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Quantity and quality limit detritivore growth: mechanisms revealed by ecological stoichiometry and co-limitation theory

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Abstract. Resource quantity and quality are fundamental bottom-up constraints on consumers. Best understood in autotroph-based systems, co-occurrence of these constraints may be common but remains poorly studied in detrital-based systems. Here, we used a laboratory growth experiment to test limitation of the detritivorous caddisfly larvae *Pycnopsyche lepida* across a concurrent gradient of oak litter quantity (food supply) and quality (phosphorus:carbon [P:C ratios]). Growth increased simultaneously with quantity and quality, indicating co-limitation across the resource gradients. We merged approaches of ecological stoichiometry and co-limitation theory, showing how co-limitation reflected shifts in C and P acquisition throughout homeostatic regulation. Increased growth was best explained by elevated consumption rates and improved P assimilation, which both increased with elevated quantity and quality. Notably, C assimilation efficiencies remained unchanged and achieved maximum 18% at low quantity despite pronounced C limitation. Detrital C recalcitrance and substantive post-assimilatory C losses probably set a minimum quantity threshold to achieve positive C balance. Above this threshold, greater quality enhanced larval growth probably by improving P assimilation toward P-intensive growth. We suggest this interplay of C and P acquisition contributes to detritivore co-limitation, highlighting quantity and quality as potential simultaneous bottom-up controls in detrital-based ecosystems, including under anthropogenic change like nutrient enrichment.

Key words: *assimilation; consumption; detritus; headwater streams; multiple resources; Pycnopsyche lepida; response surface; subsidies.*

INTRODUCTION

Resource quantity and quality are primary bottom-up constraints on consumer growth and energy flow in ecosystems (Hessen et al. 2002, Cross et al. 2006, Marcarelli et al. 2011). Nutrient supply is a key factor shaping the quantity and quality of consumers' resources. In autotroph-based food webs, elevated nutrients simultaneously increase autotroph growth and nutrient content (Hessen et al. 2002). However, elevated nutrients affect detritus-based food webs differently, because nutrients reduce detrital quantity via stimulated decomposition, yet increase detrital quality via greater detrital microbial biomass and nutrient content (Rosemond et al. 2015, Manning et al. 2016). This

"decoupling" of quantity and quality can be exacerbated by other anthropogenic stressors, such as riparian clearance, that alter detrital subsidies (Kominoski and Rosemond 2012, Larsen et al. 2016). While these bottom-up changes alter community composition and secondary production (Cross et al. 2006, Prater et al. 2015, Wallace et al. 2015), mechanistic responses of detritivores to the quantity–quality continuum remain poorly studied.

Based primarily on herbivore models, ecological stoichiometry theory uses threshold elemental ratios (TERs) to predict that lower quantity but higher quality of resources will switch animals from nutrient- to carbon (C)-limited growth (Sturner 1997, Plath and Boersma 2001, Boersma and Elser 2006). Reduced quantity imposes C limitation due to increased C relative to nutrient costs of foraging and respiration under low food availability (Sturner 1997). Increased resource nutrient contents, such as of phosphorus (P), improve diet quality and decrease growth limitation toward optimal growth (Boersma and Elser 2006). Although both quantity and

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quality can limit growth, ecological stoichiometry often assumes the element in shortest supply (C, P, or others such as nitrogen) is limiting growth at a given time, according to Liebig's law of the minimum (Sternler 1997, Sternler and Elser 2002). However, recent data suggest that herbivore growth can be more realistically described by simultaneous limitation, or "co-limitation," of multiple resources (Plath and Boersma 2001, Sperfeld et al. 2012, 2016a). Co-limitation theory remains untested among detritivores, but offers new tools to investigate continuous responses to both detrital quantity and quality, a pressing knowledge gap in ecological stoichiometry and ecosystem ecology (Venarsky et al. 2014, Sperfeld et al. 2016b), given that detritus dominates energy flow in many ecosystems (Marcarelli et al. 2011).

Resource quantity and quality may co-limit animal growth because they constrain C and P acquisition through regulation (Sperfeld et al. 2016b). Under reduced resource quantity, consumers will ingest less food due to constraints on consumption (Flores et al. 2014). Elevated resource quality may also reduce consumption because animals can relax compensatory feeding for the limiting nutrient (Plath and Boersma 2001, Liess 2014), but the evidence from detritivores is mixed (Flores et al. 2014, Halvorson et al. 2015). Reduced consumption should increase C relative to P assimilation efficiencies, because animals prioritize C acquisition to support metabolism but exhibit lower P demands due to reduced growth (Sternler 1997). Post-assimilation, animals may up- or down-regulate both C respiration and P excretion to minimize losses of assimilated elements and maintain stoichiometric homeostasis (Frost et al. 2005, Sperfeld et al. 2017). These complex responses underpin animal growth and ecosystem functions in response to resource quantity and quality (Manning et al. 2016, Sperfeld et al. 2016b).

Co-limitation may take multiple forms depending on resource categories, response patterns, and underlying mechanisms (Tilman 1982, Saito et al. 2008, Harpole et al. 2011, Sperfeld et al. 2016a). Here, we consider quantity and quality as separate factors constraining acquisition of resources like C and P, thereby ultimately co-limiting growth. The simplest form, strictly essential co-limitation, follows Liebig's minimum rule and closely related TERs by assuming abrupt switches between growth-limiting resources depending on the most limiting factor (Fig. 1A). Alternatively, quantity and quality may interactively limit growth, producing smooth transitions from limitation by one factor to the other (Fig. 1B, C). This case differs mechanistically from TERs because C and P simultaneously limit growth across the resource space. Interactive co-limitation has been demonstrated for the aquatic herbivore *Daphnia* and is likely caused by trade-offs when animals cannot invest in acquisition of each resource simultaneously (Sperfeld et al. 2012). Although the response pattern appears similar to interactively essential patterns, animals may also exhibit biochemically dependent co-limitation (Fig. 1C). Whereas

the former assumes independent resource acquisition, the latter assumes that acquisition of one resource is dependent on sufficient supply of the other, e.g., one resource is used to acquire the other through linked biochemical pathways (Saito et al. 2008, Sperfeld et al. 2016a).

We conducted a laboratory experiment to investigate effects of detrital quantity and quality on growth and underlying stoichiometric regulation of detritivorous caddisfly larvae (*Pycnopsyche lepida*). We predicted that resource quantity (C supply) and quality (diet P:C) would co-limit larval growth, owing to shifts at multiple levels of homeostatic regulation. We analyzed co-limitation patterns using factorial and gradient concepts based on Sperfeld et al. (2016a), illustrating the utility of this approach for stoichiometric data. We analyzed consumption, egestion, P excretion, body elemental composition, as well as assimilation and growth efficiencies with the same approach to gain a mechanistic understanding of co-limitation.

METHODS

Field-collected larvae were fed post oak (*Quercus stellata*) litter conditioned under three P amendments (quality treatments) and three food supply levels (quantity treatments). Leaf litter was collected after senescence in November 2010 in Washington County, Arkansas, USA and stored dry prior to cutting 13.5 mm diameter disks for conditioning in the laboratory. Every 2–3 d, 120 disks were added to mesh bags, leached for 3 d, and added to one of three tubs for 6 weeks' conditioning in 20-L aerated, dechlorinated tap water. Each tub was flushed every 2–3 d and amended with 1,000 $\mu\text{g/L}$ N as KNO_3 and 50, 100, or 500 $\mu\text{g/L}$ P (low, med, or high P treatments, respectively) as Na_2HPO_4 (Halvorson et al. 2015).

We collected fourth- and fifth-instar *Pycnopsyche lepida* (Trichoptera: Limnephilidae) individuals from Chamber Springs, Arkansas in December 2014 for a laboratory growth experiment. Subsets of individuals were randomly chosen to clear guts for 24 h and frozen to determine initial dry mass (mean \pm SE; fourth instar, 4.159 ± 0.392 mg; fifth instar, 7.529 ± 0.681 mg). Eleven fourth-instar and 61 fifth-instar individuals ($n = 72$; note all individuals were fifth instar by experiment end) were each randomly assigned to growth chambers in an environmental room at 10°C and a 10:14 light:dark cycle. Chambers were randomly assigned to the three quality treatments and three quantity treatments in a full factorial design, resulting in eight replicates per treatment combination. For low, med, and high quantity treatments, one, two, or five leaf disks of measured C and P content were fed every 2–3 d during the experiment. Growth chambers contained 100 mL stream water, with water changed at least every 5 d, were constantly aerated, and were equipped with 1-mm mesh to prevent coprophagy. On each feeding date, a subset of disks from each quality was oven-dried and homogenized into

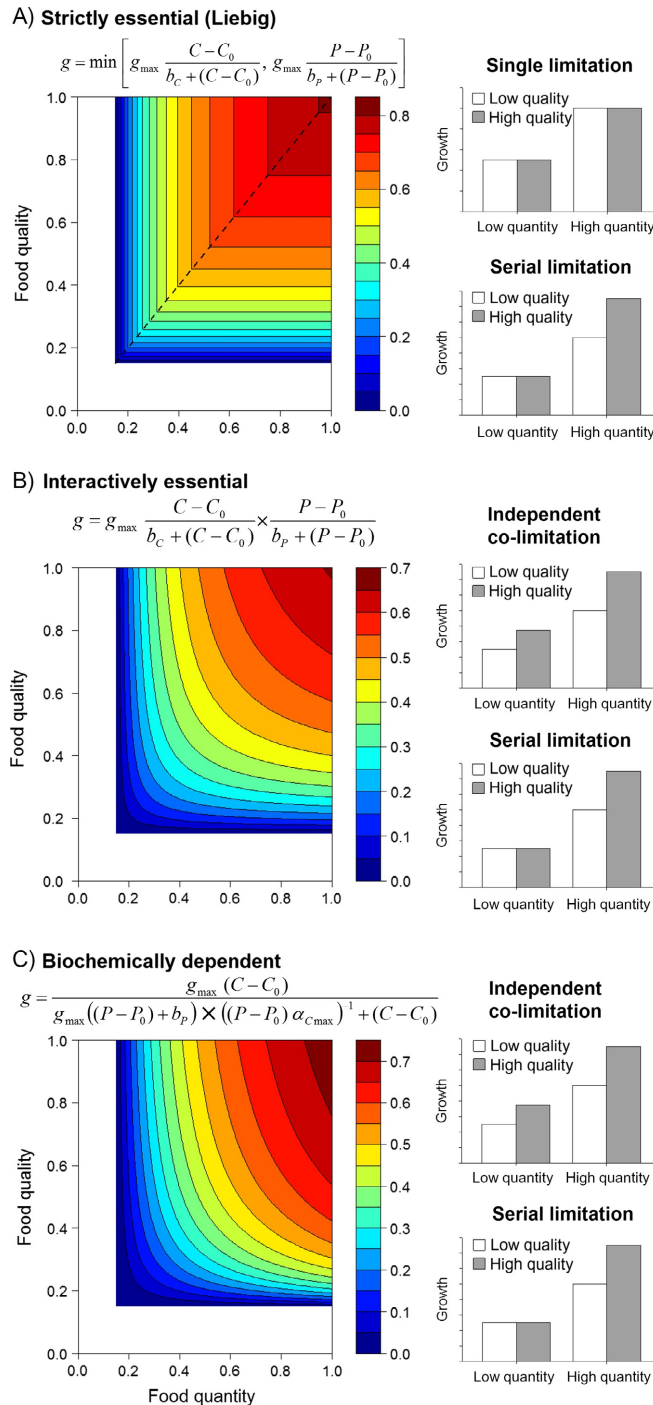


FIG. 1. Response surface types of co-limitation: (A) strictly essential resources following Liebig’s law of the minimum, (B) interactively essential resources, and (C) biochemically dependent resources (adapted from Tilman 1982, Saito et al. 2008, Sperfeld et al. 2012, 2016a). The color code indicates increasing growth depending on food quality (e.g., diet P:C) and quantity (e.g., carbon supply) and black solid lines indicate resource-dependent growth isoclines, i.e., equal growth at changing resource availability. The models assume resource thresholds for zero growth and only positive growth is shown, leaving part of the resource space blank. The dashed line in panel A separates resource space where either quantity or quality is strictly limiting, which may be described as the threshold elemental ratio (TER). Factorial limitation scenarios that are typically indicative for each co-limitation type (Sperfeld et al. 2016a) are shown next to the response surfaces. Equation terms are defined as follows: g is growth, g_{\max} is maximum growth, C is food quantity, C_0 is the quantity threshold for zero growth, P is food quality, P_0 is the quality threshold for zero growth, b_C is the half-saturation constant for quantity, b_P is the half saturation constant for quality, and $\alpha_{C_{\max}}$ is the maximum affinity for quantity that depends on quality (see Saito et al. (2008) for further details).

fine powder to determine elemental content. Once weekly, 10 disks from each quality were also collected and stored in methanol at 4°C to determine ergosterol content (indicator of fungal biomass) following Gessner (2005).

We measured consumption and egestion weekly during 2–3 d trials between feeding events. Consumption was measured as the difference between pre- and post-feeding dry mass of litter disks. Pre-feeding litter mass was determined from blotted mass and a blotted-dry mass regression. Post-feeding mass was determined from disks collected, oven-dried, and weighed after feeding. We converted small negative consumption rates (3% of measures) to zero. Egestion was measured as the production of fine particulates in filtered stream water. Egesta were collected on muffled, pre-weighed 1- μ m glass fiber filters (Pall, Port Washington, New York, USA), oven-dried, and weighed prior to determining elemental content.

After 30 d of growth, we removed litter from growth chambers and immediately commenced 3-h excretion trials with larvae. Larvae were placed in 30 mL filtered stream water, after which they were returned to growth chambers. Excretion trial water was filtered, kept on ice, and measured for soluble reactive phosphorus (SRP) using the ascorbic acid method (APHA 2005). Excretion rates were calculated as the difference in SRP between experimental chambers and five control chambers, divided by trial duration. We froze larvae at the end of 24-h gut clearance. Larvae were subsequently thawed, removed from cases, oven-dried, and weighed to determine dry mass. Dry larvae were homogenized into powder to determine elemental content. Final larval survivorship was 62.5%, 87.5%, and 96% in the low, med, and high quantity treatments, respectively. Only surviving individuals were included in analyses.

Egesta filters were cut in half and each half was weighed and analyzed for either C or P content. Total C and P was determined from measured contents of each half divided by its mass proportion. We subtracted background P content of control filters on each date. Leaf litter and larval powder were subsampled for elemental content. All samples were analyzed for C content using a Flash 2000 Elemental Analyzer (Thermo Scientific, Waltham, Massachusetts, USA) and P content using hydrochloric acid digestion, dilution, and subsequent analysis for SRP.

We calculated total C and P consumption using weekly dry mass consumption rates and litter C and P contents measured on each feeding date. Weekly measured C- and P-specific egestion rates were similarly used to calculate total C and P egested during the experiment. Total C- and P-specific consumption, egestion, and growth were divided by experiment duration to calculate

absolute molar rates (μ mol/d) for each individual. We subtracted measured C egestion and growth from C consumption rates to infer post-assimilatory C losses. We attribute these primarily to C respiration but we note this would include other unmeasured C losses like dissolved organic C excretion, exuviation (among 4th instars) and silk secretion for case construction. We also calculated C- and P-specific assimilation efficiencies (AE_C and AE_P , respectively) using the equation

$$AE_X = \frac{(\text{Consumption}_X - \text{Egestion}_X)}{\text{Consumption}_X}$$

as well as C- and P-specific gross growth efficiencies (GGE_C and GGE_P) using

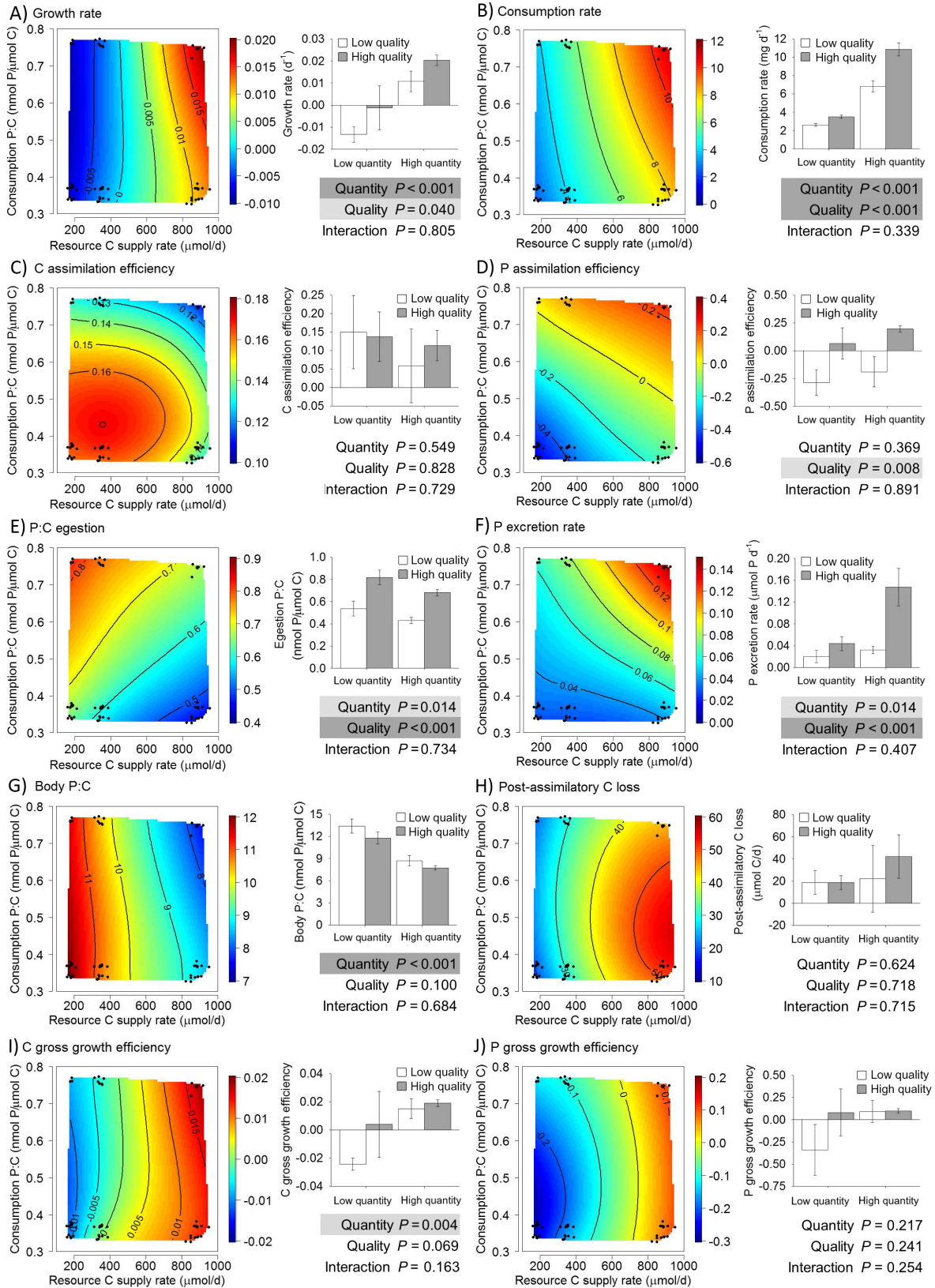
$$GGE_X = \frac{\text{Growth}_X}{\text{Consumption}_X}$$

We used the R package fields to create thin-plate splines and response surfaces (Sperfeld et al. 2016a, b) to present response variables measured from each individual caddisfly across the gradient of resource quantity (C supply rate) and quality (molar P:C ratio; note all P:C ratios are nmol P/ μ mol C). The first response surface axis of quantity describes the amount of food available for consumption, whereas the second axis describes the ratio of P, relative to C, per unit of food as a proxy of diet quality. We also used factorial contrasts from the widest set of treatment combinations, providing statistical support to interpretations from the response surfaces. These contrasts employed two-way ANOVA (factors: quantity and quality) between the fully crossed low vs. high quantity and quality treatments. Response variables were log-transformed where necessary to satisfy ANOVA assumptions. All statistical analyses were conducted in R version 3.3.1 (R Core Team 2016).

RESULTS

Resource supply rates equated to mean 181, 345, and 879 μ mol C/d in low, med, and high quantity treatments, respectively. The quality treatments spanned a wide range of increasing P:C ratios (mean P:C = 0.327–0.733 nmol P/ μ mol C), also associated with increased nitrogen contents and fungal biomass indicative of greater quality (Appendix S1: Table S1). Across this resource space, growth was primarily limited by quantity and was, on average, negative in the two lower-quantity treatments. However, increased quality additionally enhanced growth, indicating co-limitation by both quantity and quality (Fig. 2A). Consumption rates exhibited patterns similar

FIG. 2. *Pycnopsyche lepida* response surfaces and factorial contrasts of (A) growth rates, (B) consumption rates, (C) C assimilation efficiencies, (D) P assimilation efficiencies, (E) P:C egestion, (F) P excretion rates, (G) final body P:C, (H) post-assimilatory C loss rates based on subtraction, (I) C gross growth efficiencies, and (J) P gross growth efficiencies across gradients of resource quantity (C supply rate) and quality (P:C ratio). In response surfaces, each point represents one individual caddisfly. *P* values are derived from two-way ANOVA within each factorial contrast; significant *P* values ($P < 0.05$) are highlighted with gray shading. For factorial contrasts, values are means ± 1 SE.



to growth rates, but increased more monotonically with increasing quality as indicated by the more diagonal isoclines in the resource space (Fig. 2B). In the factorial contrasts, both quantity and quality showed significant effects on growth and consumption, thus indicating independent co-limitation (cf. Fig. 2A, B).

Calculated AE_C showed high within-treatment variation, but means varied little among quantity and quality treatments (Fig. 2C). In contrast, mean AE_P ranged widely among treatments and was lower and negative under low quality, yet higher and positive under high quality (Fig. 2D). Egesta generally exhibited greater P:C ratios than resources, except for the high quality, high quantity treatment (Fig. 2E). Across the resource space, increased resource quantity reduced egesta P:C, whereas increased resource quality increased egesta P:C (Fig. 2E).

P excretion rates increased significantly with both higher quantity and quality from much lower (possibly basal) rates in low quantity and quality treatments (Fig. 2F). *Pycnopsyche lepida* body P:C ratios were mainly affected by food quantity and decreased with increasing quantity (Fig. 2G). From budget subtraction, post-assimilatory C losses were on average positive and generally increased with greater food quantity, but factorial contrasts showed no significant quality or quantity effects (Fig. 2H).

Similar to growth rates, GGE_C exhibited strong quantity limitation by shifting from generally low and negative to positive values with increasing food quantity, and additionally with a weaker but notable positive effect of quality (Fig. 2I). GGE_P also increased with increasing quantity, but factorial contrasts indicated no significant treatment effects probably due to the high within-treatment variability especially under low quantity (Fig. 2J).

DISCUSSION

In our study, resource quantity and quality co-limited detritivore growth by constraining C and P acquisition toward growth and homeostatic regulation. Growth responded independently and additively to both quantity and quality, indicating a factorial scenario of “independent co-limitation” (Harpole et al. 2011), where high quality can alleviate some negative effects of low quantity. This pattern is inconsistent with strictly essential co-limitation according to Liebig’s minimum rule and supports interactively essential or biochemically dependent co-limitation (Fig. 1; Sperfeld et al. 2016a), indicating greater interplay between C and P acquisition, e.g., during assimilation. The covered resource space did not include a P:C threshold for zero growth, but other data from *P. lepida* fed oak litter support strong quality limitation, including a zero-growth threshold of 0.239 nmol P/ μ mol C and growth inhibition under high P:C (Halvorson et al. 2015; Appendix S1: Fig. S1). We affirm calls for studying detrital food webs along concurrent gradients of quantity and quality, including under anthropogenic change like riparian removal and

nutrient enrichment (Kominoski and Rosemond 2012, Rosemond et al. 2015, Larsen et al. 2016).

Our experiment points to consumption as a primary determinant of growth responses to quantity and quality, because consumption rates mirrored patterns in growth rates. At each quantity level, *P. lepida* feeds faster under elevated resource quality, depleting litter in lower quantity treatments but leaving surplus under high quantity (Appendix S1: Fig. S2). The feeding response to quality is counter to other consumers that undertake compensatory feeding on lower-quality diets (Plath and Boersma 2001, Flores et al. 2014, Liess 2014). This capacity to feed faster may reflect increased palatability and digestibility of high-quality litter (Appendix S1: Table S1). In turn, lower consumption on low-quality litter may reflect increased gut residence time to enhance assimilation (slight increase of AE_C under lower quantity and quality). Elevated feeding on high-quality litter is a notable behavior to enhance growth (Arsuffi and Suberkropp 1989, Sperfeld et al. 2017) and would increase litter breakdown with nutrient enrichment (Manning et al. 2016).

Consumption sets the limit on material available for growth, but animals may alter gut conditions to maximize assimilation of ingested nutrients (Frost et al. 2005, DeMott et al. 2010). Maximum individual AE_C was 46%, but mean AE_C rarely surpassed 20% of consumed C even under low quantity, suggesting that the recalcitrance of litter constrains detritivore up-regulation of AE_C under quantity limitation. Litter microbial biomass drives this constraint, because easily assimilated microbial C is only a small portion of bulk detrital C (Halvorson et al. 2016). Given constraints on maximal AE_C , *P. lepida* and other detritivores may possess few post-ingestive strategies to compensate for reduced quantity. Low consumption rates combine with low AE_C , causing C assimilation rates ($\text{Consumption}_C \times AE_C$) to fall below post-assimilatory C losses, resulting in negative GGE_C and mass loss (Fig. 2I; Sterner 1997). Detritivorous animals may therefore be more susceptible to severe quantity limitation relative to herbivores like *Daphnia* with greater ability to up-regulate AE_C (Sterner 1997, DeMott et al. 2010).

We found that food quality additionally limited *P. lepida* growth and affected multiple levels of C and P acquisition, but the responses surfaces indicated stronger quality effects at higher quantities, as TERs predict (Sterner 1997). This suggests quality mostly constrains growth above a threshold supply level (~400–450 μ mol C/d) necessary for *P. lepida* to achieve positive C balance. Despite this, AE_P was greater on high-quality litter regardless of quantity. Although ecological stoichiometry theory predicts lower AE_P on high P resources (Frost et al. 2005) (1) P was likely more digestible on high P:C litter because a greater proportion of P was in microbial biomass (Appendix S1: Table S1) and (2) we probably underestimated P consumption due to selective feeding on P-rich biofilm (Hood et al. 2014). Underestimation would

explain how individuals with calculated negative AE_P still showed P excretion and positive growth. A second, indirect indicator of assimilation, egesta P:C, suggests that regardless of quality, *P. lepida* also more effectively acquired P relative to C when fed higher-quantity diets. Such interplay exemplifies interactive or biochemically dependent co-limitation because acquisition of P improved with increased quantity and quality each independently (Fig. 1; Sperfeld et al. 2016a). Additionally, the response surfaces predict a lower quantity threshold for positive GGE_C compared to GGE_P , indicating distinct C costs for net P acquisition. These points suggest that C and P are “co-regulated” across quantity–quality gradients and thus growth is not limited singly by either element, as assumed by TERs and other strictly essential resource models.

Animals must convert assimilated C and P to new tissues to gain mass, but growth is constrained by losses of assimilate to metabolism and excretion, and is further constrained by the stoichiometry of new tissues (Frost et al. 2005, Halvorson et al. 2015). We did not measure post-assimilatory C losses, but calculated rates approximately doubled from ~20 to 40–50 $\mu\text{mol C/d}$ under increased quantity. Because P excretion rates increased five-fold across the resource space, P was a comparatively more sensitive post-assimilatory loss than C. Moreover, the estimated P:C ratio of post-assimilatory losses was quite high (0.75–3.49 $\text{nmol P}/\mu\text{mol C}$) compared to egestion (0.43–0.82 $\text{nmol P}/\mu\text{mol C}$), highlighting the greater relative magnitude of P excretion compared to C losses in post-assimilatory processes. The marked increase of P excretion in the high quantity and quality treatment suggests *P. lepida* excreted excess P, especially given that resource P:C was above the P:C threshold of 0.62 for optimal *P. lepida* growth at high quantity (Halvorson et al. 2015; Appendix S1: Fig. S1). As an additional indicator of regulation, the decline of body P:C at high quantity is partly a consequence of greater body size because newly grown tissues were P depleted compared to initial tissues (P:C = 11.03 $\text{nmol P}/\mu\text{mol C}$), reducing body P:C. After accounting for differences in body size, *P. lepida* exhibited higher body P:C under severe quantity limitation (Appendix S1: Fig. S3), suggesting that animals depleted body C stores, perhaps to support basal metabolism during starvation. Altered body stoichiometry may therefore be a component of consumers’ response to quantity and not just quality.

The co-limitation pattern in our study may be an integral feature of detrital-based food webs, similar to autotroph-based food webs (Hessen et al. 2002, Wallace et al. 2015). It is likely that the breadth of ecosystems, lakes, streams/rivers, caves, and even terrestrial ecosystems, span or exceed the resource space in our experiment (Appendix S1: Table S2). Among Ozark streams, where we collected *P. lepida* larvae, litter P:C ranges widely (0.362–1.011 $\text{nmol P}/\mu\text{mol C}$) and the ratio of standing detritus to detritivore biomass ranges from 13 to 283 (Prater et al. 2015). Accounting for litter

replenishment every 2–3 d, our experiment converts to an ecologically relevant range of 18–160 g litter/g *P. lepida* biomass. Within this range, we have shown that quantity and quality interactively (instead of strictly) co-limit detritivores’ ability to acquire C and P for growth. This co-limitation is shaped by reduced consumption that combines with (1) an inability to up-regulate AE_C under low quantity, (2) distinct C costs (likely metabolism) associated with P assimilation and growth, (3) post-assimilatory losses to C metabolism and P excretion, and (4) altered body P:C contents, but high-P demands for growth. Together, these patterns support interactive C and P regulation across the resource space. Our study provides mechanistic bases for how detrital energy and nutrients are channeled through food webs, and perhaps why certain systems may or may not support detritivore biomass and production along the quantity–quality continuum (Marcarelli et al. 2011, Prater et al. 2015, Wallace et al. 2015).

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