Nutrient-specific foraging by *Glossosoma intermedium* larvae leads to conspecific case grazing

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Abstract: Nutrient-specific foraging, or selection of resources based on nutritional quality, is a strategy homeostatic consumers use to meet their dietary nutritional needs. *Glossosoma intermedium* is a homeostatic caddisfly that often grazes nutrient-rich periphyton colonizing the cases of conspecific larvae. We hypothesized that case grazing may be the result of nutrient-specific foraging under conditions where streambed periphyton is nutrient deficient. To test this hypothesis, we monitored larvae in experimental streams. We measured case-grazing frequency and duration under 4 treatments of streambed periphyton: ambient (control), +N, +P, and +NP. Case-grazing frequency was significantly lower in the +NP treatment than in the other treatments, suggesting that nutritional quality influences resource selection by *G. intermedium*. However, duration of case-grazing bouts was not influenced by treatment. In addition, grazing by *G. intermedium* increased streambed periphyton C∶P and N∶P more in the +P treatment than in the other treatments, whereas grazing did not affect streambed periphyton C∶N or algal biomass differently among treatments. This result suggests that *Glossosoma* was P limited, and that it either differentially ingested P-rich periphyton or differentially retained P. Our study suggests that nutrient imbalances between streambed periphyton and grazer nutrient demand lead to case grazing by *G. intermedium* larvae and that the different strategies (case grazing, selective foraging, differential nutrient excretion/retention) that P-limited grazers use to meet their nutritional needs lead to P depletion of the surrounding periphyton mat.

Key words: *Glossosoma intermedium*, nutrient-specific foraging, stoichiometry, lotic ecosystem, grazing behavior

Homeostatic consumers, i.e., consumers that maintain a constant internal elemental balance, require specific and relatively stable proportions of C, N, and P for growth (Sterner 1990, Sterner and Elser 2002, Persson et al. 2010). To maintain this elemental homeostasis, consumers differentially excrete nutrients (Anderson et al. 2005, Boersma and Elser 2006) and alter their feeding strategies to acquire the appropriate balance and amount of C, N, and P (DeMott et al. 1998, Cook et al. 2000, Hood et al. 2014). Two often-used feeding strategies are compensatory feeding and nutrient-specific foraging (Suzuki-Ohno et al. 2012, Neeson et al. 2013, Liess 2014). During compensatory feeding, consumers increase their ingestion rate of an imbalanced resource in an attempt to acquire sufficient amounts of the limiting nutrients (Fink and Von Elert 2006, Liess 2014). During nutrient-specific foraging, organisms select complementary resources based on their internal nutritional status and nutritional requirements (Simpson et al. 2004, Neeson et al. 2013). Nutrient-specific foraging can be beneficial to terrestrial invertebrates, such as *Deroceras reticulatum* and *Locusta migratoria* (Simpson and Abisgold 1985, Cook et al. 2000, Raubenheimer and Simpson 2003), but this feeding method has been studied less frequently in lotic, benthic grazers, such as caddisflies.

Primary consumers in freshwater ecosystems often have to cope with highly variable and nutritionally imbalanced periphyton as their primary resource (Pringle et al. 1988, Frost and Elser 2002, Evans-White et al. 2005). Grazing herbivores, such as caddisfly larvae, alter their feeding behavior and resource selection to cope with resource availability. For example, homeostatic *Glossosoma* larvae preferentially move toward thick periphyton mats and consume algae, especially diatoms, rather than other organic matter (Oemke 1984, McNeely et al. 2007, Katano and Doi 2014). *Glossosoma intermedium* larvae engage in conspecific case grazing, wherein they consume P-rich periphyton (Cavanaugh et al. 2004, Mooney et al. 2014). Larvae engage in case grazing especially when ambient algal biomass is low, even though this behavior carries the risk of becoming dislodged from substrate and entering drift

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DOI: 10.1086/686699. Received 26 May 2015; Accepted 27 January 2016; Published online 7 April 2016.
Freshwater Science. 2016. 35(3):873–881. © 2016 by The Society for Freshwater Science.

(Wiley and Warren 1992, Cavanaugh et al. 2004). This behavior suggests that low food availability or possibly even low food quality leads to case grazing.

Streambed periphyton, the basal resource for *G. intermedium*, is often low in P content with high N : P ratios (Mooney et al. 2014) and can limit *G. intermedium* growth through P deficiency (Hart and Robinson 1990, Elser et al. 2000, Stelzer and Lamberti 2002). Thus, case grazing may be an example of nutrient-specific foraging by a benthic grazer in which larvae select P-rich case periphyton to supplement P-deficient streambed periphyton to meet their nutritional requirements.

Mechanisms used by grazers to avoid nutrient limitation, such as nutrient-specific foraging and differential nutrient excretion, may subsequently affect the nutrient content of periphyton through top-down and bottom-up mechanisms, respectively (Sterner 1990, Cross et al. 2005, Frost et al. 2005). Grazer presence typically increases P-content of periphyton (Liess and Hillebrand 2004). However, grazers with relatively high body C : P or N : P ratios, such as *G. intermedium* (C : P > 300) (Mooney et al. 2014), tend to increase periphyton N rather than P content and increase periphyton N : P ratios (Hillebrand et al. 2008). The decrease in periphyton P content brought on by P-limited grazers with high C : P or N : P body nutrient ratios may be partly a consequence of selective P consumption or P retention. In addition to case grazing, *G. intermedium* larvae also may selectively consume P-rich periphyton components. This behavior may allow larvae to maintain their elemental balance without ingesting more periphyton.

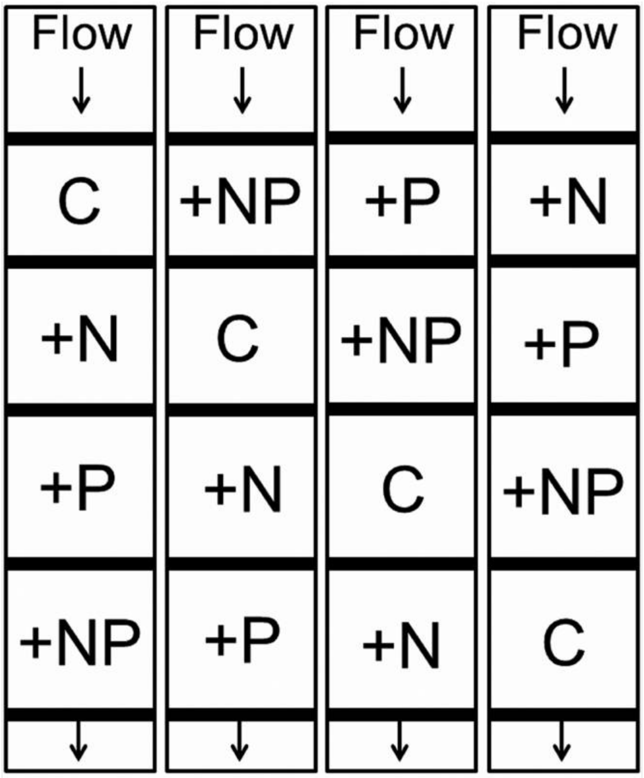
Our primary objective was to test whether *G. intermedium* larvae consumed case periphyton more frequently when streambed periphyton was nutritionally imbalanced (nutrient-specific foraging) than when it was nutritionally balanced. Therefore, we monitored larval grazing behavior while manipulating N : P of streambed periphyton with nutrient-diffusing substrate (NDS) treatments (control, +N, +P, and +NP). We hypothesized that *G. intermedium* larvae alter their resource selection (streambed or case periphyton) in response to the nutritional quality of streambed periphyton. This hypothesis led to 2 predictions: that conspecific case grazing would be: 1) more frequent, and 2) of longer duration in the control and +N periphyton treatments than in the +P and +NP treatments because P depletion of the periphyton in the control and +N periphyton would render it stoichiometrically imbalanced relative to the needs of *G. intermedium* larvae.

Our secondary objectives were to assess how larval grazing affected streambed periphyton chlorophyll *a* (chl *a*, $\mu g/cm^2$) and nutrient content among treatments. We hypothesized that grazing would deplete algal biomass similarly among all periphyton treatments. This hypothesis led us to predict that postgrazed algal biomass would be lower than pregrazed algal biomass and would not differ among treatments (prediction 3). We also hypothesized that P (or P-rich components) would be removed by larvae through selective grazing where it was readily available in streambed periphyton. This hypothesis led us to predict that grazing would increase periphyton N : P more in +P and +NP treatments than in control and +N treatments (prediction 4).

METHODS

Experimental design

We used a 4 (treatment) × 4 (row = position in experimental flume) × 4 (column = day of observation) Latin square design (Fig. 1) to test how 4 periphyton treatments (control, +N, +P, and +NP) influenced case-grazing frequency and duration of case-grazing bouts. We completed grazing trials over 4 consecutive days (1 trial/d). The primary reason for using the Latin square design was to ensure that the treatment periphyton from upstream treat-



Flow ↓	Flow ↓	Flow ↓	Flow ↓
C	+NP	+P	+N
+N	C	+NP	+P
+P	+N	C	+NP
+NP	+P	+N	C
↓	↓	↓	↓

Figure 1. The Latin square design and experimental flume set-up used for the observational experiment. Letters represent treatments (C = control, +N, +P, +NP). Rows are longitudinal positions of treatments in the flume, and columns are sampling days (day 1–4). Thick black lines between treatments represent screen separations. Water was circulated from the top of each flume through all of the separated treatments (black arrows).

ment periphyton positions in the experimental flume did not alter the behavior of larvae in downstream segments.

Altering resource nutritional quality

We deployed NDS (Tank et al. 2006) filled with nutrient-amended agar in Spring Coulee Creek, a spring-fed stream in the Driftless Area of the midwestern USA (Vernon County, Wisconsin) (Mooney et al. 2014). We chose to grow periphyton in Spring Coulee Creek because it had only a small population of grazers at the time of the study. To grow streambed periphyton with differing nutritional quality, we amended agar to low N : P (+0.5 × 10^6 μmol/L PO_4^{3-}-P), ambient N : P (no nutrient additions), moderate N : P (+8.00 × 10^6 μmol/L NO_3^--N and 0.5 × 10^6 μmol/L PO_4^{3-}-P), and high N : P (+8.00 × 10^6 μmol/L NO_3^--N) (Pringle 1987). The +NP treatment agar was amended to have an N : P of 16 : 1 because that ratio was near the ideal N : P for periphyton (18 : 1) (Kahlert 1998). Larvae excrete at ∼30:1 (N : P), which resulted in case periphyton with an N : P of ∼11:1 (Mooney et al. 2014). Agar percentages were 2% (20 g/L) for the control, +N, and +P treatments, and 3% (30 g/L) for +NP treatment (Tank et al. 2006, Capps et al. 2011). NDS were incubated for 25 d to allow periphyton to colonize the exposed area of the fritted-glass discs (3.14 cm^2). We staggered NDS deployment over 4 d to ensure that treatment periphyton for day 4 had the same incubation time as treatment periphyton for day 1.

We collected 4 fritted glass discs from the deployed NDS after the 25-d incubation period, scrubbed periphyton from the 4 discs in a known amount of deionized water, sonicated the samples, and then immediately filtered the samples (Whatman GF/F; Maidstone, UK) and dried the filters. The dried filters containing the treatment periphyton were stored in a desiccator prior to C, N, and P analyses to test whether we successfully altered periphyton nutritional composition. We collected 2 discs from each treatment to analyze pregrazed algal biomass (μg chl *a*/cm^2). The discs used in this way were dried, desiccated, and stored in covered aluminum dishes in a freezer prior to analysis. All remaining fritted glass discs (16/treatment) were used in the grazing-behavior study.

Nutrient and algal biomass analyses

We used hydrochloric acid digestion of solids followed by analysis for soluble reactive P (APHA 2005) to measure TP concentrations of nutrient-amended periphyton per unit surface area of filter segments (6-mm filters). We used a Costech® (Valencia, California) CHN elemental analyzer to measure total C and N concentration of nutrient-amended periphyton/unit surface area of filter segments. We measured algal biomass of the nutrient-amended periphyton as chl *a* content (μg/cm^2) on whole fritted glass discs spectrophotometrically (acetone extraction; APHA 2005).

Grazing behavior experiment

On the day of each observation, we removed the 16 fritted glass discs assigned to the corresponding row/column of the grazing experiment from the NDS and placed 4 discs from each treatment in a corresponding screened-in section (1 section/treatment) of the experimental flume (Fig. 1). We scrubbed the flume to remove any biofilm immediately before the addition of treatment periphyton to ensure that larvae had only 2 food choices: treatment and case periphyton. We collected 40 *G. intermedium* larvae from Rullands Coulee Creek, a spring-fed stream comparable to Spring Coulee Creek in Vernon County, Wisconsin, on each of the 4 consecutive days of observation. We placed larvae in 4 jars (10 larvae/jar) filled with stream water and stored them in a cooler for transportation to the experimental flumes. We placed 10 larvae in each treatment section and allowed them to acclimate to their treatments for 2 h before a 2-h observation period. The 2-h acclimation period and subsequent observational period should have been sufficient to induce nutrient-specific foraging. Simpson et al. (1990) found that the terrestrial locust *Locusta migratoria* altered its feeding strategy after 1 low-quality meal, and Moelzner and Fink (2014) found that the snail *Lymnaea stagnalis*, a benthic grazer, could distinguish among algal qualities in <1 h. We quantified case-grazing frequency (number of case-grazing bouts individual $[ind]^{-1}$ h^{-1}) and the duration of case-grazing bouts (total time spent case grazing/number of bouts) for each treatment during each 2-h observational period (Cavanaugh et al. 2004).

Effect of grazing on streambed periphyton

After the observation period, we collected the fritted glass discs and analyzed postgrazed nutrient and chl *a* content. We estimated grazer effects on nutritional composition and algal biomass of the periphyton (postgrazed molar ratio/pregrazed molar ratio and postgrazed chl *a*/pregrazed chl *a* content).

Statistical analyses

All analyses were completed in SPSS (version 20; SPSS, Armonk, New York) with $\alpha = 0.05$. We used a 1-way analysis of variance (ANOVA) with pregrazed C : N, C : P, N : P, and chl *a* content as the dependent variables and periphyton treatment as the independent variable to test for differences in nutritional composition and algal biomass among periphyton treatments. We used post hoc multiple comparison analysis (Tukey's Honestly Significant Difference [HSD]) to identify specific differences among periphyton treatments.

We used 3-way, fully factorial ANOVA with case-grazing frequency as the dependent variable and row and column within the Latin square design and treatment as independent variables to test whether case-grazing frequency differed among periphyton treatments. We followed the ANOVA with Tukey's HSD to identify specific differences resulting from independent variables. We used a second 3-way, fully factorial ANOVA with bout duration as the dependent variable and row, column, and treatment as independent variables to test whether bout duration differed among periphyton treatments.

We used 1-way ANOVA with grazing effect on periphyton C : N, C : P, N : P, and chl *a* as the dependent variables and treatment as the independent variable to test whether grazing effects of *G. intermedium* differed among periphyton treatments.

RESULTS

Nutrient treatment

Streambed periphyton chl *a* and C : N did not differ among treatments (Table 1, Fig. 2A, B). However, streambed periphyton C : P and N : P did differ among treatments (Table 1, Fig. 2C, D). C : P and N : P were significantly lower in the +P treatment than in the control (HSD, $p = 0.019$ and $p = 0.029$, respectively) and +N (HSD, $p = 0.010$ and $p = 0.011$, respectively) treatments, whereas periphyton C : P and N : P ratios did not differ between the +P and +NP treatments (Fig. 2C, D).

Case grazing

Larval case-grazing frequency differed among treatments (Table 2). Larvae grazed conspecific cases less frequently in the +NP treatment than in the control, +N, and +P treatments (HSD, $p = 0.037$, 0.002, and 0.031, respectively; Fig. 3A). Position in the flume did not affect larval case-grazing frequency, but day of observation did (Table 2). Case-grazing frequency was significantly higher on day 1 than on days 3 and 4 (HSD, $p = 0.027$ and 0.013, respectively). Neither treatment, position in the flume, nor day of observation affected duration of case-grazing bouts (Table 2, Fig. 3B).

Effect of grazing on periphyton

Larval grazing reduced chl *a* content and increased C : N similarly in all treatments (grazing effect was <1 and >1, respectively; Table 3, Fig. 4A, B). Larval grazing increased periphyton C : P in all treatments, but disproportionally increased periphyton C : P in the +P treatment relative to the control, +N, and +NP treatments (HSD, $p = 0.013$, 0.019, and 0.025, respectively; Fig. 4C). Grazing increased periphyton N : P in the +P treatment and decreased N : P in the control, +N, and +NP treatment (HSD, $p = 0.005$, 0.007, and 0.009, respectively; Fig. 4D)

DISCUSSION

We produced streambed periphyton communities with a significantly lower C : P and N : P in the +P than in the control and +N treatments. Thus, periphyton nutrient stoichiometry differed among treatments. Relative to our first hypothesis, case-grazing frequency was significantly lower in the +NP treatment than in the control, +N, and +P treatments (partially supporting prediction 1), but bout duration did not differ among treatments (opposing prediction 2). These results suggest that nutritional stoichiometry of streambed periphyton partially drives case grazing by *G. intermedium* larvae. Subsequently, we found that larval grazing reduced chl *a* content similarly among all treatments (supporting prediction 3) and increased C : P and N : P more in the +P treatment than in the control, +N, and +NP treatments. These results suggest that grazing

Table 1. Analysis of variance showing the effects of treatments (control, +N, +P, and +NP) on pregrazed periphyton C : N, C : P, N : P, and chlorophyll *a* (μg chl *a*/cm^2). df = degrees of freedom, MS = mean square. * indicates a significant effect.

Variable	Source of variation	df	MS	*F*	*p*
C : N	Between treatments	3	0.171	0.298	0.826
	Within treatments	12	0.573		
	Total	15			
C : P	Between treatments	3	43,138.965	6.671*	0.007
	Within treatments	12	6466.565		
	Total	15			
N : P	Between treatments	3	1329.213	5.975*	0.010
	Within treatments	12	222.465		
	Total	15			
Chl *a* (μg/cm^2)	Between treatments	3	82.760	0.763	0.536
	Within treatments	12	108.454		
	Total	15			

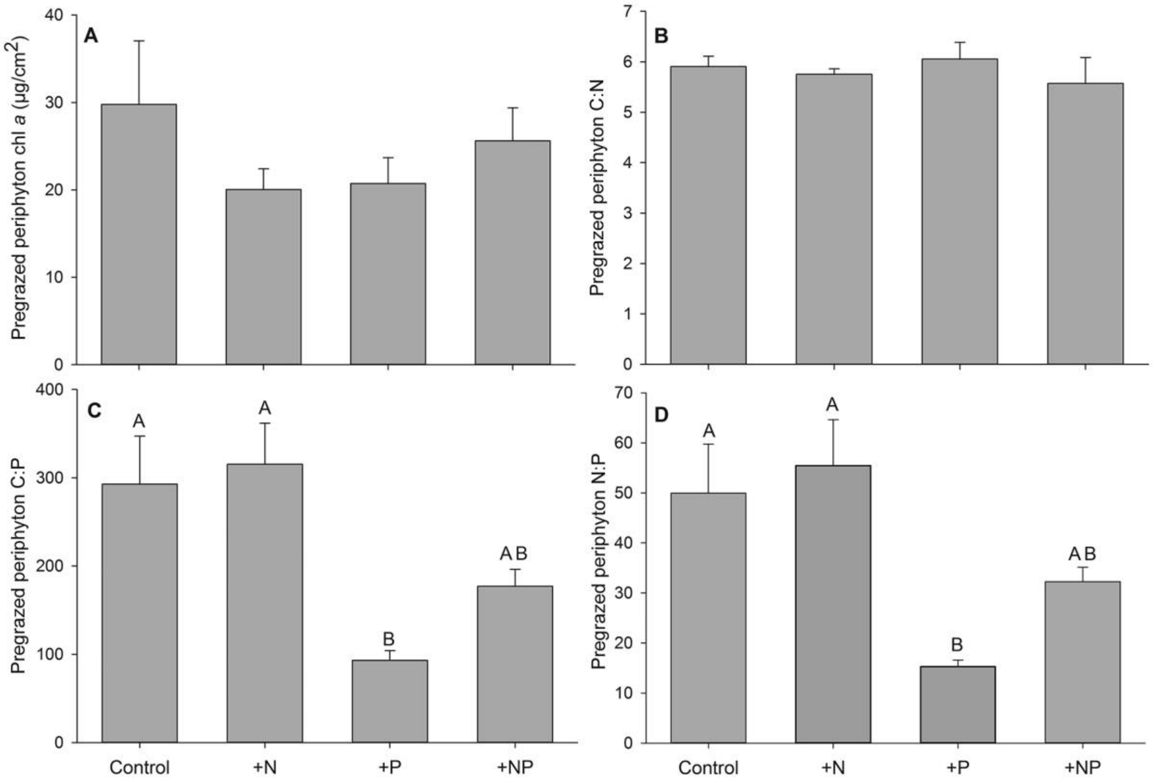


Figure 2. Mean (+1 SE) chlorophyll *a* (chl *a*) concentration (A) molar C : N (B), C : P (C), and N : P (D) of pregrazed treatment periphyton in control, +N, +NP, and +P treatments. Means with the same letters are not significantly different (Tukey's Honestly Significant Difference, $p > 0.05$).

by *G. intermedium* reduced P-content of periphyton that had the highest availability of P (partially supporting prediction 4).

Effects of resource stoichiometry on case grazing

Algal biomass (as chl *a*) did not differ among treatments, but periphyton stoichiometry did (lower N : P and C : P in +P treatment than in the other treatments). Therefore, we focused on how nutrient stoichiometry of periphyton influenced case grazing by larval *G. intermedium*.

Larvae engaged in case grazing less frequently in the +NP than in the other treatments. The +NP periphyton probably was the most stoichiometrically balanced food option for the larvae because it had an N : P ratio (33 ± 4) similar to that of *Glossosoma* larvae (N : P = 30; Evans-White et al. 2005, Mooney et al. 2014). If larvae engaged in nutrient-specific foraging, the need to consume P-rich case periphyton should have been minimal in the +NP treatment where streambed periphyton was not P-deficient relative to their needs. This expectation was reflected by our results. In contrast, N : P of periphyton grown in the +P treatment (15.27 ± 1.34) most closely resembled that of case periphyton (11.05 ± 0.8; Mooney et al. 2014). The stoichiometric similarities between periphyton grown in the +P treatment and case periphyton led us to expect minimal case grazing in the +P treatment because the stoichiometric benefits of case grazing should have been low. However, case-gazing frequency did not differ between the +P and +N treatments, despite their significantly different N : P ratios (+P: 15.27 ± 1.34, +N: 55.47 ± 9.18).

The +P periphyton may have had a higher proportion of P than necessary for the larvae and, thus, might not have been an ideal dietary resource. By the same reasoning, case

Table 2. Analysis of variance showing differences in case-grazing frequency (bouts individual^{-1} h^{-1}) and bout duration (total time spent case grazing/total instances of case grazing) among treatments, longitudinal position in the flume, and sampling day. df = degrees of freedom, MS = mean square. * indicates a significant effect.

Dependent variable	Source of variation	df	MS	*F*	*p*
Case-grazing frequency	Treatment	3	0.241	15.928*	0.003
	Position	3	0.031	2.045	0.209
	Day	3	0.133	8.753*	0.013
Bout duration	Treatment	3	6.949	3.116	0.110
	Position	3	0.554	0.248	0.860
	Day	3	9.001	4.037	0.069

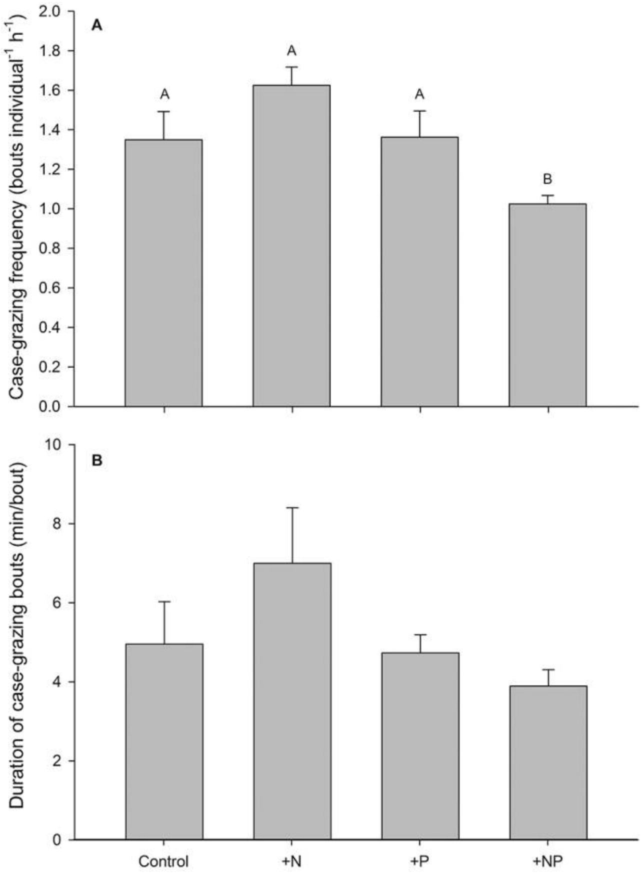


Figure 3. Mean (+1 SE) case-grazing frequency (A) and bout duration (B) over a 2-h period. Means with the same letters are not significantly different (Tukey's Honestly Significant Difference, $p > 0.05$).

periphyton may not be an ideal resource on its own but might serve as an imbalanced resource (high P content) that complements other imbalanced resources (streambed periphyton) with high N content. We observed a lower frequency of case grazing in the +NP treatment than in the other treatments, and no significant differences among the control, +N, or +P treatments. These results suggest that case grazing may be a behavior induced by general nutritional imbalances in an attempt to ingest as many resources as possible to reach a stoichiometric median. Thus, larval case grazing would be expected to be less frequent only at times when their resource is ideal (similar to our +NP treatment) and the need for the consumption of multiple types of resources is minimal.

Nutrient content of streambed periphyton did not affect bout duration. This result suggests that algal biomass, rather than nutrient content, is the key factor affecting the time a grazer spends in 1 resource patch (Hart and Resh 1980, Kohler 1984). The need to graze conspecific cases may be greater at times when streambed algal biomass is severely depleted than when streambed periphyton is nutritionally imbalanced, but our results suggest that larvae use case grazing to optimize their intake of nutritionally complementary resources.

Grazing on streambed periphyton

If compensatory feeding were the primary mechanism used by larvae to avoid nutrient limitation, larvae should have increased consumption and removed more algae when periphyton nutrient content was highly imbalanced (control and +N treatments) relative to when the nutrient content was balanced. Overall consumption of periphyton did not appear to differ among treatments despite the differing nutritional qualities of the periphyton. Instead, larval grazing increased N : P significantly more in the +P treatment than in the other treatments without disproportionally reducing algal biomass. This result suggests that larvae reduced P content when P was readily available in the periphyton mat. The mismatch between the disproportional reduction of P and consistent removal of algal biomass among treatments suggests that P-limited larvae preferentially consumed P-rich components of the periphyton mat. Thus, larvae may have used nutrient-specific foraging to increase their consumption of P without compensatory feeding. However, differences in C : P and N : P of postgrazed periphyton also can arise from differential nutrient retention/excretion by larvae in response to their food source.

Study limitations

We showed that streambed periphyton stoichiometry plays a role in case-grazing behavior, but our study was limited by the narrow range of treatment periphyton N : P

Table 3. Analysis of variance showing the effects of treatments (control, +N, +P, and +NP) on grazing effect (postgrazed/pregrazed) on periphyton C : N, C : P, N : P, and chlorophyll *a* (μg chl *a*/cm^2). df = degrees of freedom, MS = mean square. * indicates a significant effect.

Variable	Source of variation	df	MS	*F*	*p*
C : N	Between treatments	3	0.079	0.814	0.510
	Within treatments	12	0.097		
	Total	15			
C : P	Between treatments	3	11.388	6.291*	0.008
	Within treatments	12	1.810		
	Total	15			
N : P	Between treatments	3	4.459	8.477*	0.003
	Within treatments	12	0.526		
	Total	15			
Chl *a*	Between treatments	3	0.079	0.635	0.607
	Within treatments	12	0.124		
	Total	15			

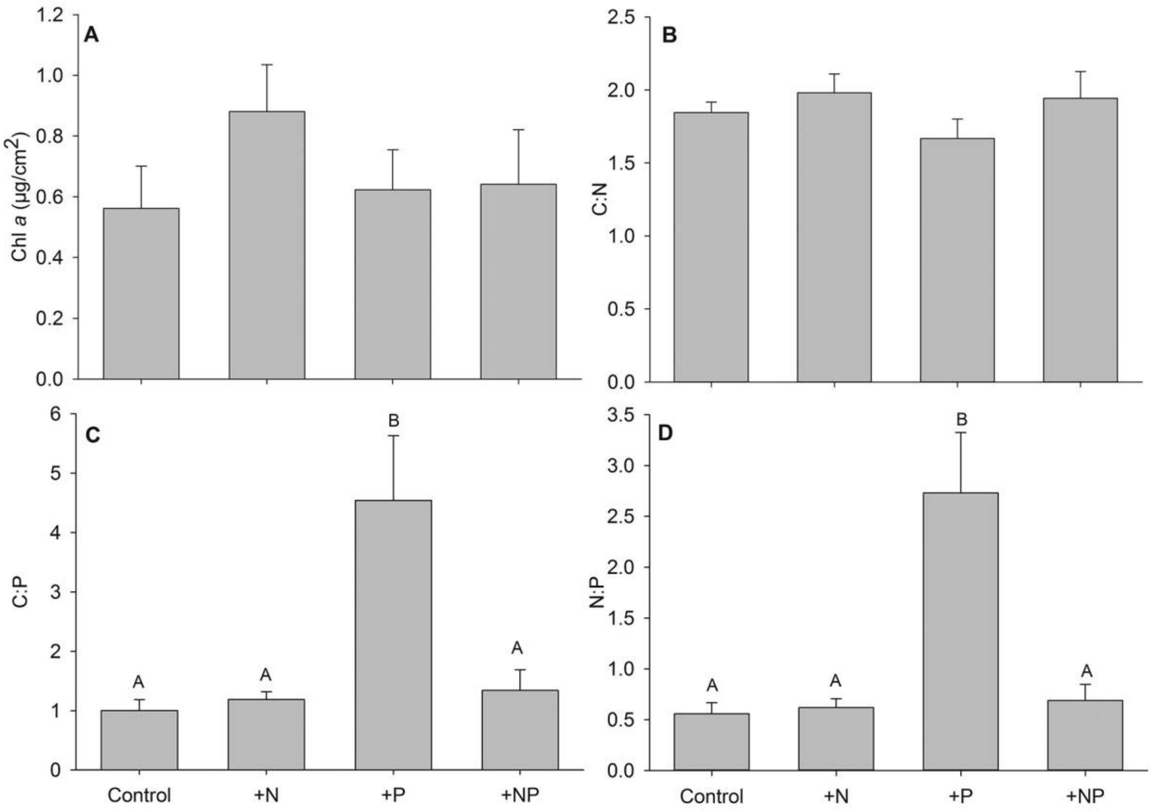


Figure 4. Mean (+1 SE) grazer effect (postgrazed/pregrazed) on chlorophyll *a* (chl *a*) concentration (A), C : N (B), C : P (C), and N : P (D) of periphyton in control, +N, +P, and +NP treatments. Values >1 indicate a positive effect, and values <1 indicate a negative effect. Means with the same letters are not significantly different (Tukey's Honestly Significant Difference, $p > 0.05$).

ratios. Larger differences in periphyton N : P among treatments might yield clearer patterns of resource selection by *Glossosoma* larvae. In addition, the time frame of our experiment was relatively short. Despite these limitations, we found that larvae have the ability to engage in nutrient-specific foraging. Thus, our relatively short, laboratory-based behavioral study may be a conservative measure of the ability of larvae to identify nutritionally beneficial resources. Fuller understanding of nutrient-specific foraging by benthic grazers may require use of longer laboratory experiments with resources that differ more strongly or in situ manipulations and observational experiments that address grazing behavior, followed by gut-content and stoichiometric analyses.

Conclusions

Similar to Cavanaugh et al. (2004), we found that *G. intermedium* graze conspecific case periphyton in response to environmental conditions. Case grazing occurs more frequently when streambed periphyton is nutritionally imbalanced relative to the needs of *G. intermedium*, a result suggesting that case periphyton serves as an important dietary supplement. Moreover, nutrient-specific foraging can lead to selective consumption of P-rich components of periphyton mats when they are readily available. We conclude that nutrient-specific grazing by *G. intermedium* larvae on selected resources (case periphyton or P-rich algal cells in periphyton) allows them to reach nutritional balance more efficiently than does compensatory feeding.

ACKNOWLEDGEMENTS

We thank the University of Wisconsin–La Crosse for funding through a Research, Service, and Educational Leadership grant. This paper was awarded the best poster presentation in basic research at the 2013 meeting of the Society of Freshwater Science in Jacksonville, Florida. We also thank Associate Editor Antonia Liess and 2 anonymous referees for providing comments and suggestions that greatly enhanced this paper.

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