. intermedium* (accepting hypothesis 2). Predicted excretion N:P was more similar to measured excretion N:P when case periphyton was used as food resource in the equation (Table 1) than when cobble periphyton was used (supporting hypothesis 2). This result suggests that case periphyton is an important food resource for P-limited

Table 2. Mean ( $\pm$  SE) % C, N, and P of larvae, case material, cobble periphyton, and stream water and mean ( $\pm$  SE) rates of N and P excretion at Coon Creek (CC), Spring Coulee Creek (SC), and Timber Coulee Creek (TC). Biomass percentages are mass % per body dry mass (DM) and case material percentages are mass % per case material DM.

Site	Nutrient	Larval biomass (%)	Case material (%)	Excreta (mg mg <sup>-1</sup> d <sup>-1</sup> )	Periphyton ( $\mu$ g/cm <sup>2</sup> )	Stream water (mg/L)
CC	N	8.64 $\pm$ 0.42	0.063 $\pm$ 0.007	0.0107 $\pm$ 0.0056	673.5 $\pm$ 143.0	1.42 $\pm$ 0.04
	P	0.37 $\pm$ 0.11	0.020 $\pm$ 0.005	0.0008 $\pm$ 0.0002	6.0 $\pm$ 1.3	0.016 $\pm$ 0.01
	C	44.77 $\pm$ 3.00	—	—	1923.4 $\pm$ 693.4	—
SC	N	10.29 $\pm$ 0.61	0.073 $\pm$ 0.005	0.0067 $\pm$ 0.0002	271.9 $\pm$ 19.5	2.25 $\pm$ 0.15
	P	0.50 $\pm$ 0.03	0.015 $\pm$ 0.002	0.0007 $\pm$ 0.0001	15.7 $\pm$ 2.4	0.018 $\pm$ 0.003
	C	53.95 $\pm$ 3.53	—	—	3928.0 $\pm$ 765.3	—
TC	N	9.89 $\pm$ 0.48	0.054 $\pm$ 0.007	0.0192 $\pm$ 0.0069	182.7 $\pm$ 28.6	1.78 $\pm$ 0.06
	P	0.32 $\pm$ 0.04	0.019 $\pm$ 0.003	0.0001 $\pm$ 0.0003	18.6 $\pm$ 4.6	0.036 $\pm$ 0.004
	C	48.39 $\pm$ 0.86	—	—	3169.4 $\pm$ 1043.7	—

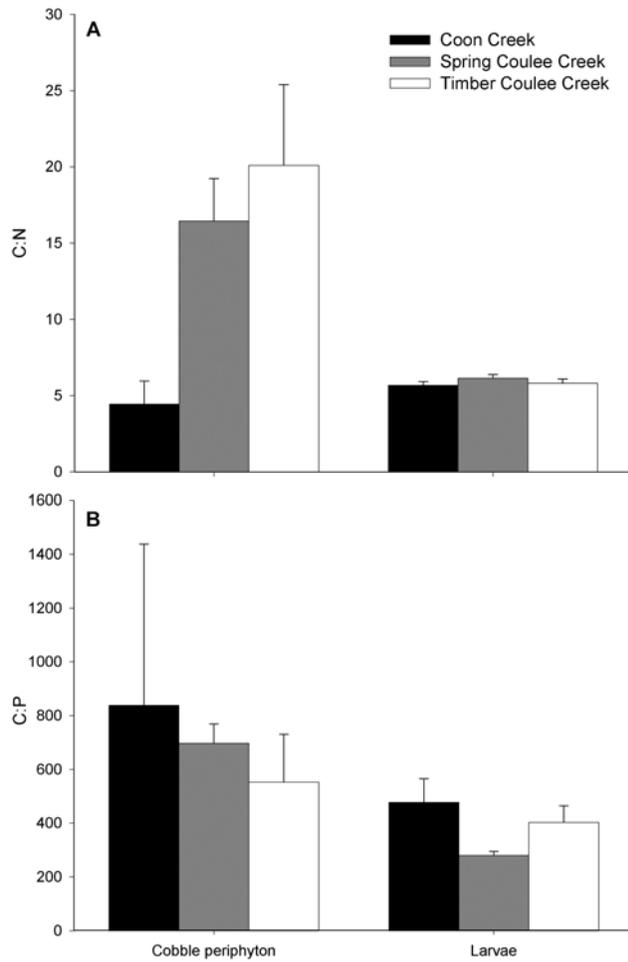


Figure 2. Mean ( $\pm 1$  SE) molar C:N (A) and C:P (B) of cobble periphyton and larvae at Coon Creek, Spring Coulee Creek, and Timber Coulee Creek.

*G. intermedium* and that case grazing facilitates P remineralization in otherwise P-limited streams.

Larval excreta were P-rich relative to the stream water at all 3 sites. The presumed assimilation by case periphyton of additional P from larval excreta decreased N:P of case periphyton at CC and SC ( $11 \pm 3$  and  $11 \pm 0.8$ ) to levels below those of the surrounding cobble periphyton ( $368 \pm 109$  and  $50 \pm 10$ ). This result suggests that case periphyton is a more P-rich dietary resource than cobble periphyton. Furthermore, the molar ratios suggest that P-rich excretion products alleviate P limitation of case periphyton in CC and SC, 2 streams that otherwise only support P-limited periphyton.

The nutritional content of periphyton has consequences for its grazers. Herbivores often change their feeding habits to cope with resources of differing nutritional content (Kohler 1992). Under conditions where dietary resources are nutrient limiting, herbivores can alter their feeding rate, resource selection, biomass growth rate, and population growth rate (Sterner and Elser 2002, Frost et al. 2005, 2006,

Wagner et al. 2013). Grazing invertebrates may preferentially graze on case periphyton because of its higher nutrient content. P-rich case periphyton may be partially responsible for the benefits to invertebrates of feeding on/near caddisfly aggregates. For example, when caddisfly larvae feed in close proximity, their individual growth rates increase (Katano et al. 2007), *Baetis* sp. nymphs have higher population densities on *Glossosoma* sp. cases than on surrounding cobbles (Poff and Ward 1988), and dense populations of *Baetis* sp. have lower mortality in the presence of *Glossosoma* sp. than in its absence (Kohler 1992). Thus, *Glossosoma* aggregations, which can reach up to 40 larvae/0.1 dm<sup>2</sup> (Morris et al. 2011), provide large patches of P-rich periphyton for themselves and for other grazers, and they may promote P turnover in P-limited streams.

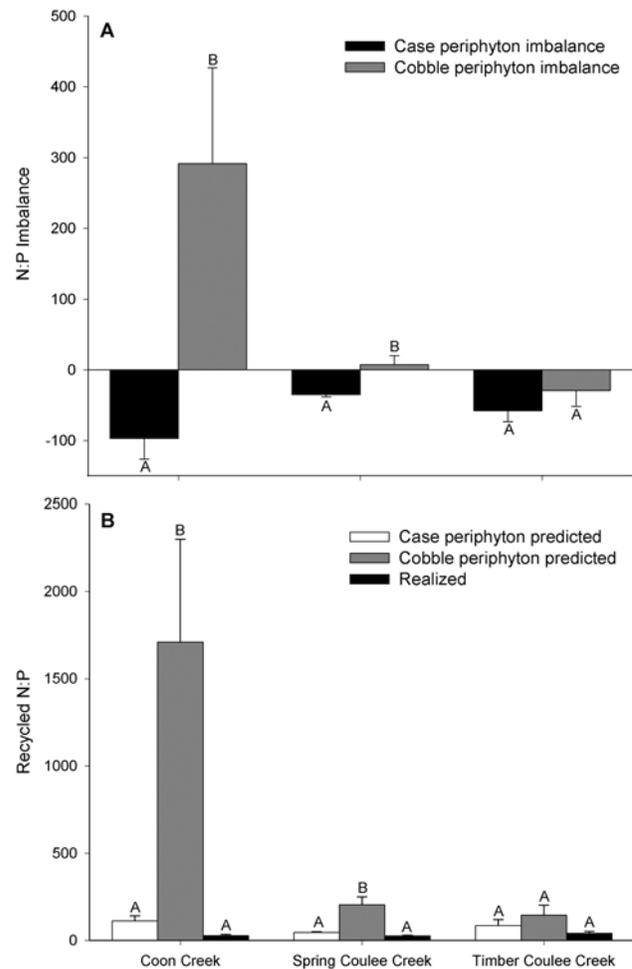


Figure 3. A.—Mean ( $\pm 1$  SE) molar N:P imbalances between cobble periphyton and *Glossosoma intermedium* and between case periphyton and *G. intermedium* in the 3 streams. Positive imbalances suggest P limitation, whereas negative imbalances suggest N limitation. Bars with the same letter within a stream are not significantly different. B.—Mean ( $\pm 1$  SE) predicted excretion N:P with consumption of cobble or case periphyton and actual excretion N:P. Bars with the same letter within a stream are not significantly different.

Homeostatic consumers maintain relatively constant body nutrient ratios, regardless of their dietary resource (Elser and Urabe 1999). C:N and C:P of larvae and cobble periphyton did not differ among stream sites. Thus, results based on C ratios were inconclusive. However, larval tissue N:P did not differ among streams despite significant differences in cobble periphyton N:P among streams. Thus, our data suggested that *G. intermedium* were homeostatic in their N and P body nutrient composition. Our results are similar to those of other studies, which show that most aquatic consumers are nutritionally homeostatic (Stelzer and Lamberti 2002, Evans-White et al. 2005, Persson et al. 2010, Veldboom and Haro 2011). Based on stoichiometric theory, nutrient ratios in a homeostatic consumer's excreta depend on the balance of nutrients in its tissue and in its food resource (Sterner and Elser 2002, Vanni 2002). However, the connections among the nutritional composition of a homeostatic consumer, its resource, and its excreta may be unclear if the consumer can choose among multiple resources of varying nutritional quality.

Stoichiometric theory predicts that a homeostatic consumer ingesting a P-deficient resource (food N:P > consumer body N:P) should excrete at an N:P greater than the N:P of its resource (Sterner and Elser 2002). The reason is that the consumer should retain as much P as possible and differentially excrete excess N. If *G. intermedium* grazed exclusively on cobble periphyton, our results from CC would be contrary to this prediction. Larval N:P ( $108 \pm 32$ ) and excreta N:P ( $27 \pm 8$ ) were lower than cobble periphyton N:P ( $368 \pm 109$ ). Furthermore, at CC and SC, the predicted excretion N:P values with cobble periphyton as a food source ( $1710 \pm 589$  and  $205 \pm 45$ , respectively) were much greater than the actual excretion N:P values at both CC and SC ( $27 \pm 8$  and  $26 \pm 4$ , respectively; Fig. 3B). However, assuming that case periphyton was being consumed by the larvae, the predicted excretion N:P at CC and SC ( $111 \pm 29$  and  $46 \pm 3$ , respectively) were similar to the actual excretion N:P (Fig. 3B). The predicted excretion N:P values suggest that consumption of case periphyton may lead to faster turnover of P than consumption of cobble periphyton. That actual excretion N:P was more similar to the predicted excretion N:P using case periphyton as food source is evidence that the larvae grazed on cases rather than on cobbles. This feeding behavior has a substantial effect on the cycling of P in these P-limited streams. This effect may be magnified if the frequency of case grazing is high, which becomes more likely when larvae form large aggregates on the stream bed.

In many midwestern USA streams, *Glossosoma* play a key role in ecosystem functioning because they directly exert both top-down and bottom-up controls by removing streambed periphyton through grazing (Hart 1981, Kohler 1992, Wallace and Webster 1996) and by exposing case periphyton to extra nutrients. We used predictions from ecological stoichiometry theory to show that periphyton col-

onizing the cases of *G. intermedium* larvae in P-limited streams is relatively P rich via P fertilization by larval excreta. This nutrient-rich, basal resource may serve as a vital food source for grazers, such as *G. intermedium*, themselves and for others during periods of low periphyton biomass, and any time a more nutrient-rich resource is needed.

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